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Leaf litter depth and low canopy cover affect the detectability of the Brazilian Lancehead *Bothrops jararaca* (Wied-Neuwied, 1824) (Viperidae) in the Atlantic Forest

Jane C. F. OLIVEIRA[1,*], Átilla C. FERREGUETTI[1,4], Rafael SANTOS[2], Mateus Leite LOPES-SILVA[2], Lorena P. Vasconcelos BARROS[3], Bárbara RISSE-QUAIOTO[2], Cátia Moura MILITÃO[1], Pedro FATORELLI[1] and Carlos Frederico Duarte ROCHA[1]

1. Departamento de Ecologia, Instituto de Biologia Roberto de Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Maracanã, 20550-019, Rio de Janeiro, Rio de Janeiro, Brazil.
2. Centro Universitário São Camilo, Paraíso, Cachoeiro de Itapemirim, 29304-910, Espírito Santo, Brazil.
3. Faculdades Integradas São Pedro - FAESA Centro Universitário, Belo, 29053360, Vitória, Espírito Santo, Brazil.
4. Department of Ecosystem Science and Management, Intercollege Graduate Degree Program in Ecology, Pennsylvania State University, University Park, Pennsylvania, USA.
* Corresponding author, J.C.F. Oliveira, E-mail: janeherpeto@gmail.com

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Abstract. Precise estimates on the abundance and population size of a species are fundamental to the reliable evaluation of its conservation status. Demographic data can provide important insights into different aspects of the ecology, life history, and evolutionary history of a species, and can help to detect changes in population size, which is important in biological conservation. Here, we present the first systematic estimate of the abundance, detectability, and site occupancy of the Lancehead, *Bothrops jararaca* (Wied-Neuwied 1824), at Serra das Torres Natural Monument in the Atlantic Forest of Espírito Santo State, southeastern Brazil. To understand better the ecological factors driving occupancy, we also analyzed the principal habitats used by *B. jararaca*. We used the Rapid Assessment method to sample a *B. jararaca* population between January and March 2018 using active searching and pitfall traps. We applied the Royle-Nichols occupancy model to estimate the abundance of *B. jararaca*, as well as single-season, single-species occupancy models to analyze the types of habitats in which *B. jararaca* was most frequently detected. We recorded 47 juveniles and adults of *B. jararaca* (1.5 snakes per sampling day) and estimated an abundance of 137 ± 25 (mean ± SE) individuals for the sampled area within the MONAST. We found higher detectability in deeper leaf litter and higher detectability where there was a low percentage of canopy cover. Our results advance the understanding of snake population dynamics and contribute to the knowledge of the abundance patterns of *B. jararaca*.

Key words: abundance estimates, detection probability, habitat use, occupancy modelling, population ecology.

Introduction

Currently, 28 *Bothrops* species occur in all ecoregions of Brazil (Costa & Bérnils 2018), distributed in habitats ranging from lowland and montane rainforest to dry habitats (Campbell & Lamar 1989). *Bothrops jararaca* (Wied-Neuwied 1824) is endemic to the Atlantic Forest ecoregion and it is a common species (Campbell & Lamar 1989, Sazima 1992), occurring from the sea level to altitudes up to 1,200 m (Sazima 1992). This Lancehead snake can be found in preserved habitats, but also in anthropic areas and small forest remnants (Puorto et al. 1991). These snakes are predominantly crepuscular and nocturnal (Sazima 1988, Marques & Sazima 2004), although they may also be active during the day to thermoregulate (Sazima & Haddad 1992). *Bothrops jararaca* is terrestrial or semi-arboreal (Sazima 1992, Martins et al. 2002), with an ontogenetic shift in habitat use (Martins et al. 2002). Juveniles are found in close proximity to streams or on trees, while adults are predominantly terrestrial (Sazima 1992), possibly due to the type of prey consumed by the different age classes (Reinert 1993, Martins et al. 2002).

Although there are important contributions regarding *B. jararaca*'s natural history (Sazima 1992, Marques & Sazima 2004, Martins et al. 2002), none have considered the species detectability or estimated its abundance in a certain area. Abundance is one of the most important parameters used to evaluate a species' conservation status (Traill et al. 2007). Although there is growing evidence that snake populations are declining worldwide (e.g. Mullin & Seigel 2009, Reading et al. 2010) relatively few data are available for most forest remnants (Reading et al. 2010), which hinders systematic comparisons between different areas. Many snake species are difficult to study in situ because of low detection probabilities due to their low densities and cryptic behavior, especially in structurally complex habitats (Guimarães et al. 2014). To compensate systematically for this negative bias, it is important to ensure reliable estimates of species distribution and abundance (Bailey et al. 2013). Given this, reliable information on detectability and habitat occupancy, as well as on the abundance of *B. jararaca*, will be important for a better understanding of the species' ecology, and in particular planning of conservation policies for the protection of this snake in nature.

