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Habitat use by the South-American rattlesnake (*Crotalus durissus*) in south-eastern Brazil

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Habitat use affects food intake, reproductive fitness and body temperature control in reptiles. Habitat use depends on both the characteristics of the animal and the environmental heterogeneity. In this study we investigated habitat use in a population of the South-American rattlesnake, *Crotalus durissus*, in a cerrado (the Brazilian savanna) remnant, in south-eastern Brazil. In general, snakes appeared to be thermal generalists. However, they showed substrate temperature preferences in the rainy season, when they selected colder substrates during the day and warmer substrates at night. Individuals were predominantly active on the surface and more frequently found under bushes. Furthermore, in general, the principal component analysis results indicate that rattlesnakes are generalists regarding the microhabitat variables examined in this study. These habitat characteristics, associated with a low thermal selectivity, indicate that rattlesnakes are able to colonize deforested areas where shade occurrence and vegetation cover are similar to those in the cerrado.

Keywords: *Crotalus durissus*; habitat use; radio-telemetry; ecology

Introduction

In general, animals exhibit a preference for locations in their environment with distinct characteristics, which may be defined as microhabitats (Reinert 1993). The understanding of the mechanisms that affect habitat selection and use has provided the framework for hypotheses and theories on evolution, community structure, as well as maintenance of species diversity (Reinert 1993). Studies indicate that habitat use is associated with climatic aspects, retreat-site availability, and abundance of prey and predators (Burghardt 1967; Reinert et al. 1984; Duvall et al. 1985; Gibbons and Semlitsch 1987; Huey et al. 1989; Chiszar et al. 1990; Reinert 1993; Webb et al. 2004).

In most tropical regions, unlike in temperate areas, ectotherms are active throughout the year because low temperature extremes (below 0°C) rarely occur. However, very limited information is available on the habitat use of neotropical species compared with their temperate counterparts. Although there are some studies on the biology of the South-American rattlesnake *Crotalus durissus* (Salomão et al. 1995; Almeida-Santos and Salomão 1997; Salomão and Almeida-Santos 2002; Vanzolini and Calleffo 2002; Almeida-Santos et al. 2004), few have been conducted in the field (Bastos et al. 2005). While rattlesnakes (genus *Crotalus*) comprise a highly diversified group in North America, only one species colonized South America

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(Wüster et al. 2005). In tropical regions, *C. durissus* exhibits a peak of activity between April and May (autumn, Salomão et al. 1995). Mating occurs from April to June (Salomão and Almeida-Santos 2002) and juvenile recruitment, from December to August (Almeida-Santos and Salomão 1997; Almeida-Santos et al. 2004). Despite being associated with open vegetation, *C. durissus* has recently colonized forested areas undergoing fragmentation (Marques et al. 2001; Bastos et al. 2005), increasing the incidence of accidents involving rattlesnakes and humans (Bastos et al. 2005).

This study aimed to investigate habitat use and selection in a population of rattlesnakes in a fragment of cerrado (the Brazilian savanna) of south-eastern Brazil.

Materials and methods

Field work was conducted at the Itirapina Ecological Station (IES: 2.300 ha; 22°13′24″S; 47°54′03″W; approximately 700 m of elevation), municipality of Itirapina, State of São Paulo, south-eastern Brazil. Regular sampling was conducted from December 2003 to December 2004. The study site represents one of the last remnants of protected cerrado in the State of São Paulo. The main vegetation types in the reserve are gallery forests, swamps, flooded areas, grasslands, shrubby grasslands, and shrubby grasslands with trees; grasslands and shrubby grasslands are the most common types. The climate is mesothermal, with two well-defined seasons, a dry–cold (April–August) and a wet-warm season (September–March). Data on habitat use were obtained from (1) rattlesnake captures during searches conducted by car along roads and firebreaks inside IES (roads and firebreaks were narrow, sometimes partially covered by grasses and cut the area in a dense network); (2) occasional encounters and (3) re-location of animals equipped with externally attached radio-transmitters. Searches by car consisted of regular sampling for 5 consecutive days, every 20 days. In each sampling period, unpaved roads in IES were covered daily between 7:00 and 24:00 hours, at a speed under 35 km/h, in a systematic manner. Captured animals were weighed, measured, and implanted with a passive integrated transponder (PIT). A total of 15 adult rattlesnakes (11 males and four females) were equipped with radio-transmitters (model SI-2; 9 g, 33 mm × 11 mm; Holohil Systems Ltd., Ontario, Canada) externally attached with adhesive tape (Tozetti 2007). The body mass of all snakes was above 250 g ensuring the device never accounted for more than 5% of the animal's body mass.

