

Seasonal activity of *Bothrops jararaca* (Serpentes, Viperidae): optimizing foraging while avoiding predators

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Abstract. The peak of activity of *Bothrops jararaca* is in the rainy season. This pitviper feeds mainly on small mammals and is preyed upon by several avian and mammal predators. However, the association between *jararaca*'s seasonal activity with that of their prey and predators remains unknown. The present study tested the hypothesis that the peak activity of *B. jararaca* coincides with that of their prey and predators, mainly due to favorable climatic conditions during this period. Snake activity was inferred from standardized searches and animals deposited in herpetological collections. Seasonal activity of prey was inferred from monthly sampling carried out over one year using pitfall and Sherman traps. Plasticine models were used to infer predation risk. Analyses of predator and prey abundance were performed, taking into account climatic variables, and models explaining this relationship were proposed. Activity of both *B. jararaca* and its prey was higher in the rainy season. Activity of the latter was positively correlated with temperature and rainfall. Predator activity, however, was higher in the dry season and negatively correlated with temperature and rainfall but positively correlated with humidity. The peak activity of *B. jararaca* in the rainy season might favor foraging activities, since this period coincides with greater prey abundance and decreased predation risk. During the dry season when resource availability is low, predators feed opportunistically, encountering dangerous prey such as *B. jararaca*. In summary, the activity pattern showed by the snake clearly increases its survival.

Keywords. Food; Plasticine models; Predation; Rodents; Seasonality; Snake.

INTRODUCTION

For some time, researchers have tried to answer the fundamental question about population ecology: What determines species abundance and distribution? Although the role of some variables has been investigated separately, population dynamics depends on several environmental conditions, both abiotic and biotic, acting together (Townsend et al., 2010). For a population to thrive, a balance between predator and prey abundance is necessary. This balance also affects natural history traits, such as survival rates and breeding success (Oro et al., 1999). Predator activity can drive prey populations into decline, and in fragmented habitats it can even determine their presence or absence (Murdoch and Oaten, 1975). In contrast, predator activity can be regulated by prey activity and abundance such that predator diets adapt to target species whose daily and seasonal activity is similar to their own (Dugan, 1981; Folsom and Collins, 1984; Lode, 1995; Womble and Sigler, 2006).

Snakes are carnivorous, feeding on a broad diversity of prey from small invertebrates to large mammals, and some species even consume eggs (Gasc, 1994). They are also preyed by a wide range of predators, including both invertebrates and vertebrates (Greene, 1997). As such, predator and prey abundance can influence snake activ-

ity. Individuals of the insular pitviper *Gloydus shedaensis* (Zhao, 1979), for instance, restrict their activity to the seasons when migrant birds, their prey, are present on the island (Shine et al., 2003).

Nevertheless, that relationship is not universal. In southern Brazil, snake activity is not synchronous with that of their amphibian prey and is instead affected by temperature, while amphibian activity is modulated by humidity (Zanella and Cechin, 2009). Accordingly, species activity can be strongly correlated with abiotic factors, such as temporal heterogeneity, which can make the environment unfavorable during certain periods, such as winter in temperate regions (Menge and Sutherland, 1976; Sun et al., 2001) or even in tropical areas (Marques et al., 2001). This seasonal effect is noticeable for several taxa, including birds, mammals, amphibians, and snakes (Fowler and Salomão, 1994; Alves and Pereira, 1998; Marques et al., 2001; Loretto and Vieira, 2005; Ximenez and Tozetti, 2015). Seasonal activity in snakes can be modulated by climatic factors, such as temperature, rainfall, and wind (Shine et al., 2003; Brown et al., 2005).

Among the 405 Brazilian snake species (Nogueira et al., 2019), the pitviper *Bothrops jararaca* (Wied, 1824) stands out due to its pharmacological and medical importance (Ribeiro and Jorge, 1990; Ribeiro et al., 1998). Additionally, the species has a wide distribution,

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occurring from Paraguay, Argentina, and Rio Grande do Sul north to southern Bahia, Brazil (Campbell and Lamar, 2004). Juveniles feed mainly on anurans and adults mostly consume rodents, and it can be predated by raptors, such as the roadside hawk (*Rupornis magnirostris* Gmelin, 1788), the laughing falcon (*Herpetotheres cachinnans* Linnaeus, 1758) and owls, and mammals, such as the opossum (e.g., *Didelphis* sp.; Sazima, 1992; Oliveira and Santori, 1999). It is nocturnal, with peak activity during the rainy season (Sazima, 1992; Campbell and Lamar, 2004); however, whether its seasonal activity is influenced by either biotic or abiotic factors is yet to be investigated.