Estimates of the abundance of *B. jararaca* will play a role as a baseline for future studies of population dynamics and time series comparisons for the detection of demographic patterns. These studies are important mainly due to the general trend of snake populations declines (Reading et al. 2010), and because the Atlantic Forest is under intense pressure due to anthropogenic changes in land use (SOS Mata Atlântica / INPE 2018). Regarding the Espírito Santo State, data on *B. jararaca* abundance are currently available only in a herpetofauna study published by our research group (Oliveira et al. 2020). Here, we provide an estimate of the abundance of *B. jararaca* in the remnant forest of Serra das Torres in the Atlantic Forest of southeastern Brazil, and the first report on its detection probability. We also predicted the predominant habitats used by *B. jararaca* through occupancy modeling. We evaluated three questions: (a) what is the estimated abundance of *B. jararaca* in the sampled area?

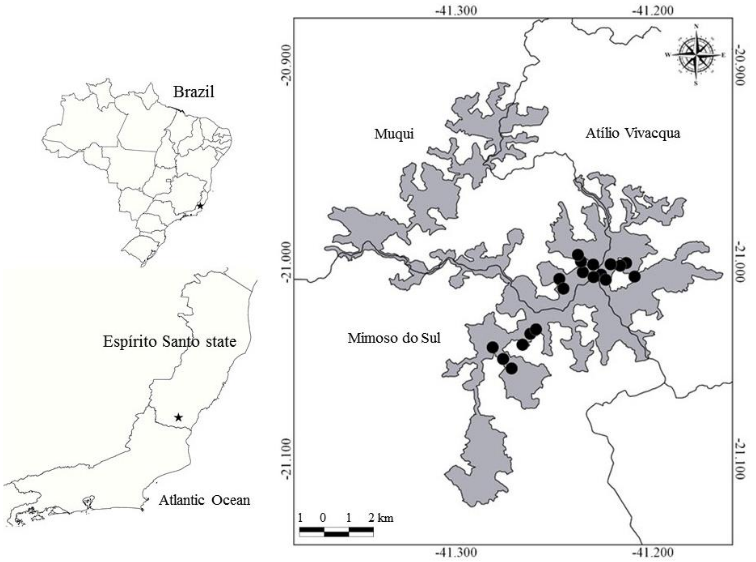

Figure 1. Location of the Monumento Natural Serra das Torres in the state of Espírito Santo (bottom left), within Brazil (top left). The limits of the MONAST are shown in relation to the municipalities Atílio Vivacqua, Mimoso do Sul, and Muqui (right). Black dots show the sampled locations.

(b) in which habitats we detected the most *B. jararaca*? and (c) whether microhabitat covariates are correlated with the detectability of *B. jararaca*?

Material and Methods

Study site

We surveyed within the Serra das Torres Natural Monument (Monumento Natural Serra das Torres; MONAST) (-21.0209N, -41.2378E), located in Atílio Vivacqua, Mimoso do Sul and Muqui municipalities in the south of the Espírito Santo State, southeastern Brazil as part of a broader herpetofaunal survey (Fig. 1; Oliveira et al. 2020).

The MONAST covers the largest complex of forest remnants found in southern Espírito Santo, with an area of approximately 10,450 hectares within the Atlantic Forest ecoregion. Several mountains within the MONAST reach more than 1,000 m asl and are covered by semideciduous seasonal forests, dense rainforests, and dense submontane rainforests (Magnago et al. 2008). The mean annual temperature in the entire forest remnant is approximately 24.5 °C and the mean annual rainfall is around 1,290 mm (Oliveira et al. 2013). The MONAST is surrounded by extensive farmlands, primarily coffee and banana plantations.

