

Ecology of the Pitviper, *Bothrops moojeni*, in the Brazilian Cerrado

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ABSTRACT.—*Bothrops moojeni* is a member of the *atrox* group that occurs in central and southeastern Brazil and adjacent Paraguay and Argentina. We describe habitat use, diel and seasonal activity, biometry, feeding habits, and reproduction of *B. moojeni*, based on field studies and analysis of 207 preserved specimens. *Bothrops moojeni* predominantly uses riparian vegetation in the Cerrado (central Brazilian savannas), such as gallery forests and adjacent wet grasslands, although they occasionally use drier interfluvial areas. Sexes are dimorphic in snout–vent length, relative tail length, relative mass, and relative head length. Main prey types were mammals, frogs, and lizards. There is an ontogenetic dietary shift from ectotherms to endotherms. Prey–predator mass ratio ranged from 0.008–1.079, and prey mass was positively correlated with predator mass. Although prey absolute mass was positively correlated with snake mass, large snakes did not eliminate small prey from their diets. There was an ontogenetic decrease in prey relative mass. Females consumed more endothermic prey than males, and this difference probably reflects size differences. The reproductive cycle is lengthy and seasonal, with recruitment restricted to the rainy season. Fecundity is positively correlated with female body size. Life-history characters of *B. moojeni* are similar to those of other members of the *atrox* group, even though *B. moojeni* occurs in the Cerrado, a drier and more seasonal biome.

Bothrops moojeni is a large pitviper from riparian areas in central and southeastern Brazil, throughout the Cerrado morphoclimatic domain (Borges and Araújo, 1998; Campbell and Lamar, 1989; Leloup, 1984). Recent systematic studies indicate that populations of *B. moojeni* from the Cerrado of southeastern and central Brazil form a monophyletic assemblage within the *atrox* species group (Wüster et al., 1996, 1999).

Few studies deal specifically with the ecology of snakes in the genus *Bothrops* (Martins and Gordo, 1993; Martins et al., 2002; Sazima, 1992; Valdujo et al., 2002). Regarding *B. moojeni*, basic information on diet, reproduction, and micro-habitat use, directed at rearing for commercial venom production, is available in Leloup (1975, 1984). Borges and Araújo (1998) studied habitat segregation between *B. moojeni* and *Bothrops neuwiedi* in the Brasília region, central Brazil, concluding that the former inhabits mostly gallery forests and adjacent areas, whereas the latter occurs exclusively in open savannas. Martins et al. (2001) reported arboreal habits in juvenile *B. moojeni*, and Martins et al. (2002) reported *B. moojeni* as occurring in gallery forests and swamps in the Cerrado.

Studies on Cerrado fauna are important given the fast rate of destruction of its natural landscapes during the last decades (Ratter et al.,

1997). We present information on habitat use, activity, diet, biometry, and reproduction of *B. moojeni* from central and southeastern Brazil. Preliminary data on the biology of *B. moojeni*, based partially on the same dataset used herein, were provided by Martins et al. (2001, 2002).

MATERIALS AND METHODS

We obtained field data at several Cerrado localities throughout the range of nominal populations of *B. moojeni* (cf. Wüster et al., 1996, 1999). All study sites were protected areas in undisturbed Cerrado, encompassing all the typical Cerrado vegetation types (see Ratter et al., 1997). We made most field observations and collections at Itirapina Ecological Station (IES, with approximately 2300 ha; 22°15'S; 47°49'W; elevation 800 m), São Paulo, southeastern Brazil; at Emas National Park (ENP, with approximately 130,000 ha; 18°15'S; 52°53'W; elevation 800 m), in southwestern Goiás, central Brazil; and at reserves in the Brasília region, central Brazil, including Águas Emendadas Ecological Station (AEES, with approximately 10,000 ha; 15°33'S; 47°34'W; elevation 1100 m), Área Alfa Cerrado Reserve (AACR, a Brazilian Navy training area with approximately 6,000 ha; 16°00'S; 47°56'W; elevation 1150 m), and IBGE Biological Reserve (IBGE, with approximately 1,350 ha; 15°57'S, 47°53'W; elevation 1100 m). We also made occasional observations in other Cerrado areas in central Brazil, including the regions of

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Chapada dos Veadeiros National Park (about 14°13'S; 47°29'W; elevation 500–1600 m) and Grande Sertão Veredas National Park (about 15°23'S and 45°54'W; elevation 700–1000 m). Cerrado areas in Brazil are characterized by well-defined dry and wet seasons (April to September and October to March, respectively; Eiten, 1972), with annual precipitation around 1500 mm.

