HERPETOLOGICAL NATURAL HISTORY

VOL. 8 2001 NO. 2

Herpetological Natural History, 8(2), 2001, pages 101–110.

WHEN AND WHERE TO FIND A PITVIPER: ACTIVITY PATTERNS AND HABITAT USE OF THE LANCEHEAD, *BOTHROPS ATROX*, IN CENTRAL AMAZONIA, BRAZIL

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Abstract. Activity and habitat use in *Bothrops atrox* are described from central Amazonia using three methods: time constrained search (TCS, in swamp forest in a stream valley and terra firme forest on a plateau), occasional sightings (OS; both in primary forest), and snakes brought to a hospital (IMTM). Results for OS and IMTM indicate that *B. atrox* is significantly less active during the dry season. The monthly number of snakes found with OS and brought to the IMTM were both correlated with rainfall and relative humidity, but not with temperature. Monthly number of individuals found with TCS did not differ from expectation and was correlated with rainfall but not with humidity or temperature. Encounter rate at night was much higher than by day. Most snakes found at night were hunting in a coiled posture, whereas most snakes found by day were moving. Juveniles were found more frequently on vegetation than adults. The higher incidence of snakebites by *B. atrox* in summer in the Manaus region may reflect this increase in activity. Unimodal seasonal activity and primarily nocturnal habits are widespread in *Bothrops*. Ontogenetic shift in microhabitat use is also common in semiarboreal lanceheads and may be related to food availability and perhaps a higher predation pressure at the ground level.

Key Words: Activity patterns; Habitat use; Rainforest; Brazil; Serpentes; *Bothrops atrox*; Snakebite.

The Amazonian lancehead, *Bothrops atrox*, is a common pitviper that occurs throughout most of the northern part of South America (Campbell and Lamar 1989; Wüster et al. 1996). Besides being an important ecological component of Amazonian rainforests (Cunha and Nascimento 1978; Duellman 1978; Martins and Oliveira 1999), *B. atrox* is the most important venomous snake in Amazonia from the standpoint of human morbidity and mortality

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(Pardal et al. 1995; Sá Neto and Santos 1995), comparable to *B. asper* in Mexico and central America (Hardy 1994*a,b*), and *B. jararaca* in southeastern Brazil (Rosenfeld 1971). Most studies on regional herpetofaunas in Amazonia provide general information on the biology of *B. atrox* (Beebe 1946; Cunha and Nascimento 1975; Dixon and Soini 1986; Martins and Oliveira 1999; Rodriguez and Cadle 1990; Zimmerman and Rodrigues 1990), although more detailed studies are rare (Martins and Gordo 1993). For instance, the available information on habitat use and activity patterns (references above and Belluomini et al. 1991; Cunha and Nascimento 1982; Duellman and Mendelson 1995; Henderson et al. 1976) is not sufficient for a good characterization of these important aspects of its biology (especially in relation to human envenomating; see Sazima 1992).

The Amazonian lancehead inhabits mostly forests, although it may be occasionally found in disturbed habitats around human settlements (Campbell and Lamar 1989; Cunha and Nascimento 1975, 1978, 1982; Duellman 1978; Martins and Oliveira 1999). Sparse information indicates that *B. atrox* shows an ontogenetic shift in microhabitat use: juveniles are found mostly on shrubs (up to 1.5 m above ground), whereas adults are found mostly on the ground, and only occasionally on the vegetation (Campbell and Lamar 1989; Dixon and Soini 1986; Duellman 1978; Henderson et al. 1976, 1979; Martins and Oliveira 1999; Zimmerman and Rodrigues 1990). It is primarily a nocturnal species, but daytime activity has occasionally been observed (Beebe 1946; Cunha and Nascimento 1975, 1978; Duellman 1978; Duellman and Mendelson 1995; Egler et al. 1996; Martins and Oliveira 1999).