Phenological studies of tropical forests have demonstrated that peak productivity occurs in the rainy season (e.g., van Schaik et al., 1993). This seasonality in resource availability appears to be linked to the seasonal activity of several groups of animals, which can be more active in the rainy season, including birds (Poulin et al., 1992) and small mammals (Naxara et al., 2009; Barros et al., 2015). The present study aimed to test the hypothesis that the activity of *Bothrops jararaca* in the rainy season, which has been reported by previous studies (Sazima, 1992; Marques et al., 2001), coincides with that of their predators and prey, whereby the benefits offered by climate conditions and availability of prey would overcome the risk of *B. jararaca* predation. To test this hypothesis, we surveyed prey abundance and predation over a year and evaluated the correlation between the climate variables and the activity of *B. jararaca* predators and prey, proposing models to explain the variation in activity based on environmental variables.

MATERIALS AND METHODS

Field work was performed from November 2014 to October 2015 at “Núcleo Pedra Grande” (23°26′45.89″S, 46°38′10.26″W), Parque Estadual da Cantareira (PEC), in the northern region of São Paulo Municipality, Brazil. The phytophysognomy is classified as Ombrophilous Dense Atlantic Forest (Fundação Florestal do Estado de São Paulo, 2009), and the climate is Subtropical Humid according to Köppen climate classification (Instituto de

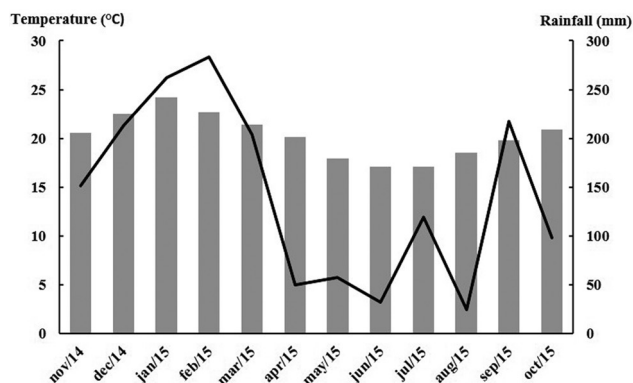


Figure 1. Mean temperature (bars) and rainfall (line) in São Paulo Municipality during the study period. Source: IAG/USP (2014, 2015).

Astronomia, Geofísica e Ciências Atmosféricas, 2016; Fig. 1).

Data from the literature indicates that *Bothrops jararaca* activity peaks in the rainy season (Sazima, 1992; Marques et al., 2001). Nevertheless, to obtain more refined data for our study area we used time constrained search and pitfall traps. Unfortunately, only four individuals were found during the study period, so we also included *B. jararaca* specimens sampled at PEC and either deposited at the Herpetological Collection Alphonse Richard Hoge from Instituto Butantan (1989–2019) or obtained through standardized sampling involving time constrained searches and pitfall traps carried out by our collaborators ($n = 13$ individuals between July 2017 and July 2018; N.F. Torello-Viera, pers. comm.). We only considered animals sampled at PEC in our analysis. The number of individuals in each season was used as a proxy to determine snake activity.

To sample *Bothrops jararaca* prey (rodents and anurans), six lines of pitfall traps (PT) were used, each composed of five 100-L buckets buried in line, 10 m apart, and linked by a drift fence. Additionally, 30 Sherman traps were installed on the forest substrate, 10 m apart from each other, in three transects near the PT lines. Both kinds of traps were inspected on three consecutive mornings every month, totaling 36 d of sampling over one year. Since the number of amphibians sampled was negligible, prey activity was inferred from the total number of rodents captured each month. Rodents captured were weighed, ear-tagged, and released, and recaptures were not included.