Vegetation types in the study areas were divided into two major categories: riparian and interfluvial areas (adapted from Eiten, 1972). Riparian areas consist mostly of gallery forests, wet grasslands (*campo úmido*), and palm marshes (*veredas*) in depressions closely associated with perennial water. Interfluvial areas are covered by several types of seasonally dry savannas, always on higher, gently sloping, well-drained terrains, ranging from grasslands (*campo limpo*) to arboreal savannas (*cerrado sensu stricto*; see Ratter et al., 1997).

We obtained snakes during time-constrained searches (TCS) and incidental sightings (Martins and Oliveira, 1999). We conducted TCS only at the main study sites (IES, Brasília region and ENP), from July 1997 to April 2001. We calculated sampling effort in TCS as the number of person-hours (p-h) spent searching (see Valdujo et al., 2002). For each specimen observed in the field we recorded: time and date of encounter, vegetation and substrate types, posture (see Oliveira and Martins, 2002), and snout–vent length (SVL). We also obtained snakes from local collectors in and around the main study sites; these collectors provided information on habitat use, time, and date of capture for most specimens.

At IES we also obtained snakes from pitfall traps with drift fences (PTDF Greenberg et al., 1994) installed in riparian (three sampling units with 24 buckets) and interfluvial areas (six sampling units with 48 buckets). We used these traps from August 1999 to April 2001. Each sampling unit of PTDF consisted of a pair of 45 m arrays, 100 m from each other. Each array had four 100-liter plastic buckets (placed every 15 m), connected by a 0.5-m high fence made of plastic mesh. Each day of PTDF sampling corresponded to 72 bucket-days. We sampled a total of 185 nonconsecutive days (13,320 bucket-days) from August 1999 to April 2001. Of these, we sampled 124 days (8928 bucket-days) during the wet season and 61 days (4392 bucket-days) during the dry season. We sampled 4440 bucket-days in riparian habitats (border of the gallery forests), and 8880 bucket-days in interfluvial habitats during the course of both seasons. At IES we implanted pit-tags (Trovan® ID 100 Implantable Transponder) in all specimens caught.

To detect eventual differences in seasonal activity using data from local collectors, we compared observed with expected monthly number

of collected snakes, after correcting for unequal monthly sampling efforts (see Seigel, 1992). We considered sampling effort the total number of days of each month, assuming that the probability of finding snakes by local collectors is the same every day. We calculated the monthly expected number of snakes by dividing the total number of snakes collected by the total number of days throughout the study (from April 1997 to April 1999), and then multiplying this value by the number of days of each month. We then compared the observed with the expected number of snakes caught during dry and wet seasons with a chi-square test. To avoid bias caused by juvenile recruitment, we excluded juvenile snakes (SVL ≤ 300 mm) from this analysis.

To obtain data on diet and reproduction, we analyzed 207 preserved specimens from various localities in the Brazilian Cerrado. We deposited all 143 specimens collected for this study in herpetological collections, except for a few in bad state of preservation (e.g., old roadkills or accidentally mutilated specimens). We obtained additional material from the herpetological collections of Instituto Butantan (IB), Universidade de Brasília (CHUNB), and Museu Nacional (MNRJ). We used only museum specimens incorporated in collections without having been previously kept in captivity for long periods.