Additional information on habitat use and activity in *B. atrox* would be helpful to our understanding of the biology of this widespread and ecologically important species. Furthermore, knowing how pitvipers use time and space would allow predictions of when and where encounters between humans and snakes are more likely to occur. This knowledge could be used to plan further field studies on pitvipers and to decrease snakebite risk during field activities. Here we present data on habitat use and activity patterns of populations of *B. atrox* from central Amazonia, including field data gathered from a primary forest population in Manaus, Amazonas, Brazil, and collections made by lay people during five years in the Manaus region.

MATERIALS AND METHODS

The field data reported here were gathered from 1990–95 at several localities in the Manaus region (see map in Martins and Oliveira 1993; see also Martins and Oliveira 1999). However, most of our field data come from a regular snake-search program (see below) in the northwestern portion of Reserva Florestal Adolpho Ducke (RFAD; 3°04' S, 59°58' W, elevation ca. 50 m; see satellite image in Martins and Oliveira 1999). It is a 100 km^2 tract of mostly undisturbed rainforest. For more details on the history and vegetation of the RFAD, see Prance (1990) and Ribeiro et al. (1999).

Regular searches for snakes at RFAD were conducted in two study areas (1.4 km apart) located in physiognomically and topographically different regions: a plateau and a stream valley (see details in Martins and Oliveira 1999). The plateau area (2 ha) is covered by terra firme forest with tall trees and a relatively sparse understory, whereas the stream valley area (1 ha) is a swamp forest with many tall palms, relatively short, thin trees, and dense herbaceous growth covering large portions of the ground. The total area sampled at RFAD, including opportunistic sightings, was less than 100 ha (i.e., less than 1% of the reserve's area).

The climate in the Manaus region has a mean annual rainfall of 2075 mm (during the period of 1931–60; DNPM 1978), and a dry season from June–November (only ca. 30% of the rain falls during these six months; Fig. 1A). The years of 1991–93 were relatively wet (ca. 20% above the mean in 1991 and 1992, 40% above this mean in 1993). Temperatures in Manaus range from 18–37°C (Leopoldo et al. 1987; monthly means 26–28°C) and the relative humidity ranges from 80–90% throughout the year (Fig. 1A).

Snake searching at RFAD was undertaken mostly from October 1991–March 1993. Additional sightings at RFAD and a few sporadic collections were made from March–September 1991 and from November 1993–August 1995. Searching at RFAD was divided into two categories: time constrained search (TCS; Campbell and Christman 1982) and opportunistic sightings (OS; see details in Martins and Oliveira 1999). During TCS, we walked 57–117 person-hours (p-hr) every month, with a total of 1613 p-hr walked in 18 mo, 472 p-hr occurring during the day and 1141 p-hr at night. Diurnal searches (n = 89) were made mostly in the after-