To assess the activity of *Bothrops jararaca* predators, plasticine models were used. Sixty snake models were placed in the field monthly, totaling 720 models (see Siqueira and Marques, 2018). The models were equally distributed along three trails and fixed 10 m apart from each other. Given that *B. jararaca* is semi-arboreal (Araújo and Martins, 2006), a randomization was previously defined in order to place models on the ground or in the vegetation (ca. 1.5 m height) in a 1:1 proportion. Even though *B. jararaca* is nocturnal active, individuals are frequently observed basking during the day (Sazima, 1988), so they are exposed to predation risk during both periods. As such, models were left in the field for 48 h, after which they were inspected and imprints left by mammals and birds were recorded. Such imprints are easily recognized by the presence of tooth or beak marks. Predator activity was estimated according to the number of models attacked per month.

Six abiotic variables were included in the analyses, including rainfall (rain), minimum (tmin), maximum (tmax), and mean (tmean) temperatures, and mean (hmean) and minimum (hmin) humidity. Daily averages of these variables were used to calculate an average for each 3-d sampling event. These data were provided by the “Instituto de Astronomia, Geofísica e Ciências Atmosféricas” of Universidade de São Paulo (IAG/USP, 2014, 2015). As the local climate is classified as Subtropical Humid, the year was divided into two seasons: (1) dry season, April–Sep-

tember, and (2) rainy season, October–March (Morellato et al., 2000).

A Chi-square test (X^2) was used to analyze the seasonal activity of the three trophic levels, namely *Bothrops jararaca*, its predators, and its prey. Correlation analysis was used to investigate the association between abiotic variables, prey activity, and predation risk. The abiotic variables were also used as predictors to model the variation in prey activity and predation risk. A multivariate approach was used, and Partial Least Squares regression (PLS) was chosen in order to control for the high correlation between predictor variables. This analysis compresses the predictor variables into Principal Components (PCs), which are regressed against the response variable (in this case, predator and prey activity). We chose the final model as the one with the PCs which showed the smallest cross-validation error (Root Mean Square Error Predicted, or RMSEP). Given that birds and mammals might be differently affected by climatic variables, three PLS analyses were performed to evaluate which climatic variables best explained bird activity, mammal activity, and prey activity. Models and correlations between abiotic variables and snake activity were not explored since data on the latter were obtained from different sources and methods. Analyses were performed using R Statistical Software version 3.5.0 (R Core Team 2020).

RESULTS

Seasonal activity of *Bothrops jararaca* and its predators and prey fluctuated over the months and showed different patterns (Fig. 2). Considering data from all sources, 27 snakes were sampled at the study area. The species was significantly more active in the rainy season ($n = 21$) than in the dry season ($n = 6$; $X^2 = 8.33$, $df = 1$, $P = 0.00389$). Concerning prey, 234 rodent specimens were captured, and their activity was significantly higher in the rainy season ($n = 161$) than in the dry season ($n = 73$; $X^2 = 16.38$, $df = 1$, $P = 0.00005$).

Predation rate upon models of *Bothrops jararaca* was 12.3% (89 of 720 models). Mammals were responsible for 58 attacks (65.1%) and birds 31 (34.9%). More attacks occurred in the dry season ($n = 65$) than the rainy season ($n = 24$; $X^2 = 9.02$, $df = 1$, $P = 0.02$). This seasonal difference is caused by the attacks made by mammals, which increased more than 600% during the dry season ($X^2 = 17.76$, $df = 1$, $P = 0.000002$), whereas no difference was observed in the number of attacks by avian predators between both seasons ($X^2 = 0.01$, $df = 1$, $P = 0.8$) or between birds and mammals in the rainy season ($X^2 = 0$, $df = 1$, $P = 1$). Regarding the substrate, models placed on the ground were more attacked during the dry season ($X^2 = 6.3$, $df = 1$, $P = 0.01$), but no difference was found between seasons for those