For each preserved specimen, we recorded the following data (see Shine, 1977a,b, 1986; Shine and Charles, 1982): (1) snout–vent length (SVL); (2) head length (HL); (3) tail length (TL); (iv) body mass after draining the excess of preservative liquid through ventral incisions and removing prey and/or embryos or enlarged follicles (Martins et al., 2001); (5) prey items in gut; (6) sex; (7) sexual maturity (see criteria in Shine, 1977a,b); (8) number of ova or embryos; and (9) diameter of largest ovarian follicle, oviductal egg or encapsulated embryo. All linear measurements were recorded to the nearest millimeter and mass to the nearest gram.

We used combined information from food items found in the stomach and in the hindgut (Martins and Gordo, 1993). The mass of partially digested prey was inferred by comparison with reference specimens of similar size (Greene, 1989). Direction of ingestion was recorded whenever possible. We also recorded tail-tip color, an indicator of caudal-luring behavior (see Andrade et al., 1996; Sazima, 1991). We divided snakes into mature males, mature females, and juveniles for most analyses. In mark-recapture studies at IES, we considered as sexually mature those snakes larger than the smallest mature museum specimen of the same sex.

We tested for sexual size dimorphism in SVL of mature specimens using a Mann-Whitney *U*-test. We tested sexual dimorphism in head length

between mature males and females with an ANCOVA, using trunk length (SVL minus HL) as the covariate and log-transformed variables. We applied the same procedure for testing sexual dimorphism in tail length (SVL as the covariate) and mass (total length as the covariate). Log-transformed variables were used as they reduce heteroscedasticity and promote linear relationships (Zar, 1984; King, 2000).

We explored the effect of snake size on prey size through linear regression analysis. We used the mass of both predator and prey as an indicator of size; both variables were log-transformed. We tested for ontogenetic shift in relative prey size using the slope of the previous regression line, using a *t*-test (see Zar, 1984). 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 used the same test to explore sexual differences in diet by comparing the frequency of prey types in mature males and females. We tested for sexual differences in relative prey mass by comparing the prey-predator mass ratios with a Mann-Whitney *U*-test.

We explored the effect of female size on litter size through linear regression analysis, with both variables log-transformed (King, 2000). We performed all statistical analyses using Statistica (Statistica for Windows, Release 5.1 J, Statsoft, Inc., Tulsa, OK, 1998), according to procedures in Zar (1984), with significance levels set at $\alpha = 0.05$.

RESULTS

Habitat Use and Activity.—We gathered a total of 69 field records of *B. moojeni*: 26 records during TCS (total of 1205.6 p-h; including four recaptures) in all study areas, 36 records from incidental sightings or interviews with local collectors in all areas, plus seven records from pit-fall traps at IES. Most snakes (92%) found during TCS were in riparian areas, where the encounter rate was 0.051 snake/p-h (22 snakes found during 461 p-h of search). By contrast, in interfluvial savannas, the encounter rate during TCS was 0.005 snake/p-h (four snakes found during 744.3 p-h of search). Snakes in riparian areas were found both in open and forested areas, mostly around gallery forests, natural lagoons, small pools, and palm marshes. We found no snake in wet areas (e.g., temporary pools and rivulets) located in interfluvial areas, far from gallery forests. We captured snakes in pitfall traps only during the wet season and always in riparian areas (1.6 snakes per 1000 bucket-days).

In all 26 observations during TCS, the snakes were exposed, either on the ground (92%; $N = 24$) or on vegetation (8%; $N = 2$); no specimen

was found sheltered or inside burrows and ground cavities. Both snakes found on vegetation were juveniles moving over twigs or grasses, 20 and 30 cm above ground, respectively. Eleven snakes (42%) were coiled in a typical ambush posture, 13 (50%) were moving, and two (8%) were apparently resting.

At IES, the encounter rate of TCS at night was 0.029 snake/p-h (16 snakes found during 547.0 p-h of search), whereas during daytime it was 0.005 snake/p-h (one snake found during 191.8 p-h of search). Also at IES, the encounter rate during the wet season was 0.030 snake/p-h (15 snakes found during 497.3 p-h of search), whereas during the dry season the encounter rate was 0.008 snake/p-h (two snakes found during 239.6 p-h of search).