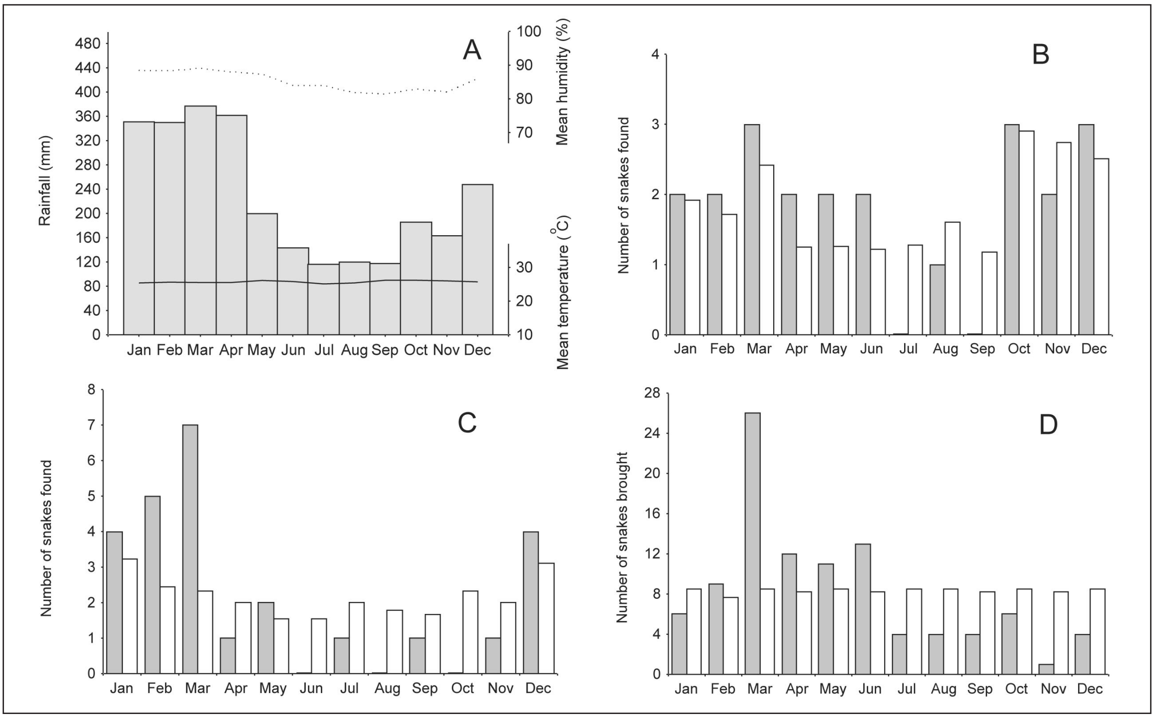

Figure 1. Climatic data for the Manaus region (A; mean for data from June 1990–May 1993) and monthly observed (dashed bars) and expected (blank bars) number of snakes for three methods: time constrained search (B; October 1991 –March 1993), occasional sightings (C; 1990–95; both at RFAD, Manaus), and snakes brought to the IMTM Hospital at Manaus, Amazonas, Brazil (D; 1990–94).

noon, and at night ($n = 95$), between 1800 and 0100 h. Opportunistic sightings occurred in various habitats and sampling effort was 234 d of fieldwork, from 1990–95.

Several snakes found during TCS and OS were caught and released soon after capture. About half of the snakes found were marked by clipping ventral scales (Spellerberg 1977). For each snake we recorded date and time of capture/sighting, location in the reserve and/or in the study area, microhabitat where the snake was first seen, activity, snout–vent length (SVL), tail length (TAL), and mass, individual (both during markings and recaptures), sex (on a few occasions), and any additional observation on behavior, natural marks, presence/absence of prey. To separate active from inactive individuals in our analyses, we assumed that an individual of *B. atrox* was active when the snake was exposed, either moving or coiled with the neck forming an S-coil, and the head lying over body coils and generally forming an angle ≥ 20° in relation to the ground (Fig. 2A). Inactive snakes were generally hidden, often loosely coiled, with the neck held straight and the head generally forming an angle < 20° in relation to the ground (Fig. 2B). Besides data gathered during fieldwork, we provide data on snakes brought to the hospital of the Instituto de Medicina Tropical de Manaus (IMTM).

Correlations were performed to investigate relationships between monthly number of snakes found and (1) monthly rainfall, (2) mean temperature, and (3) relative humidity. To describe monthly activity using data from TCS, OS, and snakes brought to the IMTM, we compared observed with expected values, after correcting for unequal monthly sampling efforts (Seigel 1992). For TCS, sampling effort was the number of hours of snake search each month; for OS, the number of days of fieldwork each month; and for snakes brought to IMTM, the total number of days of each month. TCS encounter rates at the valley and the plateau were compared for wet and dry seasons using a Mann-Whitney test. To avoid bias due to juvenile recruitment, newborn snakes (SVL ≤ 300 mm) were excluded in analyses using data from OS and TCS; however, data on snakes brought to the IMTM include newborn snakes. Ontogenetic shift in microhabitat was tested by comparing the frequencies of juveniles (TTL ≤ 600 mm, newborn snakes