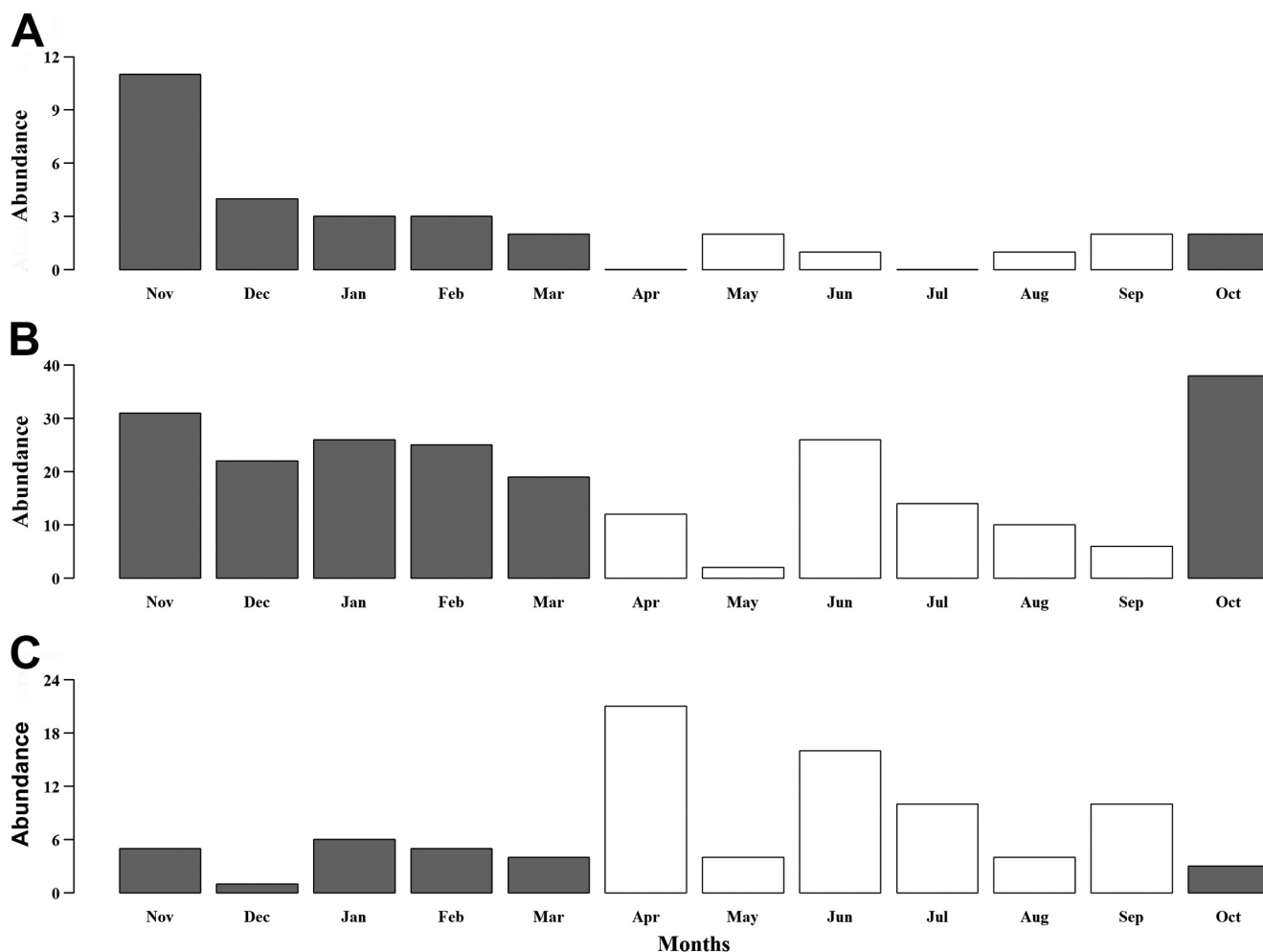


Figure 2. Seasonal activity of (A) *Bothrops jararaca*, (B) prey, and (C) predators. Dark grey: rainy season; white: dry season.