Of the snakes obtained incidentally or by local collectors for which field data were recorded ($N = 39$), 33 (84%) were in or close to riparian areas and on the ground, either resting or moving. Five were in water bodies. Two adult specimens were found moving over vegetation, up to 150 cm above ground, in or close to gallery forests, and only one snake was found in a burrow.

During TCS and incidental encounters, individuals of *B. moojeni* were active at air temperatures ranging from 18.5–25.0°C at night ($N = 11$) and at 25.0 and 29.5°C during daytime ($N = 2$). The number of snakes obtained from local collectors was higher-than-expected in the wet season and lower-than-expected in the dry season ($\chi^2 = 4.37$, $df = 1$; $P = 0.04$). No climatic variable alone seems to explain the variation in the monthly number of snakes collected (maximum temperature, $r^2 = 0.04$, $F = 1.41$, $P = 0.26$; minimum temperature, $r^2 = 0.25$, $F = 0.26$, $P = 0.62$; rainfall, $r^2 = 0.27$, $F = 3.74$, $P = 0.08$).

Sexual size dimorphism was evident in *B. moojeni* ($U = 349.00$; $P < 0.01$), with mature females (median 1034 mm; range 760–1330 mm; $N = 55$) larger than mature males (median 827 mm; range 590–1060 mm; $N = 45$). Mature females were heavier than males of similar size, with a relatively longer head, and a relatively shorter tail than mature males ($F_{1,83} = 6.47$, $P = 0.01$; $F_{1,96} = 36.57$, $P < 0.01$; $F_{1,84} = 53.82$, $P < 0.01$, respectively).

Feeding Habits.—Of 207 dissected specimens, 127 (61.3%) contained prey remains in the gut. The percentage of snakes with food was 65.7% when only the 143 specimens obtained directly from the field are considered, of which 94 contained prey remains. Twelve snakes contained remains of more than one prey item in the entire gut, and only three of these had more than one prey item in the stomach. Five (15.1%) out of 33 prey items for which direction of ingestion could be detected were swallowed tail first.

TABLE 1. Contribution of prey groups to the diet of juveniles, mature males, and mature females of *Bothrops moojeni*.

Age group	With prey	No. of prey	Centipedes	Frogs	Lizards	Snakes	Mammals and birds
Juveniles N = 81	55 (68%)	60	0	30 (50.0%)	16 (26.7%)	2 (3.3%)	12 (20.0%)
Mature males N = 53	30 (57%)	35	1 (2.9%)	10 (28.6%)	6 (17.1%)	2 (5.7%)	16 (45.7%)
Mature females N = 73	42 (57%)	49	0	6 (12.2%)	4 (8.2%)	5 (10.2%)	34 (69.4%)
Totals 207	127	144	1	46	26	9	62

We recovered 144 prey items in six major taxonomic groups (Table 1): mammals (41.0% of all prey found), frogs (31.9%), lizards (17.4%), snakes (6.2%), birds (2.8%), and centipedes (0.7%). We detected an ontogenetic shift in prey types: ectotherms (mostly amphibians) are the main prey of juveniles whereas endotherms (mostly rodents) are the main prey of adults (Table 1; Fisher exact test, $P < 0.01$). We also observed an intersexual difference in diet, with adult males consuming mostly ectotherms and adult females preying mostly on endotherms (Table 1; Fisher exact test, $P = 0.02$). This difference was not evident (Fisher exact test, $P = 0.12$) in a comparison between males and females of similar sizes (using a subsample ranging from the smallest mature female to the largest mature male).

We obtained prey mass for 28 partially or nondigested items. The ratio of prey mass: predator mass ranged from 0.008–1.079. The smallest prey was a juvenile lizard (*Tropidurus* sp.; 31 mm SVL, 1 g) eaten by an adult male *B. moojeni* (IB 61682, 700 + 132 mm, 120 g), and the largest an adult lizard *Ophiodes striatus* (Anguillidae; 136 mm SVL, 41 g) consumed by a juvenile female (IB 53139, 484 + 82 mm, 38 g). Prey mass was correlated with predator mass (adjusted $r^2 =$

0.43, $F = 21.66$, $P < 0.01$, $N = 28$). There was an ontogenetic shift in prey relative mass; the slope of the regression (0.66) of prey mass on predator mass was significantly different from one; $t = 2.25$, $P < 0.02$, $N = 28$, with juveniles tending to consume relatively heavier prey than adults.