Snake surveys

Prior to field sampling, we chose 18 different locations to sample within MONAST (Fig. 1) that could be accessed by our research team and, preferably, that were composed of the most preserved forest – most of them in the central part of the forest remnant. We determined a distance of at least one kilometer between sampling locations to avoid pseudo-replication and to cover the largest possible forest area. We used the Rapid Assessment (RA) method (Patrick et al. 2014) to assess the abundance and habitat use of *B. jararaca* because this is an efficient approach that provides reliable and replicable data in a short period of time (Patrick et al. 2014). We surveyed the MONAST in 2018 for 30 sampling days total, doing 10 consecutive days in each municipality in which the protected area is located (in January – Atílio Vivacqua; February – Mimoso do Sul; March – Muqui) with a field team that included 6 to 10 members. The surveys focused on preserved fragments of forest at altitudes ranging from *ca.* 600 m to 1,000 m asl. Additionally, we recorded individuals occasionally found in the anthropic areas neighboring the MONAST, such as plantations, roads and also next to human habitations. At each sampled location we conducted transects with standardized time-limited surveys of one hour each (Crump & Scott Jr. 1994). Transects were conducted rigorously between 09:00 and 12:00 h for the daytime samples and between 18:00 and 23:00 h for the crepuscular/nighttime samples, for a total of 1320 hours of sampling effort (considering variations in team numbers and sampling hours/day). Each transect was sampled only once, either during the day or at night. We classified the age/reproductive stage of individuals according to Sazima (1992): adult males have Snout to Vent Length (SVL) > 65 cm and adult females' SVL > 75 cm; thus, individuals of both sexes with SVL < 65 cm were considered juveniles.

Additionally, we used four sets of pitfall traps with drift fences (Corn 1994). Each set consisted of about 80 m of plastic fencing dug into the ground in a straight line, with 40 buckets (diameter 40 cm; volume 20 L) spaced 2 m from each other and positioned underneath the fence. We installed these traps three days prior to each sampling session; the buckets were opened for the whole 10-day sampling. At the end of each sampling, we removed the buckets and fences. We installed the pitfall traps in different forest fragments and at different altitudes, focusing on the most preserved habitats. The overall sampling effort for the 30 sampled days of the pitfall traps sets with drift fence was approximately 720 hours.

We deposited collected voucher specimens at the National Museum (Museu Nacional, Rio de Janeiro - MNRJ), Rio de Janeiro State, in accordance to a permit by SISBIO/RAN no. 57085-6.

Covariates

We selected four covariates to model the occupancy and detection probability of *B. jararaca*. We recorded the following covariates for each individual found (1) canopy cover (measured as the percentage of vegetation on a photograph taken with ultra-wide lens smartphones, upwards perpendicularly from the forest floor at the exact point where a snake was first detected – see Suganuma et al. (2008); (2) the type of habitat where the snake was recorded (under a rock in the forest, on a tree, or within 3m of a stream); (3) anthropic areas – as classified above and, (4) depth of the leaf litter (in mm).

Data Analysis

We used the detection and occupancy probabilities to assess *B. jararaca* population parameters. Occupancy models determine imperfect detection by interpreting a series of detection/non-detection events arising from the interaction between a species' probability of patch occupancy (Ψ) and its detection probability (P). A detection event occurs when the site (we define site as each transect) is occupied, and the species was detected ($\Psi \times P$). A non-detection occurs because (a) the species was present but not detected ($\Psi \times [1-P]$) or because (b) the species was not present and therefore, was not detected ($1-\Psi$). The maximum likelihood method, used in this occupancy modeling approach, was selected here because it provided the least-biased estimates of occupancy and detection probabilities from a series of alternative approaches (Wintle et al. 2004).

We implemented Royle-Nichols occupancy models in the PRESENCE program (Royle & Nichols 2003) to estimate abundance. These models assume that the heterogeneity in detection among sites is the result of underlying differences in abundance (Royle & Nichols 2003). This analysis estimates an index (λ) of mean abundance, considering imperfect detectability. The Royle-Nichols model assumes that: 1) the number of animals at a site follows a defined spatial distribution for which λ-hat indicates the mean abundance across all sites; and 2) the probability of detecting animals during each occasion was related to the inherent detection probability of the species, r-hat, and its total abundance.

We also verified how habitat covariates affect species occupancy and detectability. For this, single-species, single-season occupancy models were created using the "Unmarked" package (Fiske & Chandler 2011) in software R (R Development Core Team 2017). For each location, we equated each day of sampling to an occasion, based on the Mackenzie et al. (2006) approach, to construct a detection history. We constructed a set of candidate models for *B. jararaca*, which were selected by *a priori* hypotheses based on three different approaches: (1) considering occupancy probability and detectability as constant across all sites, (2) considering the variation in occupancy as a function of the habitat covariates, and (3) considering only detectability as a function of the covariates. The best models were selected using Akaike's Information Criterion adjusted for small sample size (AICc). All models with a ΔAICc value of less than 2 were considered equivalent. We also used the weight (AICcwt) of each model, which corresponds to the amount of evidence in favor of a given model, to choose the best model, which we then selected to test our hypotheses. We checked our data with 2,000 bootstraps to assess the adjustment fit and over-dispersion parameter (c-hat) (Mackenzie et al. 2006).