Rattlesnakes were re-located during each 5-day sampling period. An interval of at least 12 hours was left prior to re-location of an individual snake to minimize the effects of temporal dependence (auto-correlation) between points (White and Garrott 1990). Tracking provided visual contact with snakes, except where animals sheltered in burrows. Snakes were relocated both at day and at night to maximize the observations of behaviours and other activities typical of each period (Laundré et al. 1987). At each capture or re-location, the snakes' surface body temperature was recorded with the aid of a non-contact infrared thermometer (Raytek model RAYMT4U), which removed the need to handle the animal. Each snake was tracked until either the detachment of the radio-transmitter or shedding (Tozetti 2007).

At each observation (capture or re-location), we recorded the microhabitat in which the animal was found. Records where animals were moving when they were found were discounted, as they could reflect temporary presence in the microhabitat. Each observation was considered as a sample. Frequencies of records for each type of microhabitat were analysed with chi-square tests. Surface body temperatures of snakes in different microhabitats were compared with a Kruskal–Wallis analysis of variance and, when necessary, followed by a *post hoc* test (Zar 1999). Comparisons between dry and rainy seasons were conducted using a Mann–Whitney U-test (Zar 1999).

For analysis, the microhabitat samples were characterized by delimiting a square with side length of 3 m (with the animal at the centre) and recording the following variables: (1) percentage of woody vegetation cover (shrubs and trees); (2) percentage of grass and herbaceous cover; (3) percentage of exposed soil; (4) percentage of shadow projected on the ground at high noon; (5) substrate temperature near the snake and (6) relative air humidity at the surface level near the snake. Available microhabitats were characterized by delimiting four squares with side length of three meters each, randomly chosen from a 'grid' of 5×5 squares (a total of 25 squares), with the snake at the central square. Variables 1–6 were recorded for these four squares, and temperature and relative air humidity measured at the substrate level in the centre of squares.

Comparisons among variables recorded in used and available microhabitats were conducted with a paired Wilcoxon test (Zar 1999). The association between the presence of snakes and the percentages of shrubs, grasses, exposed soil, and projected shadows in the squares with and without snakes was examined with a principal components analysis (PCA; Manly 1994), using the software MVSP (Kovach 1999). Percentage values obtained were arcsine-square-root transformed (in degrees) (Zar, 1999).

Only data on captures during searches by car were used to analyse habitat use. For each habitat, the capture rate was estimated (number of captures per distance travelled). Capture rates were then compared with a Kruskal–Wallis analysis of variance, and when necessary, followed by a post hoc test (Zar 1999). Capture rates during the dry and rainy seasons were compared using a Mann–Whitney test (Zar 1999). Differences were considered significant at $p<0.05$ (Zar 1999) in all tests.

Results

During this study, 38 snakes were captured. Twelve were females (six juveniles and six adults) and 26 were males (five juveniles and 21 adults). A total distance of 12,000.4 km was covered by car during 224 sampling days.

A total of 15 adult rattlesnakes (11 males and four females) were monitored through radio-tracking. On average, animals were monitored for 64.9 days (range 1.0–195.0) and re-located 9.5 times (range 1.0–28.0).

During the day, snakes did not select microhabitats based on substrate temperature. Differences between temperatures (mean $\pm$ SD) measured during the day in squares with (24.3°C $\pm$ 6.0, range 12.4–44.0°C) and without snakes (25.2°C $\pm$ 6.7, range 11.3–42.9°C; $T=1858$; $p=0.12$; $n=96$ samples) were not significant. At night, however, differences were significant ($T=449.5$; $p=0.007$; $n=55$ samples), although the average temperature of selected substrates (16.4°C $\pm$ 4.5, range 8.0–23.7°C) was very similar to that of available microhabitats (16.0°C $\pm$ 4.5, range 6.5–24.1°C).

