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## Effects of Urbanization on *Bothrops jararaca* Populations in São Paulo Municipality, Southeastern Brazil

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ABSTRACT.—Quantitative and qualitative alterations in the environment may have serious ecological consequences for populations of native species. Isolated forest fragments, such as those surrounded by highly urbanized areas, may function similarly to oceanic islands with differences in species diversity compared to mainland areas. These differences may include changes in prey availability and predator pressure, with consequent effects on growth and size of species that interact with those prey and predators. Here, we investigate body size, prey availability, and predation pressure in populations of *Bothrops jararaca* in two forest fragments within an urban environment in southeastern Brazil (a completely isolated, small forest fragment and a large, well-connected forest fragment). While we found no differences in mean body size or stoutness between the two populations, we did find larger specimens in the small isolated fragment. Prey availability and predator pressure also were significantly lower in the small isolated fragment. The urban environment significantly changes the population ecology between the two locations. These results suggest that lower food availability in the isolated fragment did not decrease the growth rate of *B. jararaca*, but the low predator pressure increased longevity, resulting in a higher proportion of large snakes in this population.

RESUMO.—Alterações quantitativas e qualitativas no ambiente podem ter sérias consequências para a ecologia de populações de espécies nativas. Fragmentos florestais cercados por matriz urbana podem funcionar de modo similar à ilhas oceânicas, tendo menor diversidade de espécies do que áreas maiores. Outras diferenças incluem mudanças na disponibilidade de presas e pressão de predadores, que consequentemente afetam o crescimento e tamanho das espécies. Neste estudo investigamos o tamanho corporal, disponibilidade de presas e pressão de predadores em populações de *Bothrops jararaca* em dois fragmentos florestais dentro de um ambiente urbano no Sudeste do Brasil (um pequeno fragmento completamente isolado e um grande fragmento conectado). Não encontramos diferenças na média do tamanho corporal, nem na robustez entre as duas populações. Entretanto, espécimes maiores foram encontrados no fragmento menor e isolado. A disponibilidade de presas e pressão de predação também foram significativamente menores no fragmento menor e isolado. O ambiente urbano mudou significativamente a ecologia da população destes dois locais. Os resultados sugerem que a menor disponibilidade de presas não diminui a taxa de crescimento de *B. jararaca*, mas a menor pressão de predação pode aumentar a longevidade, resultando em uma maior proporção de serpentes maiores nesta população.

Snakes exhibit indeterminate growth (Shine and Charnov, 1992); the rate may be influenced by several ecological factors such as climate, food availability, predation pressure, and competition (Dunham et al., 1978; King, 1989). Hence, species with wide geographic distributions may diverge in growth pattern because of exposure to distinct environments (Arnold, 1977; King, 1989; Pearson et al., 2002). In addition, natural selection can result in genetic differences among populations, especially where gene flow from other populations is reduced or absent (Hendry and Taylor, 2004; Nosil and Crespi, 2004).

Oceanic islands provide good examples of morphological divergence because of population isolation. For example, island snakes can exhibit variants in body size such as dwarfism or gigantism compared to relatives elsewhere (Boback, 2003). These directional changes are driven by a complex combination of ecological factors, but diet is a particularly important cause (Case, 1983; Hasegawa and Morigushi, 1989; Kohno and Ota, 1991; Boback, 2003). This phenomenon is seen in pitvipers of the *jararaca* group in southeastern Brazil, where *Bothrops jararaca* is a mainland species and *B. insularis*, *B. alcatraz*, *B. otavioi*, and *B. sazimai* are island dwellers. The island species are significantly smaller and consume lower-calorie food (the mainland species feed on birds, anurans, lizards, and centipedes [Marques et al., 2002, 2012; Martins et al., 2002; Barbo et al., 2012]).

*Bothrops jararaca* is a medium-sized snake species, reaching up to 1,600 mm, with females being substantially larger than males (Campbell and Lamar, 2004). These pitvipers are predominantly rodent eaters, and dwell in Atlantic forest, but can occur in disturbed areas such as forest remnants surrounded by humandominated landscapes (Puorto et al., 1991). This species is relatively abundant in São Paulo Municipality, occurring in some forest fragments within the urban area (Barbo et al., 2011).