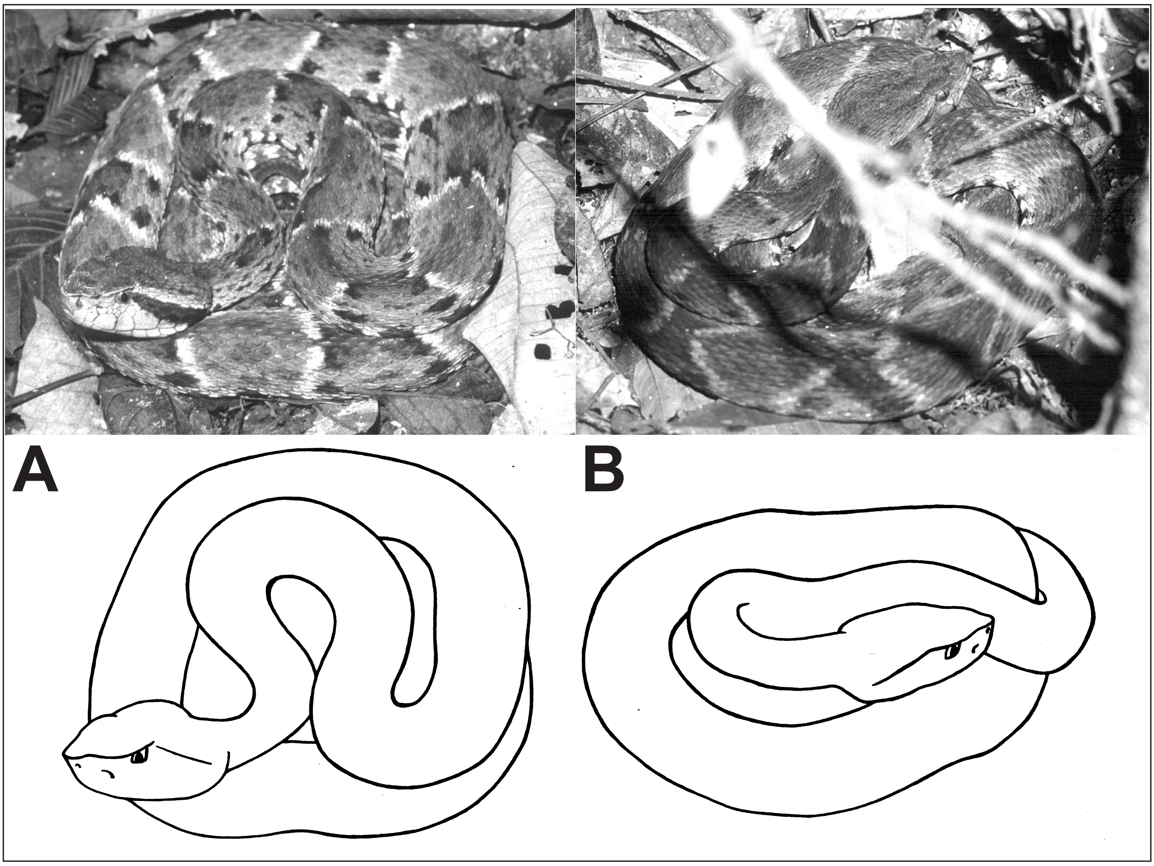

Figure 2. (A) Active individual of *Bothrops atrox* (adult female, total length ca. 1500 mm). Note the neck forming an S-coil, and the head lying over body coils and forming an angle of more than 20° in relation to the substrate. (B) Inactive individual of *B. atrox* (subadult female, total length ca. 1000 mm). Note the neck held straight and the head forming an angle of less than 20° in relation to the substrate. When found by day, inactive individuals are less prone to strike defensively. Drawings were made using the original diapositives.

included) and adults found on the vegetation and on the ground with a Chi-Square test; these include snakes found by other researchers working at the RFAD and other localities around Manaus. All computations were made in Statistica (StatSoft 1998).

RESULTS

From 1990–95, a total of 60 records of 50 active individuals of *B. atrox* were made at RFAD during TCS (n = 34 records of 25 individuals) and OS (n = 26 records of 25 individuals). Newborn snakes were found in December (n = 6), January (n = 2), and February (n = 1), all but one in the stream valley. Six of these young were found on the same night along 400 m of the trail in the stream valley, and are probably from one or two litters.

