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# Habitat Selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil

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**Tropical rainforests often appear relatively homogeneous on satellite images, but responses to landscape characteristics may be found on finer scales if habitat characteristics are considered as continuous variables. In this study, we used 30 uniformly distributed plots and 16 plots beside streams to evaluate the effects of distance from stream, litter depth, altitude, slope, and tree density on abundance of Amazonian Lancehead Pitviper (*Bothrops atrox*). We estimated densities and probabilities of detection of snakes in riparian and upland plots in Reserva Ducke, Manaus, Amazonas, Brazil. Apparent density of individuals of *B. atrox* was about 6.4 times higher near streams, but the number of individuals in the landscape more than 10 m away from streams was about 3.9 times higher than the number of individuals within 10 m of streams. Movement data from two adult *B. atrox* evaluated by radio telemetry indicate that individuals can disperse out of plots and away from streams over a period of several months. Detectability of *B. atrox* varied little among riparian and upland plots, so differences in detectability are unlikely to be responsible for large differences in encounter rates of snakes between riparian and non-riparian areas. There were small differences in body size of individuals near streams and individuals far from streams. The distribution of *B. atrox* is not uniform within the forest. However, as with most other tropical-forest organisms studied to date, this species occurs across wide environmental gradients and shows only subtle habitat specificity.**

**E**NVIRONMENTAL variation is usually only recognized by applying general classifications of habitat at discrete scales, such as “ecoregions” and “terra-firme forest.” However, within those habitat categories, many organisms make differential use of available sites and occupy only limited portions of ecological gradients (Gentry, 1988; Tuomisto et al., 1995; Costa et al., 2005; Kinupp and Magnusson, 2005; Menin et al., 2007; Keller et al., 2009; Fraga et al., 2011; Bueno et al., 2012).

The Amazonian Lancehead Pitviper (*Jararaca-da-Amazônia*) *Bothrops atrox* (Linnaeus, 1758) is widely distributed throughout the Amazon basin, and in central Amazonia has been reported as the most frequently recorded snake species (Oliveira and Martins, 2001; Fraga et al., 2011). It is primarily a forest species, but relatively adaptable to human occupation (Duellman, 1978; Campbell and Lamar, 1989; Martins and Oliveira, 1999). Lancehead Pitvipers, especially juveniles, sometimes climb into understory vegetation (Martins and Oliveira, 1999; Oliveira and Martins, 2001), but are thought to mainly use the ground to rest (especially during the day), hunt, and move. As the species hunts by ambush, depth of the leaf-litter is likely to influence patterns of habitat use. Because *B. atrox* is abundant and relatively easy to find in comparison to other snakes in central Amazonia (Fraga et al., 2011), it is a useful model for determining the factors that influence habitat use. The distribution of the species is also of concern for public health, since this species causes the most serious cases of snakebite in Amazonia (Pardal et al., 1995; Sá-Neto and Santos, 1995).

Several studies have reported on habitat use by *B. atrox*, and concluded that the species occurs in most available habitats, but is mainly found on the ground or on vegetation in forests (up to 2 m high). However, these studies were very general; conclusions were not based on

standardized sampling, or habitat dimensions were recorded only on discrete scales (e.g., Cunha and Nascimento, 1975, 1982; Dixon and Soini, 1986; Zimmerman and Rodrigues, 1990; Martins and Oliveira, 1999; Borges and Araújo, 2008; Turci et al., 2009). These approaches are useful for determining general aspects of the ecology of the species or habitat-use patterns influenced by historical, biogeographic, or phylogenetic factors, but are less useful to determine specific use of local resources (Luiselli and Filippi, 2006). Habitats measured as continuous variables contain more information and generate patterns of habitat use at finer scales, and this approach may be more directly applicable to conservation (Semlitsch and Bodie, 2003; Fraga et al., 2011).