In the rainy season, the substrates in microhabitats used during the day were colder (26.7°C $\pm$ 5.7, range 13.6–44.0°C) than available ones (28.4°C $\pm$ 6.0; range

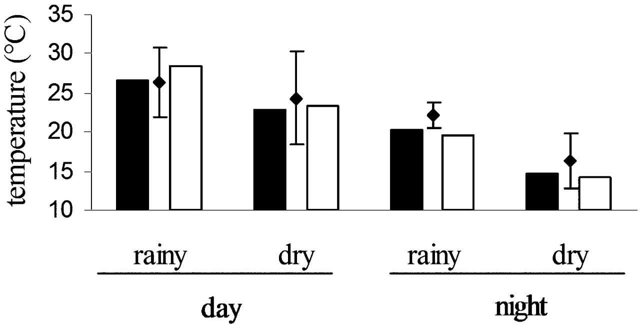

Figure 1. Average substrate temperature (°C) in the microhabitats used by *Crotalus durissus* (black columns) and available microhabitats (white columns); and mean ± SD of body-surface temperature (°C). Data obtained from radio-tracked rattlesnakes at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

13.6–42.9°C; $T=217$; $p=0.04$; $n=37$ samples), while at night, the substrate in microhabitats used were slightly warmer (20.2°C ± 3.7, range 11.0–23.7°C) than available ones (19.6°C ± 3.7, range 10.3–24.1°C; $T=28$; $p=0.01$; $n=18$ samples; Figure 1). In the dry season, microhabitats were not selected based on substrate temperature during the day (used = 22.8°C ± 5.7, range 12.4–35.0°C; available = 23.2°C ± 6.4, range 11.3–41.5°C; $T=810$; $p=0.73$; $n=59$ samples) or at night (used = 14.6°C ± 3.6, range 8.0–20.0°C; available = 14.2°C ± 3.7, range 6.5–21.2°C; $T=241$; $p=0.09$; $n=37$ samples; Figure 1).

At night, the surface body temperature of snakes varied significantly between seasons. The average temperature was lower during the dry (16.3°C ± 3.4, range 11.6–21.0°C) than during the rainy season (22.1°C ± 1.6, range = 19.8–24.2°C; $U=10$; $p=0.001$; $n=27$ samples). During the day, there was no significant difference between surface body temperature of snakes measured during the dry (24.3°C ± 6.0, range 12.8–35.5°C) and rainy (26.3°C ± 4.4, range 14.6–32.7°C; $U=419.5$; $p=0.20$; $n=67$ samples) seasons. Surface body temperatures did not vary significantly among snakes in different microhabitats ($H_{[3;93]}=3.9$; $p=0.27$; Figure 2).

During the day, microhabitats selected by rattlesnakes had higher relative air humidity (20.7% ± 12.0, range 5.0–62.0%) compared with available microhabitats

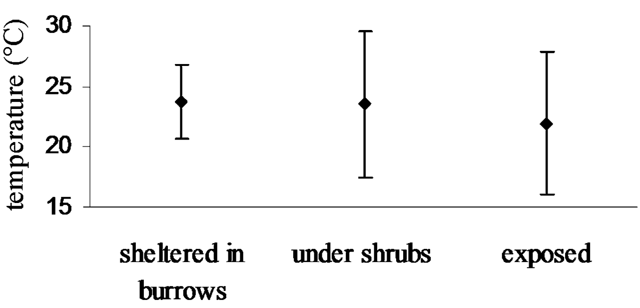

Figure 2. Mean ± SD of body-surface temperature (°C) of *Crotalus durissus* in different microhabitats. Dots represent averages (°C) and bars, SD. Data obtained for captures and re-locations of rattlesnakes at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

(18.9%±10.4, range 3.7–43.7%; $T=691$; $p=0.03$; $n=69$ samples). At night, no significant differences were observed between the relative air humidity in used (33.3%±10.9, range 12.0–50.0%) and available (33.1%±10.0, range 12.2–45.7%; $T=375$; $p=0.83$; $n=39$ samples) microhabitats. In the rainy season, no significant differences were observed between the relative air humidity in used and available microhabitats during the day (used=21%±14.5, range 5.0–62.0%; available=20.4%±12.2, range 3.7–43.7%; $T=114$; $p=0.86$; $n=28$ samples) or at night (used=32.9%±11.9, range 12.0–50.0%; available=31.5%±11.3, range 13.0–44.2%; $T=30$; $p=0.48$; $n=12$ samples). In the dry season, relative air humidity of selected microhabitats during the day (20.5%±10.1; range 7.0–42.0%) was higher than that of available ones (17.9%±9.0, range 6.7–40.2%; $T=202$; $p=0.008$; $n=41$ samples), while at night, no significant differences were observed in relative air humidity between used (33.4%±10.7, range 14.0–48.0%) and available (33.8%±9.5, range 12.2–45.7%; $T=179.5$; $p=0.82$; $n=27$ samples) microhabitats.