We recorded tail-tip color for 126 snakes (31 juveniles, 95 adults). White tail tips occurred in most juveniles (70.9%) but were rare in adults (2.2%). Specimens having white or partially white tail tips ranged in size from the smallest individual (265 + 47 mm; CHUNB 03594, juvenile female) to an adult female (810 + 130 mm; IB 61686). Snakes with a tail tip color not different from the color of the remainder of the tail ranged from 305 + 46 mm (CHUNB 19296, juvenile female) to the largest individual (1330 + 180 mm; IB 60443, adult female).

Reproduction.—The reproductive cycle of *B. moojeni* was lengthy and seasonal (Fig. 1). The vitellogenic period starts around May, in the beginning of the dry season, with ovulation occurring around July. Births were concentrated around December and January, in the middle of the rainy season, as full-term embryos were present only in females collected in December. Some females collected during the breeding season had nonvitellogenic follicles, indicating that only part of the mature female population reproduces each year, although our sample was small. Litter size ranged from three to 32 young (mean 15.6 ± 7.9 , $N = 21$) and was dependent on female body size (adjusted $r^2 = 0.45$; $F = 17.34$; $N = 21$; $P < 0.01$).

DISCUSSION

Habitat of *B. moojeni*, a relatively common species throughout the Cerrado, was poorly known until recently. Leloup (1984) was the first to suggest that the typical habitat of *B. moojeni* is riparian areas in the Cerrado. More recently, Borges and Araújo (1998) suggested that *B. moojeni* occurs mainly in and around gallery forests. Our results and those in Martins et al. (2002) strengthen these conclusions. The lack of

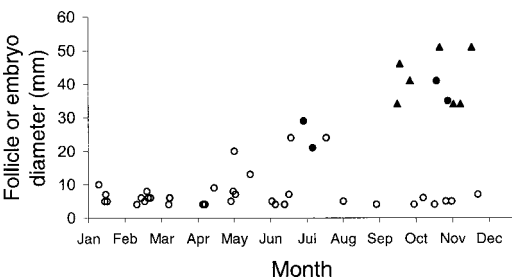


FIG. 1. Reproductive cycle of *Bothrops moojeni*: seasonal variation in diameter of ovarian follicles (empty circles), early embryos (yolk only, embryos undetectable; dots), and developing embryos (triangles) from 41 adult females.

observations of *B. moojeni* around water bodies located in interfluvial areas corroborates the association of this pitviper to gallery forests. However, our study also indicates that *B. moojeni* can occasionally be found in dry interfluvial savannas. Although occupying the Cerrado domain, widely dominated by interfluvial savannas (Eiten, 1972), *B. moojeni* occurs mainly in forested habitats, as those occupied by other members of the *atrox* species group (e.g., *Bothrops atrox* and *Bothrops leucurus*; Martins et al., 2002).

Bothrops moojeni is active at relatively high air temperatures compared to sympatric congeners (e.g., *Bothrops alternatus* and *Bothrops itapetiningae* found active at 15 and 12°C, respectively, at IES, *B. alternatus* and *Bothrops neuwiedi pauloensis*, both found active at 13°C at ENP, and *Bothrops neuwiedi goyazensis* active at 14°C in the Brasília region; pers. obs.). Other species of the *atrox* group are also active at high air temperatures (e.g., *B. atrox*; Oliveira and Martins, 2001).

Our microhabitat data indicate that *B. moojeni* are occasionally found in the water of streams and ponds located in riparian areas (Leloup, 1984). Our observations also confirm that both juveniles and adults may occasionally be found moving on the vegetation (over twigs, grasses, and eventually higher branches; see Leloup, 1984; Martins et al., 2001). Similar observations were described for *B. atrox* in Amazonia (e.g., Martins and Oliveira, 1999).