Forest fragmentation is mainly of anthropogenic origin (e.g., urban growth; Wade et al., 2003). Urbanization brings additional consequences, such as isolation, making forest remnants island-like and altering prey–predator dynamics and community richness (McKinney, 2002, 2006; Chace and Walsh, 2006). Hence, urbanization is an important conservation issue.

The aim of this study was to test for an island effect on *B. jaracara* in a forest fragment by comparing body size in two populations in urban fragments of different size and degree of isolation and by evaluating prey availability and predation pressure in each of these fragments. We expected differences in prey availability and/or predation pressure between the two forest fragments as well as consequential differences in body size of the two populations.

### MATERIALS AND METHODS

*Study Site.*—We conducted field work in two parks of different size and degree of isolation in São Paulo Municipality: Parque Estadual das Fontes do Ipiranga (PEFI), a small forest fragment

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FIG. 1. Map showing the localities of the two study areas of *Bothrops jararaca*: Parque Estadual da Cantareira (PEC, yellow) above and Parque Estadual das Fontes do Ipiranga (PEFI, red) below.

completely isolated and surrounded by an urban matrix, far from any other forest patch; and Parque Estadual da Cantareira (PEC) a large and well-connected forest fragment (Fig. 1). The PEFI is in southeastern São Paulo City ( $23^{\circ}38'40.48''S$ ;  $46^{\circ}26'05.34''W$ ). Prior to urbanization it was a cultivated area, and the implementation of the Conservation Unit aimed to ensure the preservation of local water sources and the regeneration of the native forest from the 19th Century onward (Godoy and Trufem, 2007). This small park (540 ha), with altitudes ranging from 770 to 825 m, is now covered by rain forest (Dense Ombrophilous Atlantic Forest). The climate is humid mesothermal with an average annual temperature of 19.1°C (Governo do Estado de São Paulo [GESP], 2008; Instituto de Botânica de São Paulo, 2016). This forest patch is at least ~4.5 km from any other *B. jararaca* habitat.

The PEC is in the northern region of the city (23°26′01.63″S; 46°37′49.50″W) and also includes parts of other municipalities. This large park (7,917 ha), situated at altitudes from 875 to 1,250 m, is also covered by similar rain forest. The climate of this region is also classified as humid mesothermal, with an average temperature of 19.9°C (GESP, 2009). Therefore, apart from size, the two sites are comparable in general characteristics.

*Sampling of* Bothrops jararaca.—Data on body size (measured as snout–vent length, SVL) and mass of snakes captured between 2003 and 2007 were obtained from a previously published study (Barbo et al., 2011). Measured snakes included those recorded

specifically in PEFI or PEC as well as those found by citizens in the vicinity. We considered snakes belonging to those populations only if found in the immediately adjacent neighborhood and no other available habitat was near. Snakes with unreliable locality were discarded.

We obtained additional data (not included by Barbo et al. [2011]) at the Coleção Herpetológica of Instituto Butantan, São Paulo. We also included data obtained at PEFI by Fundação Parque Zoológico de São Paulo from specimens that received a microchip tag and were tracked by radio for a few months but were not collected. Finally, we conducted fieldwork in both study areas to collect additional original data on snakes.

*Field Work.*—Search methods included visual search (VS), occasional encounters (OE), and pitfall traps (PT). All methods were rigorously replicated in both locations, aiming to avoid any bias because of different sampling effort, and were performed monthly during four consecutive days in both locations over 1 yr of data sampling (November 2014 to October 2015).

We performed VS for snakes during the daytime along the roads and paths inside the park areas. A total of six PT were installed in each park to capture both *B. jararaca* and their potential prey. Each pitfall set was made up of five buckets, with 100-L capacity each, and with a Styrofoam plate inside to prevent animals from drowning; they were buried in a line, 10 m apart, and connected by a drift fence (Cechin and Martins, 2000; Oliveira and Martins, 2001; Anthony et al., 2005; Sawaya



FIG. 2. Plasticine replicas used in the experiments of predators' pressure on *Bothrops jararaca*. The replica represents the front portion of an adult individual, and it is placed with a wire to improve substrate fixation. (A) Standard model; (B) mammal attack; (C) bird attack; and (D) rodent bite easily distinguished by the incisive teeth.

et al., 2008). Pitfalls remained open during four consecutive days and were checked every morning.