In this study, we quantified habitat use by *B. atrox* in 25 km<sup>2</sup> of tropical rainforest in central Amazonia and investigated the influence of local characteristics of the landscape on the abundance of individuals. We used visual surveys and distance sampling (Buckland et al., 2001) to estimate snake probabilities of detection. This approach is useful for studies of snakes, because it provides reasonable estimates of detection even when it is not possible to detect all individuals (Thomas et al., 2010; Isaac et al., 2011), and the models generated in the software Distance (Thomas et al., 2010) can provide detection probabilities. Distance sampling assumes that no subsets of individuals have zero probability of detection. Therefore, we used additional data from two radio-tracked individuals to confirm that individuals do not spend long periods underground where they would not be detected by visual surveys.

## MATERIALS AND METHODS

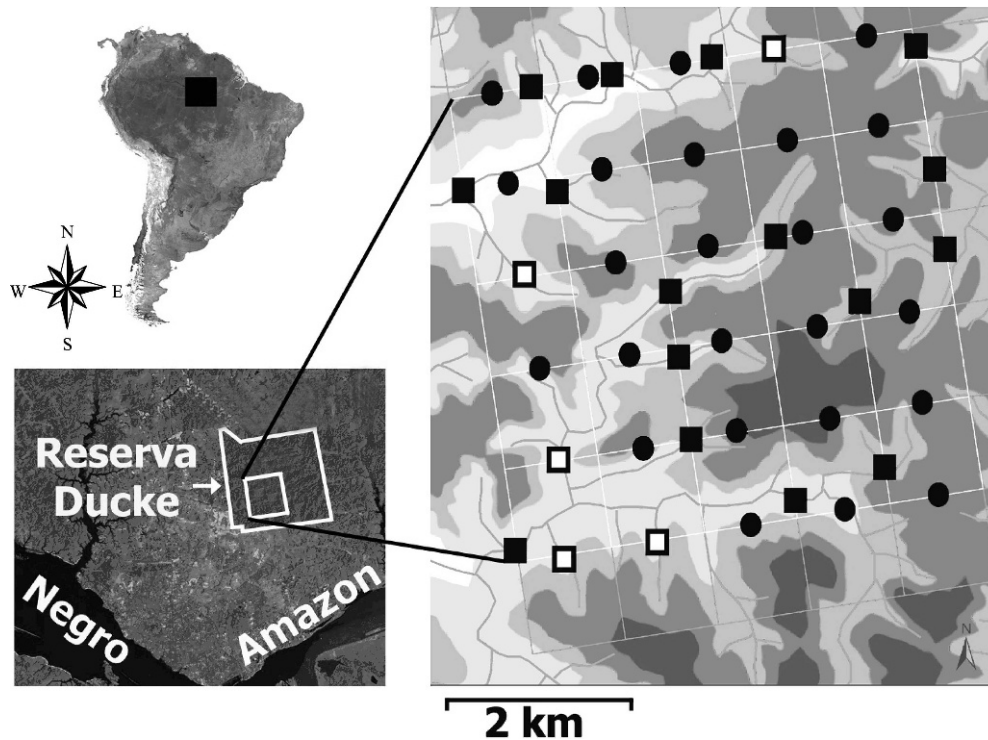
**Study area.**—Reserva Ducke, administered by the Instituto Nacional de Pesquisas da Amazônia (INPA), is located

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**Fig. 1.** Location of Reserva Ducke, Manaus, Amazonas, Brazil, highlighting the 25 km<sup>2</sup> RAPELD grid. Circles represent uniformly distributed plots, black squares represent riparian plots, and open squares indicate uniformly distributed plots located close to streams.