Rattlesnakes were observed under shrubs, exposed, and sheltered in burrows. The number of records obtained was lower than that expected for the use of burrows (obtained=27; expected=53; $\chi^2=21.6$; $df=11$; $p<0.03$) and for exposed microhabitats (obtained=42; expected=61; $\chi^2=21.8$; $df=11$; $p<0.04$), and higher than expected for snakes under shrubs (obtained=88; expected=53; $\chi^2=42.3$; $df=11$; $p<0.001$; Figure 3). In the dry season, the number of records obtained (16) was lower than expected (33.3) for the use of burrows ($\chi^2=13.7$; $df=4$; $p<0.008$) and exposed microhabitats (obtained=29; expected=41.7; $\chi^2=12$; $df=5$; $p<0.03$). Also, in the dry season, the number of records obtained was higher than expected for rattlesnakes under shrubs (obtained=55; expected=33.3; $\chi^2=26.7$; $df=4$; $p<0.001$). During the rainy season, the number of records obtained (33) was higher than expected (19.7) for snakes under shrubs ($\chi^2=15.5$; $df=7$; $p<0.03$). No significant differences were observed between obtained and expected values for use of burrows (obtained=11; expected=19.7; $\chi^2=7.8$; $df=7$; $p=0.34$), or exposed microhabitats (obtained=13; expected=19.7; $\chi^2=9.8$; $df=7$; $p=0.20$).

During the day, the number of records obtained (63) was higher than expected (37.7) for snakes under shrubs ($\chi^2=37$; $df=11$; $p<0.001$). No significant differences were found between observed and expected number of records for the use of burrows (obtained=11; expected=23.7; $\chi^2=9.2$; $df=6$; $p=0.16$), or for exposed microhabitats (obtained=26; expected=29.3; $\chi^2=6.5$; $df=9$; $p=0.7$). At night, no significant

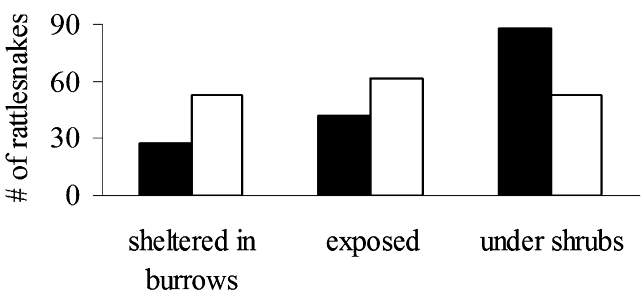

Figure 3. Observed (black columns) and expected (white columns) numbers of rattlesnakes (*Crotalus durissus*) in the different microhabitats at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

Table 1. Autovalues and percentages of variance explained by the six principal components (axes 1–6) of the variation in percentage of shrubs, grasses, trees, exposed soil, projected shadow on the ground, and air humidity associated with microhabitats with and without rattlesnakes (*Crotalus durissus*) obtained at the Itirapina Ecological Station, State of São Paulo, South-eastern Brazil.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Autovalues	3.886	1.589	0.712	0.462	0.05	0.008
Percentage	57.94	23.686	10.621	6.886	0.748	0.118
Cumulative %	57.94	81.626	92.247	99.133	99.882	100

differences were found between observed and expected number of records for any microhabitat (burrows: observed=16; expected=12.3; $\chi^2=9.1$; $df=6$; $p=0.16$; exposed: observed=15; expected=16.3; $\chi^2=8.6$; $df=8$; $p=0.4$; under shrubs: observed=22; expected=16; $\chi^2=13.4$; $df=8$; $p=0.09$).