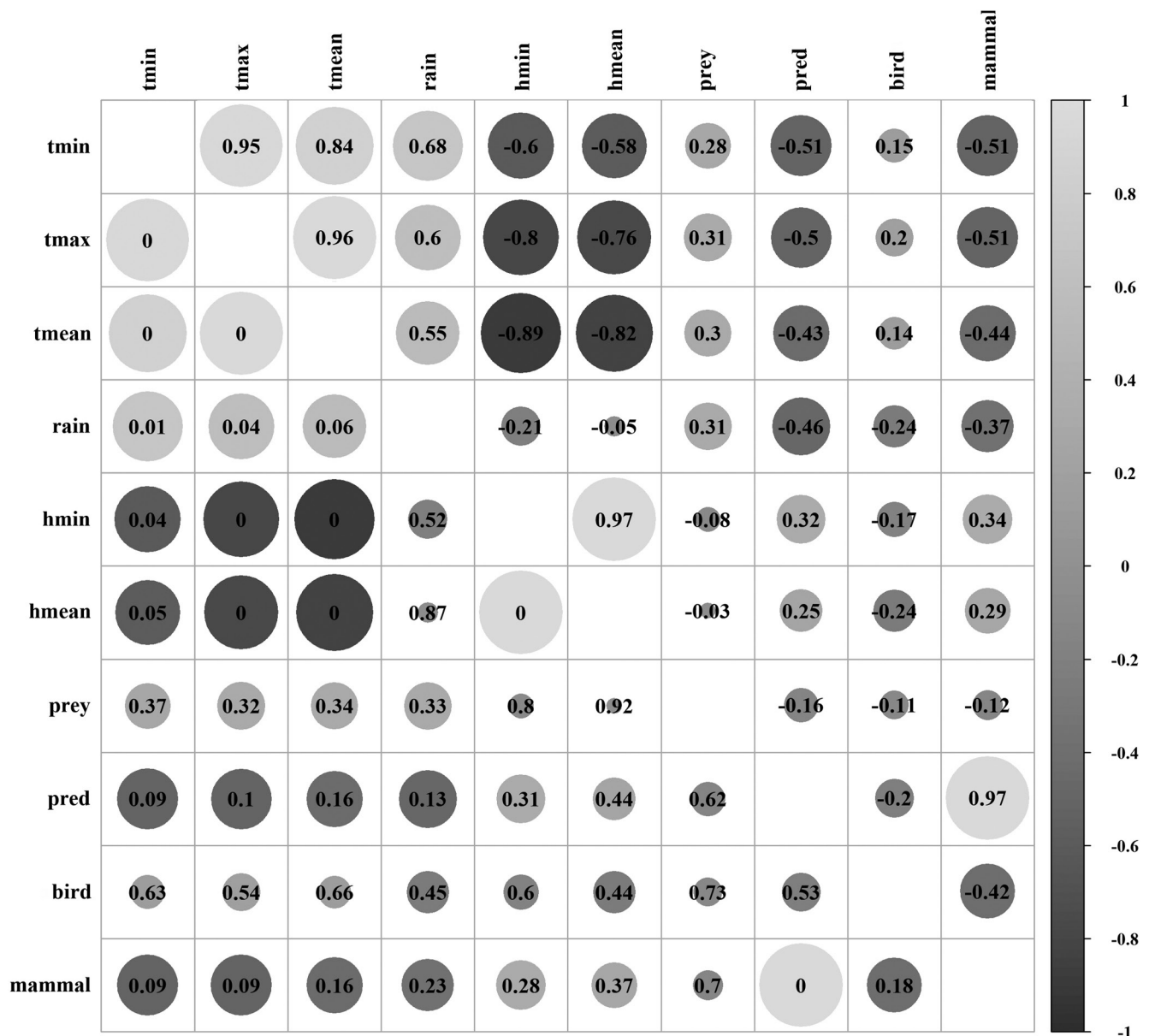


Figure 3. Correlations between *Bothrops jararaca* prey (prey) and predators (pred, bird, mammal) activity and the abiotic factors of minimum (tmin), maximum (tmax), and mean (tmean) temperature, rainfall (rain), and minimum (hmin) and mean (hmean) humidity. Grey scale bar and numbers represent the correlation coefficient, numbers in upper triangle are correlation coefficient (r), and in the lower triangle are the P value.

placed in the vegetation ($X^2 = 2.07$, $df = 1$, $P = 0.14$), or between those on the ground and in the vegetation in the rainy season ($X^2 = 0$, $df = 1$, $P = 1$).

Prey activity was positively correlated with all abiotic factors except humidity. In contrast, predator activity was negatively correlated with temperature and rainfall and positively correlated with humidity (Fig. 3). Correlation (r) strength varied from weak to medium for both prey ($r = -0.03$ – 0.31 , $df = 10$, $P > 0.05$) and predator activity ($r = -0.16$ to -0.51 , $df = 10$, $P > 0.05$).

PLS analysis showed quite similar results for all models. Altogether, the six PCs (corresponding to the abiotic variables) explained little variance in the response variables (38.6% of prey activity and 36.2% and 58.9% of avian and mammal predator activity, respectively). The best fits were found in the intercept in all cases, which means that the smallest errors were reached when no components were

accounted for (Table 1). This indicates that our predictor variables alone are not adequate to account for the data.