adjacent to the northern suburbs of the city of Manaus, Amazonas, Brazil (coordinates of headquarters 59°52'40" and 59°58'00"W, 03°00'00" and 03°08'00"S). It is predominantly covered by tropical rainforest not subject to seasonal flooding for long periods. Three general plant associations have been recognized for Reserva Ducke, and these are associated with distinctive soil characteristics and topography (Ribeiro et al., 1999). Forests on plateaus are 35 to 40 m high, with emergent trees up to 45 m, and the understory is dominated by sessile palms. Riparian forests occur in valleys, with canopy in the riparian zone recognized by botanists between 20 and 35 m high, with few emergent trees. The understory is quite dense, dominated by riparian plants, represented by families such as Rapateaceae, Marantaceae, and Cyclanthaceae. However, different taxa apparently use different widths of riparian zones within the riparian forests, which do not necessarily coincide with the botanical or legal definitions of the riparian zone (Drucker et al., 2008; Fraga et al., 2011). Slope forests occur in the transition zones between riparian and plateau forests.

The average annual temperature fluctuation in Reserva Ducke is less than 5°C, and average annual rainfall is between 1500 and 2500 mm, with the heaviest rains from November to April (Alencar et al., 1979; Ribeiro and Adis, 1984).

**Sampling design.**—A 25 km<sup>2</sup> trail grid (Fig. 1) was installed in Reserva Ducke as part of the Programa de Pesquisas em Biodiversidade (PPBio, 2007), which uses RAPELD methodology (Magnusson et al., 2005). This approach is based on standardized sample units, and has been applied to both short- and long-term studies (Costa and Magnusson, 2010). Thirty plots were uniformly distributed throughout the grid. Each plot was 250 m long by 10 m wide and its centre line followed the altitudinal contour to avoid variations in

habitat characteristics, such as soil structure, vegetation, and water-table depth (Magnusson et al., 2005).

Because of their standardized spatial distribution, only five uniformly distributed plots were located near streams. To compare estimates of densities and detection of *B. atrox* between uplands and riparian plots, we installed 16 additional riparian plots along the margins of streams (250 × 20 m). The location of the riparian plots was defined by logistical constraints; we chose streams that cross the tracks to access plots. The centerline in riparian plots was on average 3.5 m (SD±1.12) from the stream margins. Riparian plots did not follow the altitudinal contour because of the gentle downstream slope. For some analyses, we grouped the five uniformly distributed plots near streams with the riparian plots, resulting in 21 riparian plots and 25 upland plots. However, as different predictor variables were available for different subsets of plots, we generally analyzed the 30 uniformly distributed plots (including the five near streams) separately from the 16 riparian plots.

We conducted six surveys, with durations between 30 and 35 days each (January–February 2006, March–April 2006, July–August 2006, November–December 2007, April 2008, and July–August 2008). In each period, we visited all 46 plots. In the first three surveys, we surveyed three plots per day only during the night (1830–0200 h), and in the remaining three surveys, we surveyed two plots per day during the day, and repeated the same plots at night (1300–1800 h; 1830–0200 h). The average time of search was 79 min per plot (SD±25.2) per visit, with an average walking speed of 208.5 m/h (SD±65.6).

Individuals were located by space-constrained visual search, with detailed inspection of each plot, exploring the widest possible plant strata and substrates, to detect animals at rest or moving (adapted from Campbell and Christman, 1982). Distance searched was 10 m in the horizontal plane

for each side of the centerline of the plot, and 5 m vertical. Surveys were undertaken by R. Fraga, with an additional observer. For all snakes encountered we took snout-vent length (SVL) and sex data. We marked about 60% ( $n = 33$ ) of snakes using ventral-scale clipping and released them at the capture site on the same day.

**Environmental variables.**—Distance from streams and litter depth were measured for both uniformly distributed and riparian plots. For uniformly distributed plots only, data were available from previous studies on altitude, slope, and tree density. For riparian plots, we recorded only litter depth and stream size.