The general encounter rate of *B. atrox* during TCS (October 1991–March 1993) was 0.025 snake/p-hr (one snake every 40 p-hr; including newborn snakes). Monthly number of active individuals found with TCS (newborn snakes excluded) did not differ from expected ($\chi^2 = 4.56$, df = 11, $P = 0.951$; Fig. 1B). Monthly number of individuals found with TCS was correlated with rainfall ($r = 0.571$, $P = 0.053$), but not with humidity or temperature ($r = 0.482$, $P = 0.112$ and $r = 0.203$, $P = 0.527$, respectively).

With OS, snakes were found in significantly higher than expected numbers from December–March and in May, and lower than expected numbers in April and from June–November ($\chi^2 = 20.01$, df = 11, $P = 0.045$; Fig. 1C, newborn snakes excluded). Monthly number of snakes found was significantly correlated with humidity and rainfall ($r = 0.766$, $P = 0.004$, and $r = 0.765$, $P = 0.003$, respectively), but not with temperature ($r = 0.281$, $P = 0.376$).

In the Manaus region, *B. atrox* were brought to the IMTM in significantly higher than expected

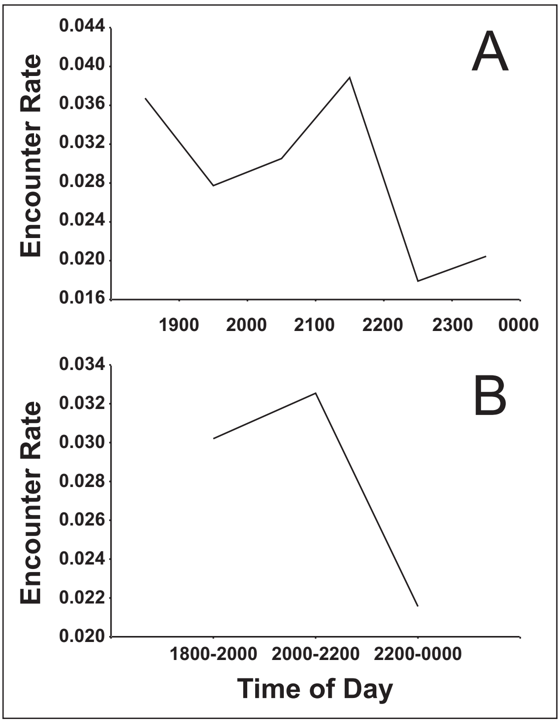

Figure 3. Encounter rates of *Bothrops atrox* at the Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil, from October 1991–March 1993 from just after dusk (1800h) to midnight, in 1-h (A) and 2-h intervals (B),

numbers from February–June and lower than expected numbers from July–January ($\chi^2 = 58.68$, df = 11, $P < 0.001$; Fig. 1D). An apparent peak occurred in March (Fig. 1D). The monthly number of snakes brought to the IMTM was significantly correlated with monthly humidity ($r = 0.623$, $P = 0.031$), marginally significantly correlated with monthly rainfall ($r = 0.564$, $P = 0.056$), but not with mean temperature in the same period ($r = 0.142$, $P = 0.659$).

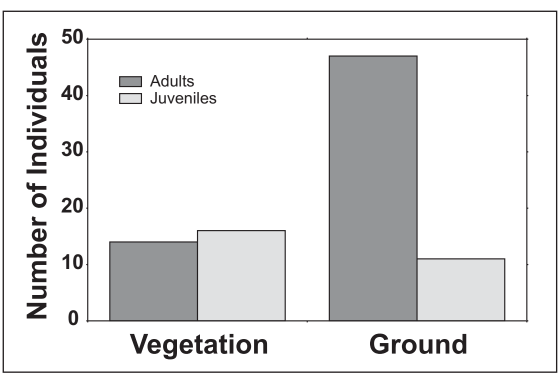

Figure 4. Occurrence of juveniles and adults of *Bothrops atrox* on the ground and on vegetation at the RFAD, Manaus, Amazonas, Brazil, from 1990–95.