Results

We recorded 47 individuals of *B. jararaca* during our field surveys. The overall encounter rate was 0.035 ind./hour or 1.5 ind./day. Juveniles comprised 17% (N = 8) of the individuals, and adults were 83% (N = 39). The estimated abundance (N-hat derived from the Royle-Nichols occupancy model) for the sampled locations in the MONAST was 137 ± 25 individuals (95% CI = 112–162 individuals).

Most individuals of *B. jararaca* recorded were on leaf litter (N = 21), followed by anthropic areas (N = 9), next to streams (N = 8), on trees (N = 8) and finally, under a rock (N = 1). Leaf litter was 0–12 cm deep with a mean of 4.10 cm (± 0.5). Only juveniles were recorded next to streams, and only adults were recorded in anthropic areas. No snakes were collected in the pitfall traps, although two juveniles were found at the edge of the buckets.

Occupancy was best described by only one habitat covariate, i.e., occupancy increased with increasing depth of the leaf litter (Table 1). Detectability was affected by two covariates: (1) leaf litter depth, with a positive effect (Fig. 2A) and (2) canopy cover, with a negative effect (Fig. 2B, Table 1). Canopy cover varied from 0–100% with a mean of 68.7% (± 5.3).

Table 1. Single-season occupancy and detectability models estimated for *Bothrops jararaca* in the Natural Monument Serra das Torres, southeast Brazil. Covariates: microhabitat types (habitat), leaf litter depth (litter), and canopy cover (canopy). Ψ = occupancy, p = probability of detectability, AICcw = Akaike weight. C-hat = 1.22 and model adjustment fit = 0.38.

Model	AICc	ΔAICc	AICcw	n°parameters
Ψ(habitat) p(litter; canopy)	315.12	0.00	0.76	5
Ψ(habitat) p(litter)	315.18	0.06	0.08	4
Ψ(habitat) p(canopy)	315.85	0.73	0.18	4
Ψ(habitat; litter) p(litter; canopy)	316.42	1.30	0.17	6
Ψ(.) p(.)	317.96	2.84	0.16	2
Ψ(habitat; litter) p(habitat; litter; canopy)	318.96	3.84	0.02	7
Ψ(habitat) p(habitat; litter; canopy)	319.02	3.90	<0.01	7
Ψ(.) p(litter; canopy)	320.41	5.29	<0.01	4
Ψ(habitat) p(.)	320.53	5.41	<0.01	3
Ψ(habitat; litter; canopy) p(habitat; litter; canopy)	328.01	12.89	<0.01	8

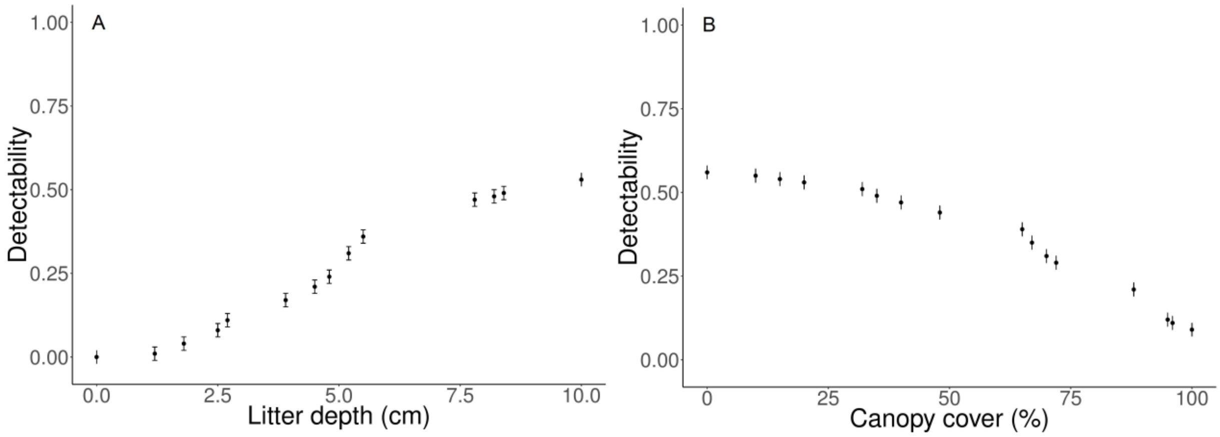

Figure 2. Relationship between detectability of *Bothrops jararaca* and leaf litter depth (A) and canopy cover (B).