Altitude above sea level was determined per plot by a professional topographer. Slope was measured with a clinometer at six equidistant points per plot, and analyses were based on mean values per plot. Tree density was measured by counting the trees in sub-plots of three different widths, depending on the diameter class at breast height (DBH) of trees. For trees with DBH > 30 cm, plots were 250 m long and 40 m wide. For trees with DBH between 10 and 30 cm, plots were 250 × 20 m, and for trees with DBH between 1 and 10 cm plots were 250 × 4 m. For this study, we considered the total numbers of trees estimated for a 250 m × 40 m plot by extrapolating the data from the subplots for the smaller size classes.

The index of litter depth was the mean distance between the highest point of the leaves and the soil surface measured with a ruler at 12 equidistant points per plot. We measured the distance between each plot and the nearest stream at six equidistant points (50 m apart) per plot. The width of streams adjacent to riparian plots was measured with a tape measure stretched from one bank to the other at six points located at 50 m intervals along the plot. Depth of streams was measured at three equidistant points across the stream, the distance between them depending on the width of each stream, at the same points where width was measured, giving a total of 18 depth measurements per plot. Mean values of measurements per plot were used in all analyses. The product of the average width and average depth of streams was used as an index of stream size. The streams were measured in November 2007 after a period of four days without rain.

We used software ArcGIS 9.3 to create a 10 m buffer around streams on an image of the 25 km<sup>2</sup> grid. This was used to estimate the area of riparian zones within 10 m of the streams, because most *B. atrox* detected in riparian plots were less than that distance from streams.

**Radio telemetry.**—Visual surveys may indicate different patterns of habitat use than radio telemetry. Before starting the visual surveys, we radio-tracked two individuals found near streams to determine whether visual encounters revealed the same patterns as radio telemetry, or if individuals spent long periods in locations where they could not be detected by visual searches. The individuals were originally encountered >400 m apart near different streams. Results were similar for the two individuals, but data for two months were lost due to an accident in the laboratory, and we only present data for the first and last months (July and November 1987). The radios were about 20 g (Wildlife Materials Inc.) with a 10 cm whip antenna, which was extended subcutaneously along the snake, to avoid compromising internal organs (Webb and Shine,

1997). The weight of radios was equivalent to a maximum of 6% of the weight of tracked individuals. Snakes were anesthetized by Halothane inhalation and the transmitters were surgically implanted in the abdominal cavity. Snakes were maintained in captivity for two weeks to ensure that they had recovered from surgery, by which time surgical wounds had healed and the snakes had each eaten a mouse. One individual, a female was 104 cm SVL (about 500 g), and the sex of the other of approximately 80.5 cm SVL (about 300 g) was not recorded. The snakes were released 18 and 19 July, respectively, and their positions determined 24 July. Positions of both snakes were recorded on 10 October, 18 October, 24 October, and 1 November 1987. Locations were recorded as distance along the stream, which is larger than straight-line distances because of stream meanders, and distance from the stream measured with a tape graduated in cm. Stream distances had been mapped in a previous study (Magnusson and Lima, 1991).

**Data analysis.**—Some data were not available for riparian plots, so we used different multiple-regression models for different subsets of the data. Riparian plots had negligible slope, and data on tree densities were only available from a long-term study of uniformly distributed plots. We tested a simpler model in analyses of all plots combined, using litter depth and distance from the stream as covariates; a second model for uniformly distributed plots, using litter depth, distance from stream, altitude, slope, and tree density; and a third model for riparian plots, using litter depth and stream size.

For uniformly distributed plots, litter depth (Pearson  $r = 0.47$ ,  $P = 0.05$ ), and altitude (Pearson  $r = 0.55$ ,  $P = 0.01$ ) were correlated with distance from the streams, indicating colinearity, but conclusions from multiple regressions were the same for models that included or excluded these variables.

We estimate the abundance of individuals for the entire study area, using the formula  $a = i/n/p*s*1000$ , separately for riparian and upland plots, where  $i$  = number of detected individuals,  $n$  = number of plots,  $p$  = area of each plot in m<sup>2</sup>, and  $s$  = total area of a habitat in m<sup>2</sup>. To estimate densities, we used  $a/s$ .