In the PCA, axis 1 explained more than half (58%) of the variance of the used and available microhabitats (Table 1); this axis was related mainly to the amount of tree and shadow cover (Table 2; Figure 4). Axis 2 explained an additional 24% of the variance and was related mainly to the amount of exposed soil (Table 2; Figure 4). The points with snakes appeared scattered throughout axis 1 (i.e., no trend is apparent in relation to the amount of tree and shadow cover) and mostly restricted to low values in axis 2 (i.e., no trend is apparent in relation to the amount of exposed soil; Figure 4). Furthermore, in general, the PCA results indicated that microhabitats used by rattlesnakes were not markedly distinct from available microhabitats, although many of the unused available habitats were in more open areas (with a lower amount of tree and shadow cover; Figure 4).

Rattlesnakes were captured predominantly in campo cerrado (open savanna; 0.0048 rattlesnakes/Km), campo sujo (grassland with some shrubs; 0.0007 rattlesnakes/Km), altered areas (0.0019 rattlesnakes/Km), and wetlands (edges of gallery forests and marshes; 0.0014 rattlesnakes/Km), although differences in capture rates among habitats were not significant ($H_{[3;24]}=4.34$; $p=0.23$). On the other hand, the capture rate of snakes in altered areas was higher in the rainy season

Table 2. Autovectors of the six principal components (axes 1–6) of the variation in percentage of shrubs, grasses, trees, exposed soil, projected shadow on the ground, and air humidity associated with microhabitats with and without rattlesnakes (*Crotalus durissus*) obtained at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Shrub	**0.151**	**0.154**	−0.259	0.94	0.049	−0.005
Grass	0.011	**−0.156**	0.016	−0.023	0.957	−0.241
Tree	**0.659**	−0.001	0.745	0.101	−0.023	−0.022
Exposed soil	**−0.172**	**0.955**	0.17	−0.09	0.147	−0.022
Shadow	**0.717**	**0.2**	−0.589	−0.312	0.033	0.023
Humidity	−0.003	−0.021	0.037	0.007	0.24	0.97

Note: The most important variables in Axis 1 and 2 are in boldface.

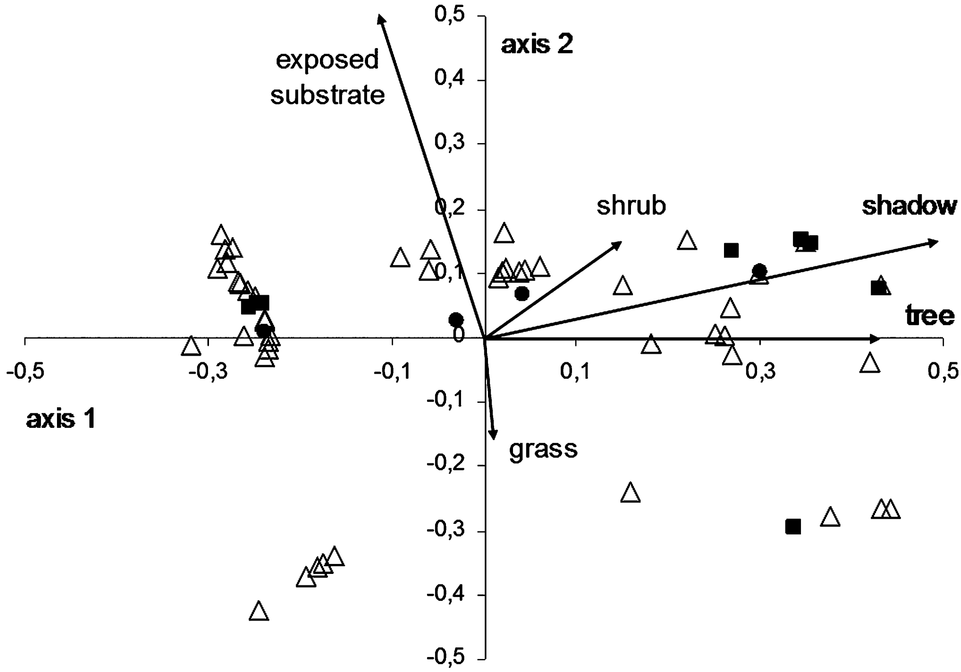

Figure 4. Biplot of available (Δ; without snakes) and used (■ samples of males, ● samples of females) microhabitats along first and second axes of the Principal Components Analysis (PCA), generated from records of *Crotalus durissus* at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

(0.003 rattlesnakes/Km; U=1.5; p=0.05; n=12 samples), but no significant differences were observed in capture rates between dry and rainy seasons for the remaining habitats (campo sujo: rainy=0.0004 rattlesnakes/Km; dry=0.001 rattlesnakes/Km; U=13; p=0.34; n=12 samples; campo cerrado: rainy=0.005 rattlesnakes/Km; dry=0.001 rattlesnakes/Km; U=16.5; p=0.86; n=12; wet area: rainy=0.002 rattlesnakes/Km; dry=no captures; U=15; p=0.4; n=12 samples; Figure 5).