Monthly encounter rates in TCS were not significantly different in the stream valley and the plateau ($Z = 1.18$, $P = 0.237$). During the dry season, the monthly encounter rates were not significantly different in the plateau and the valley ($Z = 0.48$, $P = 0.631$), whereas in the wet season the encounter rate in the plateau was significantly lower than that in the valley ($Z = 2.56$, $P = 0.010$).

During five years of fieldwork at RFAD, 22 records (21%) of *B. atrox* were made during the day and 85 (79%) at night. During TCS (including newborn snakes), encounter rate by day (0.004 snake/p-hr or about one snake every 236 p-hr) was about five times lower than at night (0.020 snake/p-hr or about one snake every 50 p-hr). Encounter rate during the first half of the night (1800–2400 h; total of 1126 p-hr of search) was highly variable, with apparent peaks at 1800–1900 h and 2100–2200 h (Fig. 3A); however, when data are grouped into 2-h intervals, the encounter rate decreased abruptly in the last interval (2200–2400 h; Fig. 3B).

Of 21 diurnal records for which activity was inferred (see Methods), in seven instances (33%) the snakes were coiled and inactive (Fig. 2B), whereas in 14 instances (67%) they were moving. Included in the latter are two pairs that were copulating (both in April; A. Weber and R. Vogt, pers. comm.) and one juvenile that had just envenomated a teiid lizard (*Ameiva ameiva*; M. Gordo, pers. comm.). Of 77 nocturnal records for which activity was inferred, in 64 instances (83%) the snakes were coiled in a hunting posture (Fig 1A), in 11 instances (14%) they were moving, and in two instances (3%) they were apparently inactive on vegetation. Of the 11 individuals that were moving, five were clearly foraging (frequently probing the substrate with their tongues), and one of them was very close to an envenomated hylid frog (*Phyllomedusa tomopterna*).

All active individuals found by day ($n = 13$) were on the ground, except for one individual that was on a fallen log. Most inactive individuals found by day were under the leaves of herbs and low shrubs ($n = 6$), along fallen logs ($n = 2$), and within buttresses ($n = 1$). At night, active individuals ($n = 42$) were exposed on the ground, several of them in the margins of small ponds ($n = 11$), under buriti palms (*Mauritia flexuosa*) where many fallen fruits were present ($n = 2$), or in swampy areas ($n = 29$), mostly close to the stream. The only two inactive individuals (adults) found at night were on the vegetation (1.2 and 1.3 m above the ground).

At RFAD, 30 individuals were found on the vegetation at 5–150 cm above ground, most of them at night. Juveniles were found significantly more frequently on the vegetation than adults (χ^2 = 11.0, $P < 0.001$; Fig. 4).

DISCUSSION

The results for two sampling methods (OS, IMTM) indicate that the activity of *Bothrops atrox* in the Manaus region decreases during the dry season, despite the fact that most of our data are from relatively wet years (see Materials and Methods). We see no reason for our conflicting results for TCS, since sample size was similar to that for OS and sampling effort was high (over 1600 p-hr of searching). Cunha and Nascimento (1975) also reported on seasonal activity in *B. atrox* in eastern Amazonia (decrease from June–November) and data in Fitch (1970) indicate a decrease in activity in *B. atrox* from May–July in western Amazonia (Perú; but see comments below on results in Henderson et al. 1978). Thus, the results provided herein for the Manaus area may apply for other Amazonian localities as well.

Although we have very limited data on the reproductive cycle of *B. atrox* in central Amazonia, mating was observed from February–May and females with well developed embryos were found from August–December (MEO, unpublished data). Thus, it would be expected to find variations in the activity of adults during these periods (e.g., higher activity of males related to search for females and of females related to thermoregulation during late pregnancy), and perhaps some of our results reflect these variations. However, we have very few sexed adults to test this hypothesis.