DISCUSSION

Several studies have demonstrated strong synchrony between the activity of predators and their prey (Cheah and McClure, 2000; Develey and Peres, 2000; Womble and Sigler, 2006) and between climate and species abundance (Zanella and Cechin, 2009), but few have focused on snakes. Our study is the first to compare snake activity considering three trophic levels, evaluating both predation risk and prey abundance simultaneously. This is relevant since it has been shown previously that climatic variables alone might not explain seasonal activity of tropical snakes (Brown and Shine, 2002).

Table 1. Partial Least Square (PLS) models with six abiotic variables built to explain variation in *Bothrops jararaca* prey and predator abundance, including the percentage of the cumulative contribution of the components to explain the observed data. The best model was the one with the smallest Root Mean Squared Error Predicted (RMSEP). NCOMP: number of components; *: best fit.

MODEL	NCOMP	% VARIANCE EXPLAINED	RMSEP
BIRD PREDATORS	0	-	1.508*
	1	6.86	1.732
	2	13.84	1.747
	3	28.43	1.854
	4	31.12	2.167
	5	34.44	2.819
	6	36.22	3.447
MAMMAL PREDATORS	0	-	6.618*
	1	18.28	6.647
	2	23.67	7.730
	3	27.35	8.192
	4	47.78	8.045
	5	50.92	7.302
	6	58.99	8.421
PREY	0	-	11.02*
	1	7.62	11.95
	2	13.40	11.30
	3	25.34	12.26
	4	34.89	13.38
	5	37.49	22.34
	6	38.62	26.13

Corroborating previous reports (Sazima, 1988; Marques et al., 2001), we found a marked peak in *Bothrops jararaca* activity in the rainy season. More rodent prey were also sampled during this period, revealing a positive association between snake activity and prey abundance and confirming our initial hypothesis. In tropical forests, food availability (e.g., fruit production and arthropod abundance) is highly seasonal (Karr, 1976; Develey and Peres, 2000) and may have a direct influence upon the abundance of species (Blake and Hopes, 1986). This could explain greater abundance of rodents in the rainy season, synchronizing their activity with the period of higher food availability. Surprisingly, we sampled very few anurans throughout the study. A strong correlation has been demonstrated between the activity of tropical anurans and the wet season (e.g., Sazima and Eterovick, 2000; Brown et al., 2002). Nevertheless, the present study was carried out in a period of uncommon drought (Coelho et al., 2016), which might have compromised our sampling.

Like *Bothrops jararaca*, the common lancehead (*B. atrox* Linnaeus, 1758) is more active during the rainy season in Amazonia (Oliveira and Martins, 2001), even though climatic variation is smaller at low latitudes. This same activity pattern has also been reported for the other pit vipers at high latitudes in southern Brazil (Hartmann et al., 2004; Rocha et al., 2014), where climatic variation (mainly temperature) is much more severe. In Amazonia, the monthly abundance of *Bothrops* found in the field was correlated with rainfall, but not temperature (Oliveira and Martins, 2001). Low temperatures in Amazonia during the

dry season are rarely less than 20°C; therefore, it might not restrict the activity of snakes (Fisch et al., 1998). Thus, prey availability might explain this correlation at low latitudes. In contrast, at high latitudes minimum temperature reaches less than 10°C during the dry season in several localities in southern Brazil. Low temperatures can reduce the metabolic rate of snakes considerably and, consequently, constrain their activity (Lillywhite, 1987). Thus, higher activity of *Bothrops* in southern Brazil during the rainy, warmer season may be explained by both the food availability and climatic conditions. Accordingly, it has been shown that another tropical ambush-foraging snake, *Acanthophis praelongus* Ramsay, 1877, reduces activity in the dry season, when prey are scarce (Christian et al., 2007).

Given that more models were attacked in the dry season, we refuted our initial hypothesis that the risk of *Bothrops jararaca* predation would be higher in the rainy season. Given that the phytophysiognomy of the study site is classified as ombrophilous dense forest (Fundação Florestal do Estado de São Paulo, 2009), the canopy is perennial (Ellenberg and Mueller-Dombois, 1967), so it is unlikely that phytophysiognomy would influence predation risk. Consequently, to understand these results we must take into account which species may prey on *B. jararaca* in our study area, and also their foraging mode. Birds of prey such as *Herpetotheres cachinnans* are common in the area and are considered effective snake predators (Daval et al., 2006; Costa et al., 2009). However, it is known that some opportunistic species also prey on *B. jararaca* (Sazima, 1992). This is in accordance with our findings, since imprints made by mammals on the models were identified as opossum bites. Omnivorous animals, such as opossum, switch their diet according to the seasonal availability of different items (Cáceres, 2002; Ceotto et al., 2009). Therefore, it is expected that in periods of resource scarcity predators might be less selective and feed opportunistically in order to avoid starvation, even dealing with dangerous prey such as snakes. A similar situation was reported for predation on coral snake models in Argentina, which underwent a higher incidence of predation during the dry season (Buasso et al., 2006).