**Distance sampling.**—For 32 individuals, we measured the perpendicular distance between the center-line of the plot and the location at which the snake was detected. We used the program Distance 6.0 (Thomas et al., 2010) to estimate detection probabilities, which has the following assumptions. Snakes directly on the center-line of the plots were always detected; movement of snakes before being detected is unlikely as 78% were found stationary and coiled. For snakes encountered while moving (22%), position at first sighting was considered the detection distance, so detection distances were measured accurately (Buckland et al., 2001; Thomas et al., 2002). The resulting detection probabilities are for individuals potentially detectable. Any that were in subterranean retreats would not have been detectable even if they were on the center-line. However, snakes with radios were detected in over 90% of track sessions. As at least part of them was potentially visually detectable by human observers, the software Distance can account for differences in detectability because there was not a large proportion of individuals with zero detection probability.

To estimate detection probability of snakes, we assumed that detection along the center-line of transect (through

**Table 1.** Models for General Estimating of Detection Probabilities Based on Distance Sampling, Using Combinations of Key Functions and Adjustment Terms. AICc = corrected Akaike's Information Criterion, DP = general detection probability (all plots). Bold = best model by the fit of AICc value.

Model	AICc	DP
Half-normal + Cosine	96.735	49.4
Half-normal + Simple polynomial	97.532	25.1
Half-normal + Hermite polynomial	97.532	25.1
Uniform + Cosine	95.289	44.2
Uniform + Simple polynomial	97.049	43.6
Uniform + Hermite polynomial	97.049	43.6
<b>Hazard-rate + Cosine</b>	<b>88.866</b>	<b>79.7</b>
Hazard-rate + Simple polynomial	93.898	77.5
Hazard-rate + Hermite polynomial	91.333	79.7

which observers move) was 1, and decreased with increasing distance from the center-line. The detection function was based on the relationship between the number of snakes detected and perpendicular distance from the center line. The software Distance calculates effective plot width to estimate detection probabilities (Buckland et al., 2001). Using distance sampling, we assume that all individuals have the same detection function. This may seem inappropriate because the models miss heterogeneity (Thomas et al., 2010); however, the software offers options for parametric key functions paired with zero or more adjustment terms that can take into account heterogeneity. We ran nine general models (without distinction between riparian and uniformly distributed plots) using different combinations of key functions (Table 1) and adjustment terms to estimate detection probabilities. We used the lowest corrected Akaike Information Criterion (Hazard rate + Cosine AICc = 88.866) to select the model that best fit the data structure, and then estimated detection probabilities separately for riparian and uniformly distributed plots. We used a model including no covariate, a model including SVL, and a model including

sex. If the detectability function differed between habitats, then the average distance at which individuals were detected is expected to differ between habitats, and we tested this with a Kolmogorov-Smirnov test.