Other factors may be responsible for seasonal activity of *B. atrox*. Rainfall, which is highly correlated with air humidity ($r = 0.905$, $P < 0.001$, in this study) is often suggested as an important factor determining the seasonal incidence of tropical snakes (e.g. Henderson et al. 1978; Martins and Oliveira 1999; Sazima 1988, 1992; Strüssmann and Sazima 1993). Our results indicate that in central Amazonia *B. atrox* is more active when the amount of rainfall and air humidity are higher (see similar situations in *Naja* spp. [Luiselli and Angelici 2000] and *Micrurus corallinus* [Marques 1996]). For Iquitos, Perú, Henderson et al. (1978; including data from Fitch 1970) found conflicting results for *B. atrox* using different rainfall data, including a negative correlation between rainfall and the number of *B. atrox* collected. Rainfall in the Iquitos region is almost evenly distributed throughout the year (see, data from Oliver 1947; Henderson et al. 1978), which may make the relation between rainfall and snake activity less obvious than in more seasonal regions such as central Amazonia. Even so, the negative correlation found by Henderson et al. (1978) for *B. atrox* is surprising and deserves attention in future snake studies in that area.

The effect of rainfall on snake activity may be indirect, by affecting prey availability (Henderson et al. 1978; Marques 1996). Henderson et al. (1978) found a positive relationship between amount of rainfall and the number of snake stomachs containing anurans suggesting this. Alternatively, other factors, such as a general reduction in forest productivity in the dry season (see Janzen and Schoener 1968) and even the dry weather per se (see Henderson et al. 1978), may simultaneously affect the activity of most animals, including snakes and their prey.

A higher level of activity of *B. atrox* during the wet season in the Manaus region may be responsible, at least in part, for the higher incidence of snakebites by the species during this period (see Sá Neto and Santos 1995). These authors suggested that the increase could be related to rising water levels in rivers, which would result in shortened migration by *B. atrox* and a higher incidence of encounters between these animals and humans. However, the flooding patterns of Amazonian rivers are highly variable. In the Manaus region, for instance, rivers that flow from the northern hemisphere (e.g., the Negro and some of its tributaries) have a flooding peak during the dry season, whereas those flowing from the southern hemisphere (e.g., the Marañon/Solimões/Amazonas and most of its tributaries) have a flooding peak during the wet season. Besides local flooding patterns other factors may be involved in a higher activity level in *B. atrox* and, consequently, a higher incidence of snakebites. These may include those factors we suggest above, as well as human activity patterns. In fact, the incidence of snakebites varies extensively among different localities in the State of Amazonas (Borges et al. 1999).

Besides occurring in other neotropical snakes (e.g., Marques 1996), the unimodal seasonal activity pattern observed in *B. atrox* was also observed in the closely related *B. moojeni* in southeastern and central Brazil (C.C. Nogueira, pers. comm.), in

B. jararaca in southeastern Brazil (Sazima 1988, 1992), in *B. neuwiedi pauloensis* in southeastern and central Brazil (P.H. Valdujo, pers. comm.), and in *B. n. pubescens* in extreme southern Brazil (M.T. Almeida, pers. comm.), but not in *B. jararacussu* in southeastern Brazil (O.A.V. Marques, pers. comm.), which may suggest that the ancestor of *Bothrops* was seasonally active.

Our results also indicate that *B. atrox* is primarily nocturnal, although diurnal activity is not rare (see also Egler at al. 1996). The highly cryptic color pattern of *B. atrox* (Greene 1988; Henderson et al. 1976; see also plates in Martins and Oliveira 1999) may make this species difficult to find by day. However, two radio-implanted individuals (one adult and one subadult) tracked for 8 and 16 mo at the RFAD, were found almost always partially hidden and inactive by day, whereas at night they were exposed and active (pers. obs). Nocturnal habits were reported for *B. atrox* in eastern and western Amazonia (Cunha and Nascimento 1975, 1978; Dixon and Soini 1986; Duellman 1978) and are widespread (and most probably plesiomorphic) in *Bothrops* (Sazima 1988, 1992; pers. obs).