Snakes found in the field were sexed, measured, and weighed, then were given a tag (numbered subcutaneous chip) and released right after the procedure. Some of the small mammals captured in PT and Sherman Live Traps (SLT) were collected for separate analysis of karyotype. The remainder was released after being weighed and receiving a numbered earring tag in the left ear. All methods we used were previously authorized by appropriate authorities, including ethics in animal use and research permits.

We assessed potential prey availability over a year of field work. We used PT and SLT to capture rodents. The PTs were the same ones used for snakes. Additionally, 30 SLTs were equally distributed among three trails per park (10 units per trail, 10 m apart). We placed bait composed of banana, corn flour, and peanut candy inside each SLT. We inspected each SLT every morning during four consecutive days. For the analysis, we considered only rodents, the main prey of adult *B. jararaca* (Sazima, 1992; Martins et al., 2002).

Plasticine replicas of anterior portions of snakes with triangular-shaped heads were used to compare relative predation pressure between sites (cf. Guimarães and Sawaya, 2011; also see Valkonen et al., 2011). All replicas were blackish-brown and were 25 cm in length and 1.5 cm in diameter, representing an adult-sized snake and avoiding bias because of differential predation on snake sizes. To prevent removal by predators, models were anchored to the ground with wire (Fig. 2). A total of 60 models were placed monthly at 10-m interval along three transects (total of 720 models in each park). The models were molded in an "S" shape and haphazardly placed in the same proportions in two different substrates: on the forest ground or on tree branches.

The models remained exposed for 48 h, were collected, and then later examined for marks of predator attacks. Predator type was determined by imprints left on the model such as teeth (mammals) and beaks (a "V" or "U" shaped mark made by birds; cf. Brodie, 1993; Valkonen et al., 2011). Other marks left by nonpredators (e.g., small rodents) were excluded from the analysis (Fig. 2B–D). We compared three variables between parks: 1) total attacks, 2) predator type, and 3) substrate.

Data Analysis.—Because of sexual size dimorphism, we made separate comparisons for males and females of SVL and mass between localities. Also, to avoid bias because of newborn recruitment, only adults were analyzed, i.e., males >650 mm and females >750 mm SVL (see Sazima, 1992). A *t*-test was utilized for comparing body size between localities. Stoutness was evaluated through linear regression of body size and mass, and then the regression coefficient was compared by *t*-test between the two populations. A chi-square ( $\chi^2$ ) test for independent groups was used for examining differences in the distribution of each population by size class. The number of classes was determined by calculating the square root of the sample by sex. Posteriorly, the range of SVL was equally divided into the number of class intervals. We report summary statistics as means  $\pm$  SD.

Prey availability was estimated using the relative density index (RDI) for both parks (Gomez et al., 2008): RDI = (number of captures/number of traps  $\times$  number of days)  $\times$  100. We considered each monthly campaign as one sample and, after testing for normality (Shapiro-Wilks method), we used a *t*-test to investigate differences in total prey abundance and mass. Although juvenile *B. jararaca* can consume anurans and lizards,



FIG. 3. Comparison of SVL (mm) between *Bothrops jararaca* males (M) and females (F) of Parque Estadual das Fontes do Ipiranga (PEFI) and Parque Estadual da Cantareira (PEC). Lines represent averages, boxes are standard deviation, and whiskers are total range.

our analysis was composed only of adults; therefore, we did not include juveniles in our analysis. We tested the difference between sites in predation pressure with a G-test of the proportion of models at each site that was attacked.