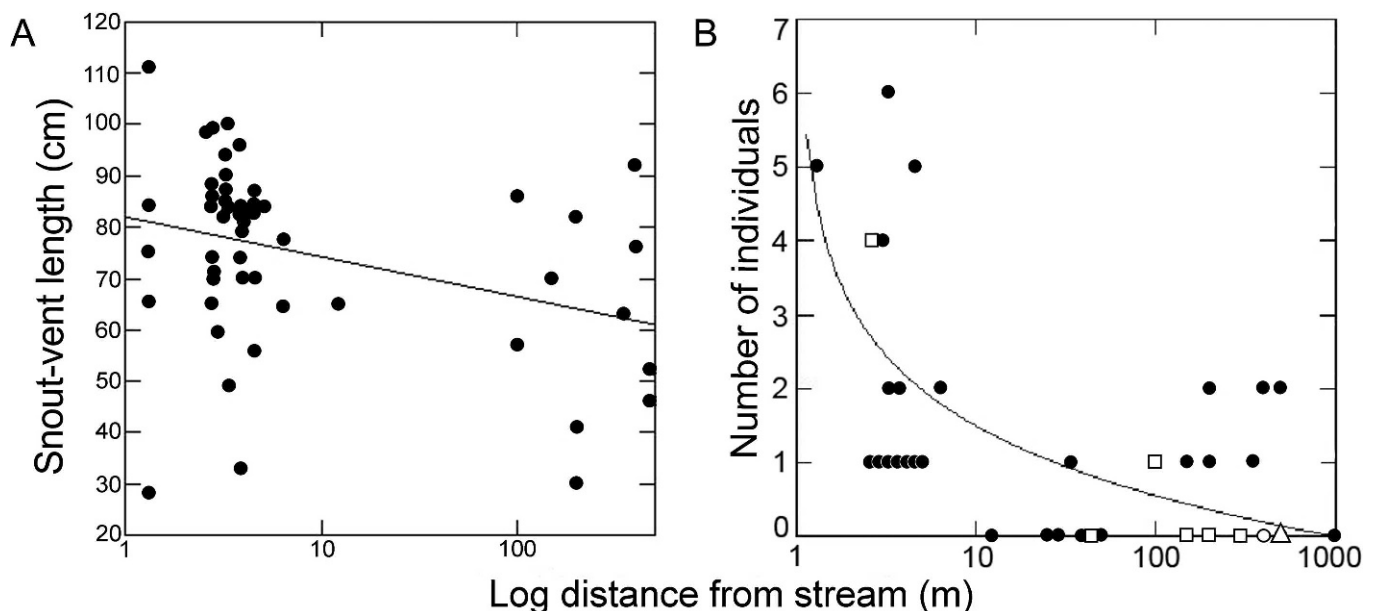
## RESULTS

We recorded 53 individuals of *B. atrox*. Twelve were recorded in uniformly distributed plots and 41 in riparian plots. The mean number detected per plot was higher in riparian plots than uniformly distributed plots (ANOVA  $F_{1,44} = 35.1$ ,  $P < 0.001$ ), and individuals were larger in riparian plots (ANOVA  $F_{1,50} = 6.692$ ,  $P = 0.01$ ), with larger snakes closer to streams. However, little of the variation in SVL ( $R^2 = 0.08$ ,  $P < 0.02$ ) was associated with whether the plot was within 10 m from streams or more than 100 m from streams (Fig. 2A).

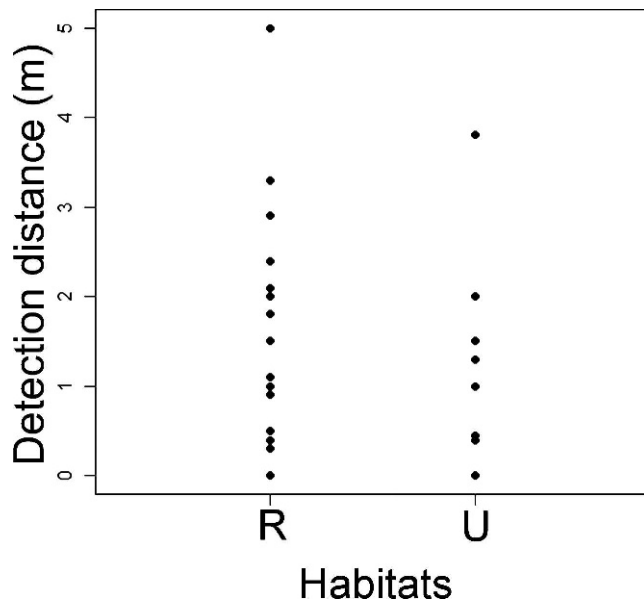
For all plots combined, litter depth (L) and the logarithm of distance from streams (logD) explained about 20% of the variance in the number (N) of snakes encountered ( $N = 3.33 + [-0.23] L + [-0.003] \log D$ ,  $R^2 = 0.2$ ,  $P = 0.008$ ). The evidence for an effect of litter depth alone was equivocal ( $P = 0.07$ ), but the number encountered had a strong negative and nonlinear relationship (Fig. 2B) with distance from the stream ( $P = 0.003$ ). Within uniformly distributed plots and within riparian plots, none of the variables influenced the number of individuals encountered ( $P > 0.28$  in all cases).