Our preliminary results for TCS during the night indicate that the activity of *B. atrox* may decrease after 2200 h, although we lack data for the interval 2400–0600 h. Higher temperatures and greater prey activity (e.g., anurans; pers. obs) could be responsible for the peak in activity in the first hours after sunset (Gibbons and Semlitsch 1987).

The ontogenetic shift in microhabitat use reported here (juveniles more arboreal than adults) was suggested for *B. atrox* in several studies (Campbell and Lamar 1989; Dixon and Soini 1986; Duellman 1978; Henderson et al. 1976, 1979; Zimmerman and Rodrigues 1990). This shift also occurs in the closely related *B. moojeni* (Leloup 1984; C.C. Nogueira, pers. comm.), *B. jararaca* (Sazima 1992), and *B. asper* (e.g., Campbell 1998). Besides differences in mass (the light weight of juveniles may facilitate locomotion on the vegetation; see Lillywhite and Henderson 1993), differences in food availability between the leaf litter and the vegetation also could be responsible for the ontogenetic shifts in microhabitat recorded for some species of *Bothrops* (see Henderson et al. 1979; Reinert 1993). In the case of *B. atrox* in central Amazonia, where juveniles forage during the evening, small frogs (the main prey of *B. atrox* juveniles; pers. obs) are found more frequently on the vegetation than on the leaf litter (especially *Eleutherodacylus fenestratus*, a common prey of *B. atrox* at RFAD; pers. obs). Frogs may be lured by the distinct tail tip of young *B. atrox* (see Martins and Oliveira 1999: Plate 108; Sazima 1991, 1992). However, differential predation pressure may also be involved. For instance, Martins (1993) suggested that several species of forest snakes sleep on the vegetation in central Amazonia to avoid contact with terrestrial predators (mainly carnivorous ants and spiders). Adults of *B. atrox* were the only snakes found resting on the ground at night during a long-term study at the RFAD, where 52 species of snakes were recorded (Martins and Oliveira 1999). Other factors also may be involved, such as physiological constraints to vertical displacement in adults (Lillywhite 1993; Lillywhite and Smits 1992).

The methods used in this study (mainly visual search) may provide biased results due to differential probability of encounter of individuals of different size, in different microhabitats and/or at different times of the day. However, a study on a few radio-implanted individuals (two adults, one subadult, one juvenile) in the same study area provided results on daily activity and microhabitat use that strongly corroborate those presented herein for microhabitat use and patterns of daily and seasonal activity (pers. obs).

The results presented herein, associated with reports from the literature (Cunha and Nascimento 1982; Duellman 1978), indicate that encounters between humans and *B. atrox* are more likely to occur at night (perhaps, during the first hours after sunset) and during the rainy season. Furthermore, our results show that small individuals of *B. atrox* are more likely to be found on low vegetation in the forest understory and that by day individuals are generally inactive (and less prone to strike defensively; pers. obs). Thus, besides the usual recommendations to decrease risks of being bitten by pitvipers (see Greene 1997; Hardy 1994*a*,*b*), field activities can be planned in time and space in a way that the risks of bites by *B. atrox* are largely reduced.

ACKNOWLEDGMENTS

W.Y. Oda, S.G. Egler, and J.B. Rocha provided invaluable help in fieldwork. M. Gordo, L. Schiesari, A. Webber, R. Vogt, K.-H. Jungfer, M. Carmosina Araújo, and H. Küchmeister kindly provided useful field data obtained at RFAD. L.

Luiselli, O.A.V. Marques, and an anonymous referee made helpful comments and criticisms on a previous draft of the manuscript. Instituto Nacional de Pesquisas da Amazonia allowed our work at Reserva Ducke. The Empresa Brasileira de Pesquisas Agropecuárias (Manaus) provided the meteorological data used herein. During part of this study, CAPES/UA provided a fellowship to MEO, and CNPq to MM. This study is part of the project Natural History and Evolution of *Bothrops*, funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (grant 95/09642-5).

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