In contrast, the use of ground cavities as retreats (see Leloup, 1984) was reported only once in our study, although the use of this microhabitat is commonly observed in other Cerrado species of *Bothrops* from interfluvial habitats (Borges and Araújo, 1998; Valdujo et al., 2002). The use of ground cavities may be an efficient way to reduce water loss and avoid exposure to predators and temperature extremes in open habitats (Vanzolini, 1948; Valdujo et al., 2002). However, gallery forests are wetter, more shaded, and show less variation in temperature than interfluvial areas, which may make the use of ground cavities less important for *B. moojeni*. Furthermore, ground cavities in riparian habitats are flooded during most of the year, making them unavailable to the snakes. The Amazonian *B. atrox* was observed using ground cavities on very few occasions (Martins and Oliveira, 1999).

Although limited, our mark-recapture data indicate that *B. moojeni* use small areas for long periods. The small number of *B. moojeni* captured in pitfall traps is probably caused by the low mobility of the species. Our results indicate that *B. moojeni* is mainly nocturnal and is active mostly during the warmest and wettest months (October to April), as are other species of *Bothrops* (Oliveira and Martins, 2002; Sazima, 1992; Valdujo et al., 2002).

Previous studies indicate that *B. moojeni* has a generalist diet (Leloup, 1984; Andrade et al., 1996). However, the relative contribution of prey categories in the diet of *B. moojeni* has not been determined, except for preliminary data provided by Martins et al. (2002). An ontogenetic dietary shift in *B. moojeni* (Martins et al., 2002; this study) was inferred previously by Andrade et al. (1996) from anecdotal information and generalizations based on the diet of related species. The diet of *B. moojeni* (Martins et al., 2002; this study) is similar to that observed for *B. atrox* (Martins and Gordo, 1993; Martins and Oliveira, 1999). These similarities in diet may reflect common ancestry, as well as similar prey availability in humid forests occupied by *B. atrox* and *B. moojeni*.

Sexual size dimorphism in *B. moojeni* (Vanzolini, 1991; this study) may be related to reproduction, since larger body size in females may lead to increased fecundity (Seigel and Fitch, 1984). Leloup (1975) observed births in *B. moojeni* from October to January, with over 60% of them in December, in agreement with our data. Leloup (1975) suggested that the gestation period in *B. moojeni* lasts about 200 days (see also Almeida-Santos and Salomão, 2002), which does not correspond strictly to the interval between copulation and birth (March through May and December through February, respectively; Almeida-Santos and Salomão, 2002; this study). Thus, fertilization is apparently delayed until June and July, when ovulation occurs (Almeida-Santos and Salomão, 2002; this study). Indeed, morphological changes that occur after copulation (uterine muscular twisting, see Almeida-Santos and Salomão, 2002), in the distal portion of the oviduct of female *B. moojeni*, indicate the occurrence of long-term sperm storage. A seasonal reproductive cycle is widespread in *Bothrops* (Almeida-Santos and Salomão, 2002), occurring even in species from less seasonal habitats, such as the Atlantic forest (*Bothrops jararaca*, Sazima, 1992; *Bothrops jararacussu*, O. A. V. Marques, pers. comm.) and the Amazon (*B. atrox*, M. E. Oliveira, pers. comm.). Recruitment is synchronic with a peak in amphibian abundance (Sazima, 1992; Andrade et al., 1996), which would ensure high food availability for neonate snakes. However, both snakes and their potential prey could respond to other environmental factors (rainfall, humidity, temperature, and any combination of these), with no causal relationship between prey abundance and snake recruitment (see Oliveira and Martins, 2002; Valdujo et al., 2002).

Our results indicate that *B. moojeni* in the Cerrado (a seasonal and relatively dry biome) are ecologically similar to other forest-dwelling

members of the *atrox* group, ranging from the Atlantic forest to Amazonia. These similarities may be caused by phylogeny or similarities between the habitats occupied by *B. moojeni* in the Cerrado and the forests occupied by other species of the *atrox* group, or both. The presence of gallery forests in the Cerrado may have provided suitable habitat for the dispersal (probably from northern forests) and maintenance of this forest-dwelling lineage in Cerrado areas of central and southeastern Brazil.

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