For 32 individuals we found no difference in detection distance (Fig. 2B) between riparian and uniformly distributed plots (Kolmogorov-Smirnov = 0.31,  $P = 0.47$ ). Distance sampling showed variation of less than 11% in detection probabilities between riparian and uniformly distributed plots, in models without covariates (9.8%), including SVL (4.9%) and sex (10.6%).

Although the density of individuals was much higher within 10 m of streams (512.5 ind/km<sup>2</sup>) than in plots away from streams (80 ind/km<sup>2</sup>), only 0.97 km<sup>2</sup> (3.88%) of the study area was within 10 m of streams. Assuming similar detectability in riparian and uniformly distributed plots (Fig. 3), the density of *B. atrox* individuals was about 6.4 times higher near streams, but the total number of



**Fig. 2.** Relationships between snout-vent length of individuals of *Bothrops atrox* (A) and number of individuals per plot (B), and  $\log_{10}$  distance from the streams. Black circles = one plot, squares = two overlapped plots, triangle = three overlapped plots, white circle = four overlapped plots.



**Fig. 3.** Detection distance of individuals of *Bothrops atrox* per habitat. R = riparian plots, U = uniformly distributed plots.

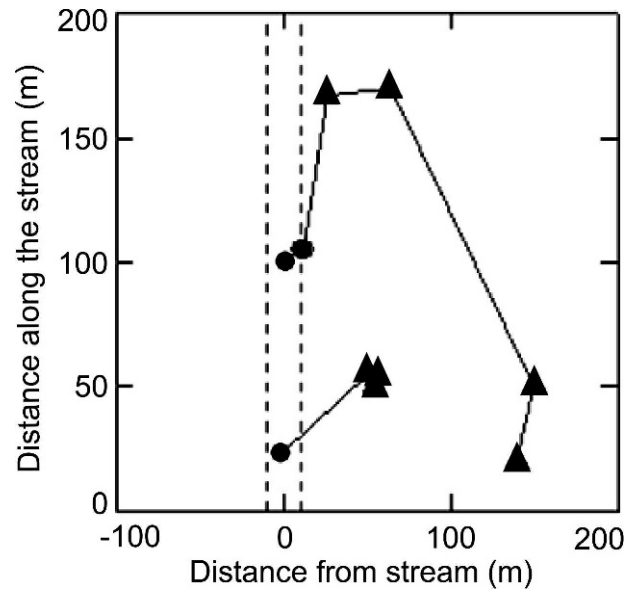
individuals more than 10 m away from streams (N estimated = 1922) was about 3.9 times higher than the number of individuals within 10 m of streams (N estimated = 497).

The positions of the radio-tracked snakes were plotted in relation to distance along, and distance from, streams (Fig. 4). This slightly distorts the distances moved because distances along streams are longer than straight-line distances, but this procedure permits plotting the positions of both snakes on the same map, and shows the positions of the snakes in relation to a strip 10 m wide on each side of the stream (Fig. 4: dotted lines). Both snakes were initially captured near streams, and did not move far from streams between locations in July (Fig. 4: circles). However, locations used in October–November, four months later, were far from the streams, and snakes that moved such distances would have had little chance of being detected in repeat surveys within plots (Fig. 4: triangles). The patterns of movement during the two other months, for which the data were lost, were similar, and snakes did not use subterranean retreats in any period.