#### RESULTS

*Morphology.*—Average body size of adult snakes from PEFI and PEC, respectively: males = 785.1 ± 81.9 mm (range = 666–740 mm, n = 17) and 824.6 ± 75 mm (range = 710–969 mm, n = 12); females = 1,149.6 ± 177.2 mm (range = 765–1,425 mm, n = 20) and 1,097.5 ± 138.9 mm (range = 855–1,362 mm, n = 14; Fig. 3). No significant difference in mean body size was found between the populations for either males ( $t_{27} = -1.321$ , P = 0.19) or females ( $t_{32} = 0.92$ , P = 0.36). Similarly, there was no difference in stoutness for both males ( $t_{25} = -0.10$ , P = 0.9) and females ( $t_{30} = -0.20$ ; P = 0.8; Fig. 4). In contrast, the populations differed significantly in size-class structure for both sexes ( $\chi^2 = 41.123$ , P < 0.001, df = 5 for males and  $\chi^2 = 14.808$ , P = 0.01, df = 5 for females). There were proportionally more large females in PEFI (Fig. 5).

*Prey Availability.*—We recorded a total 263 rodents distributed in eight genera (*Akodon, Blarinomys, Euryoryzomys, Juliomis, Oligoryzomys, Rhipidomis, Thaptomys,* and *Phyllomys*) during the study. We captured 29 (11%) potential prey items in PEFI and 234 (89%) in PEC (Fig. 6A). Prey availability in PEFI (RDI = 1.3) was significantly lower than in PEC (RDI = 10, t<sub>11.91</sub> = 5.4948, *P* < 0.0001). The same was observed for total prey mass (Fig. 6B). Total mass in PEFI (556.9 g) was significantly lower than in PEC (6,568 g, t<sub>11.51</sub> = 5.2651, *P* = 0.0001). We also captured other prey items such as anurans; they were discarded, however, as this group is more preyed upon by young *B. jararaca* and constituted an insignificant part of our data.

*Predation Pressure.*—Models were significantly less attacked in PEFI (predation rate 5.7%, n = 41) than in PEC (predation rate 12.3%, n = 89;  $G_1 = 19.9087$ , P < 0.0001; Fig. 7A). Mammals were responsible for most attacks in PEFI ( $G_1 = 41.949$ , P = 0.04) and in PEC ( $G_1 = 83.215$ , P = 0.004; Fig. 7B). One model that was attacked by both a mammal and a bird was counted twice. The models placed on the ground received more attacks in PEFI ( $G_1 =$ 



FIG. 4. Stoutness of *Bothrops jararaca* males and females represented by the relationship between body size and mass of both parks. Open circles = Parque Estadual das Fontes do Ipiranga (PEFI) population; closed circles = Parque Estadual da Cantareira (PEC) population; hashed line = best fit to PEFI population; solid line = best fit to PEC population; MM = males; FF = females.

41.940, P = 0.04), but no significant difference was observed in PEC ( $G_1 = 32.672$ , P > 0.05; Fig. 7C).

#### DISCUSSION

Snake body size can be limited by food availability (Queral-Regil and King, 1998) but, despite higher prey availability in PEC, the two populations of *B. jaracara* did not differ in average body size. This lack of difference in mean body size and stoutness suggests that lower abundance of prey in PEFI is not a constraint for growth of *B. jararaca.* This may affect population density, but we did not evaluate this parameter in this study.

Resource availability also influences reproductive traits; for example, females reproducing in years of higher food abundance are in better body condition (Shine and Madsen, 1997) and produce larger clutches or offspring. A longer, morefocused study is needed to clarify whether variations in availability of resources affect fecundity or other life-history traits of these populations.

The effects of human activities on animal populations are variable. Small rodents can use forest patches or human-created



FIG. 5. Proportional distribution of *Bothrops jararaca* males (MM; left) and females (FF; right) by body size class of both parks: above the population structure and below the cumulative proportion by the increasing size. Black bars = Parque Estadual das Fontes do Ipiranga (PEC); grey bars = Parque Estadual da Cantareira (PEC).

habitats as well, such as good-quality home gardens which provide food and shelter and act as source populations in the absence of good-quality habitat patches (Baker et al., 2003). Other species such as bumblebees and common frogs can experience population increases in urban environments because of good-quality garden habitats and green areas (Goddard et al., 2009). In contrast, our results indicate that PEFI and adjacent human-altered areas are not suitable for maintenance of high rodent populations.