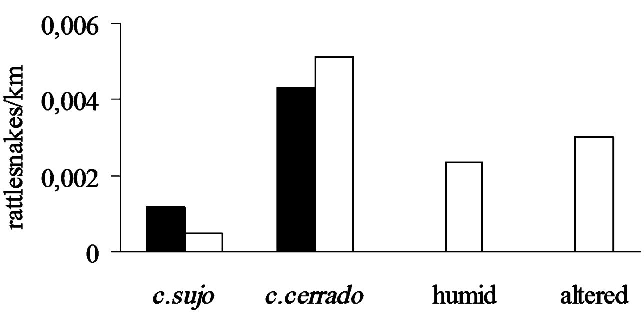

Figure 5. Capture rates of rattlesnakes (rattlesnakes/km) during the dry (black columns) and rainy seasons (white columns) obtained from searchers by car in roads and firebreaks at the Itirapina Ecological Station, State of São Paulo, south-eastern Brazil.

Discussion

In the rainy season, monitored rattlesnakes apparently reduced the risks of overheating by selecting colder microhabitats during the day, and avoided lower temperatures at night by selecting warmer microhabitats. They did not, however, seem to select microhabitats based on substrate temperature during the dry season, which is the coldest season of the year. This indicates they are thermal generalists, at least during this season. The fast decrease in air temperature between sunset and dawn in the dry season may result in a homogenization of substrate temperature. Thus, if after selecting a microhabitat the snakes remained motionless during most of the night, significant variations between the temperatures of used and available substrates would be detected only during the first hours of the night (see Webb et al. 2004).

The surface body temperature of *C. durissus* at night varied between dry and rainy seasons; this did not occur during the day. Assuming that our surface body temperature measurements reflect the core temperature of the snakes, this indicates that they control their body temperature to prevent overheating during the day. This might be a common strategy in non-fossorial snakes of open ecosystems like the cerrado, as they are more exposed to overheating than those living in forested areas. The fact that rattlesnakes were found more frequently in more humid microhabitats during the day might be a consequence of selecting microhabitats less exposed to the sun.

Rattlesnakes were observed predominantly on the surface. Only a few snakes were in burrows, even during the driest and coldest months of the year. Despite concentrating their activity on the surface, rattlesnakes avoided exposed microhabitats, being frequently observed under shrubs. These probably offer simultaneously hunting opportunities at night, thermoregulation during the day, and constant protection against predators (i.e. birds of prey). The selection of habitats and retreat sites varies widely among species of the genus *Crotalus* such as *C. atrox, C. molossus*, and *C. tigris* (Beck 1995). Despite being associated with dry habitats (Vanzolini et al. 1980), some individuals of *C. durissus* tracked with radio-transmitters were observed in completely flooded habitats. Indeed, in general, the PCA results indicate that rattlesnakes are generalists regarding the microhabitat variables examined in this study, which may maximize their capacity to invade altered areas. This ability may explain the presence of rattlesnakes in man-altered areas of the Atlantic Forest (Marques et al. 2001; Bastos et al. 2005). The combination of shaded and exposed substrate as a mosaic could increase the thermoregulatory possibilities for rattlesnakes in man transformed Atlantic Forest areas. Future studies should focus on habitat characteristics that favour the colonization of man-altered areas of the Atlantic Forest.

The absence of ontogenetic variation in diet may also facilitate the recruitment of juveniles into newly colonized areas. Unlike most Brazilian species of pitvipers of the genus *Bothrops*, which feed frequently on amphibians when young (Marques et al. 2001), juveniles of *C. durissus* may survive in dryer areas provided rodents are available, and this prey type is abundant in man-altered areas. Therefore, other factors likely associated with microhabitat use in rattlesnakes, such as the presence of chemical trails of prey or conspecifics, should be explored in future studies (Burghardt 1967; Brown and Maclean 1983; Reinert et al. 1984; Chiszar et al. 1990; Clark 2004).

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