## DISCUSSION

The low number of juveniles detected (7.5%) indicates that they may be largely undetectable by visual surveys, possibly because they tend to be more arboreal than adults (Oliveira and Martins, 2001). Therefore, our conclusion should only be applied to large individuals (>30 cm SVL).

Detectability of individuals of *B. atrox* varied little among habitats, and we detected no effect of leaf-litter depth, the variable that we expected to show the greatest effect on detectability. Individuals were marked at the beginning of the study, but only one of 33 were recaptured. The low recapture rate may result from frequent movement of individuals out of survey plots, from low detectability coupled with high densities, or a combination of these factors. Although we radio tracked only two adult individuals, their patterns of movement were similar, and inconsistent with the hypothesis that individuals spend long periods in subterranean retreats where they would be



**Fig. 4.** Positions of the two radio-tracked individuals of *Bothrops atrox* in relation to distance along and from the streams. Dotted lines = strip 10 m wide each side of the stream, circles = positions in July, triangles = positions in October–November.

undetectable by visual surveys. Movement rates of the two adult *B. atrox* evaluated by radio telemetry indicate that individuals would frequently disperse out of plots over a period of several months. Although we cannot discount some effect of detectability on differences among habitats, differences in detectability are unlikely to be responsible for the very large differences in encounter rates between riparian (41 snakes) and non-riparian areas (12 snakes).

Estimates of density and probabilities of detection indicated that the riparian zone used by *B. atrox* may be relatively narrow (up to 10 m from each bank of the stream) compared to riparian zones used by the assembly of snakes in the same study area of (up to 100 m, Fraga et al., 2011). For populations of *B. atrox*, as well as other congeneric species, riparian zones are used as aggregation sites (Nogueira et al., 2003; Campbell and Lamar, 2004; Fraga et al., 2011). Therefore, they may be important for maintaining numbers of *B. atrox*, despite the species being independent of water to complete its life cycle. The species is not restricted to riparian habitats, has a generalist diet (Martins and Gordo, 1993; Martins and Oliveira, 1999), and is frequently found in a variety of habitat categories (Duellman, 1978; Campbell and Lamar, 1989; Martins and Oliveira, 1999).

*Bothrops atrox* is more frequently encountered around streams and this may be relevant for the placement of trails to avoid snakebite. Data on movements would be necessary to determine whether this results from movements by individual snakes or occurs because individuals have activity centered in different habitats. Radio-telemetry data from two snakes and unrecorded observations on two others indicate that individuals found around streams can move to locations more than 50 m from the stream, but we detected only low densities of *B. atrox* in plots between 10 and 100 m from streams. It therefore seems that the high density of sightings around streams occurs because individuals can spend much of their time very close to streams, and not necessarily because there is a higher density within 100 m of streams.

*Bothrops atrox* shows ontogenetic variation in the use of plant strata (Campbell and Lamar, 1989; Zimmerman and Rodrigues, 1990; Oliveira and Martins, 2001), and we found differences in the sizes of snakes related to distance from streams. However, the reasons for this are not clear. Many studies have investigated the importance of habitat segregation in tropical forests (Akani et al., 1999; Heard et al., 2004; Jankowski et al., 2009), but variation in densities of species generally occurs along subtle gradients. Few organisms show strong segregation among habitats subjectively determined by humans, such as the frequently used classification of plateau, slope, and valley bottom (e.g., Ribeiro et al., 1999). Riparian zones appear to be one of the most distinctive habitats within the forest, and influence the densities of many organisms, including *B. atrox*. However, the effects are relatively subtle and it is not possible to evaluate how much most of the species depend on riparian zones, as opposed to taking advantage of riparian zones when they are available. Although effects of environmental gradients are detectable (e.g., John et al., 2007), in central Amazonia most plant species appear to be habitat generalists with wide environmental tolerance (Kinupp and Magnusson, 2005), and this appears to also apply to *B. atrox*.

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