Discussion

The abundance of *B. jararaca* recorded in the sampled site can be considered relatively high in comparison with previous studies in other Atlantic Forests remnants in southeastern Brazil where higher sampling effort was carried out. The species was seemingly rare in other herpetofauna studies, for example at Serra do Mendanha, in Rio de Janeiro State, where only 10 individuals were recorded during 62 months of sampling (Pontes & Rocha 2009). On Cardoso Island, in São Paulo State, only six individuals were recorded during 12 months of sampling (Rocha et al. 2008). A higher abundance was recorded however, at Jureia-Itatins Ecological Station where a herpetofauna study recorded 60 individuals in 3 years of sampling (1993–1996), although the total efforts of the study are not clear. Additionally, a study focusing on *Bothrops jararaca* population data, in Campinas – São Paulo State, recorded 77 individuals in 29 months of sampling (Sazima 1992). What factors determine these differences in the abundance of *B. jararaca* between seemingly similar forest remnants is still unclear. It is important to highlight that none of the previous studies on *B. jararaca* abundance considered the imperfect detection of individuals in the wild. Snakes are among the most difficult groups of reptiles to study in the wild due to their cryptic habits (Durso et al. 2011), which means that population estimates with narrow confidence intervals are rare (Dorcas & Willson 2009) or absent for most species, even those considered common such as *B. jararaca*. Here, we present the first estimate of a population size of this Lancehead snake that considers imperfect detection, which should improve the consistency of the results.

The abundance of *B. jararaca* recorded in the MONAST (including both adults and juveniles), suggests suitable conditions to maintain a population in the future and indicates that this area is a potentially important site for the conservation of this endemic species in the Atlantic Forest ecoregion of Brazil. But, additionally to the lack of abundance data, another concern is regarding the non-standardization of methods used to obtain this data, which makes comparisons between areas more difficult. The pitfall traps were not an adequate method to sample *B. jararaca*, and we suggest that it may be mainly because of the sedentary behavior of the viperids (Campbell & Lamar 1989), but may be also due to the large body size of this Lancehead compared to the buckets used that may allow snakes to avoid falling into the traps or getting out. Therefore, we recommend that future studies consider using the Rapid Assessment method with active search in similar forest remnants to collect *B. jararaca* abundance data, for aggregating data to comparative analysis.

Deeper leaf litter explained the occupancy probability of *B. jararaca* and also had a positive effect on detectability. We also found that low canopy cover was more related to detectability of this Lancehead snake. *Bothrops jararaca* is a predominantly terrestrial snake that typically thermoregulates by indirect sunlight (Sazima 1992). The fact that most individuals were found on the leaf litter and under low canopy cover is probably related to the availability of food and adequate temperatures in these habitats. In fact, *B. jararaca* feeds mostly on small terrestrial vertebrates, especially rodents (Sazima 2002, Hartmann et al. 2003) that are, in general, associated with the leaf litter and relatively complex habitats (Bonvicino et al. 2008, Emmous & Francois 2007). The use of trees and surroundings of streams by juvenile *B. jararaca* is probably related to the ontogenetic variation in its diet (Hartmann et al. 2003), and may reflect the feeding habitat of juveniles that feeds on frogs in the surroundings of streams and on trees, whereas the adults feed on rodents in the leaf litter. Anthropic areas were the second habitat most used by *B. jararaca* in the MONAST, and it is probably a result of the intense rodent activity found near farms, as well as the ecological flexibility of the species to live in disturbed habitats (Sazima 1992).

Abundance is an important parameter for assessment of the conservation status of a species (Traill et al. 2007), or for the evaluation of population decline. Here, we have presented the first estimate of the abundance of *B. jararaca* in southeastern Brazil that includes an evaluation of detectability and site occupancy probability. *Bothrops jararaca* is endemic to the Atlantic Forest ecoregion and our findings represent an important advancement in the understanding of ecological requirements of this Lancehead snake. Our results also provide important data for comparisons between *B. jararaca* populations from other regions, and emphasize the need for further investigations on the population parameters of this and other *Bothrops* species.

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