The intense forest fragmentation resulting from urban sprawl exerts a negative effect on rodent populations (Connor and McCoy, 1979; Bender et al., 1998; Baker et al., 2003). Hence, the higher degree of fragmentation and isolation of the PEFI may drastically reduce rodent populations in this park (Fahrig and

Merrian, 1985; Gonzales, 2000). The nature of land use around those fragments is also important. Economic activity (periurban, agriculture, cattle) and property ownership (peri-urban, low income rural producers, affluent rural producers) had subtle effects on species composition and species richness in Atlantic Forest remnants (Vieira et al., 2009).

Other factors also play a role in influencing rodent abundance in forest fragments. Castro and Fernandez (2004) showed that lack of connectivity is the major factor responsible for local extinction in Atlantic forest fragments. Predators, including introduced ones, if in high densities can also reduce rodent populations (Diller and Johnson, 1988; Dickman, 2009). Habitat quality is also important. Jellinek et al. (2004) showed that a lizard community was affected by vegetation variables (e.g.,



FIG. 6. Comparison of *Bothrops jararaca* potential rodent prey availability between the Parque Estadual das Fontes do Ipiranga (PEC) and Parque Estadual da Cantareira (PEC) over the period of the study. (A) Total Individuals captured and (B) total mass.



FIG. 7. Number of models attacked in the two study sites: (A) total number of attacks; (B) by bird (black bar) or mammal (grey bar); and (C) by substrate type: forest floor (black bar) or vegetation (grey bar).

introduction of exotic plants) more than by habitat isolation, and species that require native plants will become increasingly vulnerable to extinction.

Predator pressure, inferred in this study by the experiment with models, is an important factor that influences population size (Andersson and Erlinge, 1997). The higher number of attacked models in PEC can be explained by the larger area of this park. In general, habitat area and biodiversity are positively correlated (Connor and McCoy, 1979). This relationship has been validated for several vertebrate groups (Andrén, 1994; Nupp and Swihart, 1996; Kjoss and Litvaits, 2001; Laurance and Vasconcelos, 2009) including *B. jararaca* prey and predators. Therefore, larger habitats might support more predators.

The area effect is especially relevant for avian predators. Askins et al. (1987) found that small patches tend to exhibit a lower richness and density of birds that are typically restricted to the forest interior. The way birds respond to fragmentation may vary. In general, understory species are more sensitive because they are affected by connectivity because of ecological corridors between areas (Uezu et al., 2005). Naturally, that absence of corridors may result in local extinctions.

On the other hand, urbanization also may create new niches. Generalist species can survive in small patches using resources in adjacent areas (Andrén, 1994). The hawk *Buteo magnirostris*, which feeds on *B. jararaca* (Sazima, 1992), was recorded in PEFI. This species uses the park area for hunting, sleeping, and reproductive activities (Argel-de-Oliveira, 1995). In Australia, house cats (*Felis catus*) became an important predator on natural suburban populations and were responsible for decreases of rodent and bird populations (Dickman, 2009).

Artificial night lighting also may be an important differential in PEFI. Some predators such as skunks and owls hunt during dark periods (Emmons and Feer, 1997). So, the strong illumination surrounding and inside this park (LHCS, pers. obs.) may change the daily activity of predators (Rotics et al., 2011) and decrease the frequency of predation on *B. jararaca*.

Although snakes can grow throughout their lives, growth rate is highest early in life and tends to slow down as size increases (e.g., Von Bertalanffy growth model; Shine and Charnov, 1992). Hence, larger snakes are usually older snakes. The lower incidence of predators detected in PEFI presumably resulted in increased survival of snakes, allowing them to attain large body sizes as shown by the higher proportion of large snakes in this population.

Our study shows that the ecology of *B. jararaca* may be affected by the degree of isolation of forest fragments. Human activity modifies the dynamics of animal assemblages with respect to predator–prey interactions and, therefore, may have a large evolutionary impact on snake populations. This points to the importance of implementing the conservation guideline suggested by Ribeiro et al. (2009) regarding the management of the matrix surrounding patches; the matrix is vital for persistence of natural populations of animals, but suitable matrix generally is absent in urban environments.

The São Paulo Municipality comprises many patches of different sizes and degrees of isolation (Prefeitura de São Paulo, 2018), a condition that must apply to several other cities. Therefore, the results of this study and implications for conservation discussed here may be important for other localities.

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