The opossum *Didelphis aurita* (Wied-Neuwied, 1826) feeds mainly on invertebrates (present in 100% of the feces), fruits (53.8%), and vertebrates (30.8%; Santori et al., 1995). Biomass of both invertebrates and fruits in forests commonly peaks during the rainy season (Karr, 1976; Develey and Peres, 2000). Likewise, the frequency of these items in fecal samples is higher in this period, so that, for instance, the percentage of fruits in scats may decrease from 92% in the rainy season to 58% in the dry season (Cáceres and Monteiro-Filho, 2001). This same study showed that opossum scats contained remains of the blind snake *Liotyphlops beui* (Amaral, 1924) twice as frequently in the rainy than in the dry season. Nevertheless, *L. beui* is a fossorial species which remains underground during the dry season and is active on the surface during the rainy season, probably due to food availability and soil saturation by increased rainfall (Parpinelli and Marques,

2008), which would increase the chances of their capture by an opossum.

In any event, considering the general scarcity of food items during the dry season, opossums are expected to search for alternative food sources, including snakes (Almeida-Santos et al., 2000; Cáceres, 2002), which might explain the higher risk of *Bothrops jararaca* predation by mammals during the dry season. Additionally, models placed on the ground were attacked more frequently in the dry season, which could be explained by the different foraging strategies used by the opossum. Despite also being scansorial, the use of vegetation by *Didelphis aurita* seems to be related to flood regimen, which is not a concern at our study site (Leite et al., 1996).

Risk of predation by birds did not vary seasonally; however, vagility is greater in avian predators than non-volant species, enabling them to search for food sources other than snakes in different localities. It has also been shown that snakes with triangular heads are attacked less frequently by avian predators (Valkonen et al., 2011), what might have caused persistent avoidance of the models by birds. Accordingly, most of the attacks in the present study were inflicted by mammals.

The prey and predators of *Bothrops jararaca* are composed of different taxa (Sazima, 1992) with different evolutionary and ecological histories and probably respond differently to climate changes. For example, unlike marsupials (predators), the abundance of rodents (prey) is fairly constant over the year (Fonseca and Kierulff, 1989). This lack of seasonality in rodent activity might even be a result of species showing different seasonal activity patterns. For example, in two rodent species that occur in the Atlantic Forest, *Akodon cursor* (Winge, 1887) is more active in the rainy season, while *Necromys lasiurus* (Lund, 1840) is in the dry season (Feliciano et al., 2002). Such scenarios could explain why PLS analyses failed to fit models that properly predict prey activity and predation risk. This indicates that none of the abiotic variables could explain either prey activity or predation risk, which might be influenced either by biotic variables or other abiotic variables we did not consider. For instance, bird predation on lizards has been best explained by intensity of attendance at army-ant swarms (Poulin et al., 2001), and activity of bats can be explained both by biomass of insects and minimum nightly temperature (Hayes, 1997). Moreover, the fitting problem could be a consequence of small sample size, whereby the high variance of the data could have influenced the model optimization.

In summary, we found that the activity peak of *Bothrops jararaca* coincides with that of prey abundance in the rainy season. We had hypothesized that risk of predation would also be higher in the rainy season and still the benefits of better climate conditions and abundance of prey would overcome the risk of being predated; however, the peak of activity of the snakes overlapped with low predation. This pattern of avoiding activity during the time when predators are more active has been demonstrated in several groups employing different strategies, such as altering activity time (Clarke, 1983; Hudgens and Garcelon,

2011) or employing warning signals (Ratcliffe and Nydam, 2008). Additionally, the fact that predator activity peaks in the dry season suggests that they shift to dangerous prey when other food resources are scarce. The present results are important not only to evidence when each species or group of species is more active and is influenced by which abiotic variables, but also to highlight the complex relationship involved when three or more correlated trophic levels are evaluated.

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