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Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil

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ABSTRACT

The main objective of this study was to examine the natural history and the ecology of the species that constitute a snake assemblage in the Atlantic Rainforest, at Núcleo Picinguaba, Parque Estadual da Serra do Mar, located on the northern coast of the state of São Paulo, southeastern Brazil. The main aspects studied were: richness, relative abundance, daily and seasonal activity, and substrate use. We also provide additional information on natural history of the snakes. A total of 282 snakes, distributed over 24 species, belonging to 16 genera and four families, has been found within the area of the Núcleo Picinguaba. Species sampled more frequently were Bothrops jararaca *and* B. jararacussu. *The methods that yielded the best results were time constrained search and opportunistic encounters. Among the abiotic factors analyzed, minimum temperature, followed by the mean temperature and the rainfall are apparently the most important in determining snake abundance. Most species presented a diet concentrated on one prey category or restricted to a few kinds of food items. The large number of species that feed on frogs points out the importance of this kind of prey as an important food resource for snakes in the Atlantic Rainforest. Our results indicate that the structure of the Picinguaba snake assemblage reflects mainly the phylogenetic constraints of each of its lineages*

Keywords: Assemblage; Snake; Diet; Habitat use; Activity.

INTRODUCTION

One of the objectives of the study of community ecology is to identify patterns of resource use and the mechanisms by which these patterns are achieved. Apparently, several factors operate simultaneously to structure natural communities (Begon *et al.,* 1996). The study of vertebrate assemblages composed by species from the same lineage (taxocenes), and thus sharing at least part of their evolutionary history, may provide valuable information about the different ways by which distinct species respond to biotic and abiotic factors. South-American snake assemblages have been studied mainly in Amazonian forested areas (*e.g.,* Duellman, 1978; Henderson *et al.,* 1979; Dixon & Soini, 1986; Zimmerman & Rodrigues,

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1990; Martins & Oliveira, 1999; Bernarde, 2004), but also in the Cerrado (*e.g.,* Vanzolini, 1948; Sawaya *et al.,* 2008), Caatinga (*e.g.,* Vitt & Vangilder, 1983), Pantanal (*e.g.,* Strüssmann & Sazima, 1993), Atlantic Forest (*e.g.,* Marques, 1998; Argôlo, 2004), Araucaria Forest, grasslands, and forests in Southern Brazil (*e.g.,* Cechin, 1999; Di-Bernardo, 1999). Different approaches were used in these studies, such as species lists (with taxonomic emphasis), analyses of resource use, characterization of daily and seasonal activity patterns, diversity, and characterization of morphological patterns.

The Atlantic Forest in the Serra do Mar mountain range is recognized for being a region rich in fauna with about 80 species of snakes (Dixon, 1979; Marques *et al.,* 2004), but still has many areas that have been poorly studied, especially with regard to its herpetofauna. Even though the amount of studies on natural history and ecology has notably increased in the last few years, many characteristics about the life of the snake species that inhabit this region are still unknown. This study aimed to analyze the natural history and ecology of species from the snake assemblage at Núcleo Picinguaba in the Serra do Mar State Park, State of São Paulo, Brazil. We also discuss the factors responsible for the structure of Neotropical snake assemblages.

MATERIAL AND METHODS

Study site

The study was carried out at Núcleo Picinguaba (47,000 ha), a division of the Serra do Mar State Park, located on the northern coast of the State of São Paulo, southeastern Brazil (23°23'S, 44°50'W). The Núcleo Picinguaba encompasses areas is dominated by escarpments that reach the sea in the bay of Picinguaba. Elevation varies from sea level to 1,200 m, but our snake samplings were restricted from sea level to 200 m. The sampled area has approximately 4,000 ha and encompasses the following vegetation types: dense rainforest, restinga forest (rainforest on coastal sandy soils) and transitional vegetation between dense rainforest and restinga forest.

The climate is tropical-wet, with a high rainfall well distributed throughout the year (Koeppen, 1948). The Núcleo Picinguaba covers an area of coastal zone, seasonally controlled by equatorial and tropical systems, presenting the characteristic humid climate of coasts exposed to the Tropical Atlantic air mass. The mean annual precipitation is 2634 mm (1961-1990), ranging from 1773 to 3854 mm. During this study, the total annual precipitation was 1774 mm in 2001 and 2459 mm in 2002. The mean monthly rainfall is generally more than 200 mm from October to April and between 80 and 160 mm from May to September. The highest precipitation occurs from December to March (about 380 mm/month). The relative humidity is greater than 85% throughout the year. The mean annual temperature is 21.9°C. Lower temperatures occur in the drier season, resulting in a rainy/warmer season from October to April and a drier/colder season from May to September. The area is affected little by the polar masses (about 30 to 40% of annual participation). During the study the precipitation was 1773 mm in 2001 and 2459 mm in 2002 (Fig. 1). The climatic data were obtained from the Instituto Nacional de Metereologia, from the meteorological station of the Instituto Agronômico de Campinas, at Ubatuba (23°27'S, 45°04'W).

Data collection

Snake sampling was carried out from January 2001 to December 2002, corresponding to 189 days of fieldwork. The period from January to September 2001 was dedicated to preliminary data collection. Regular sampling was carried out between October 2001 and December 2002, with a sampling effort of 9 to 12 days per month. The snakes were photographed, captured, measured and released or killed and preserved. For each snake we registered the following information: species, date and time of observation, habitat and microhabitat, snout-vent length and tail length, mass, sex, and activity. Each captured snake was dissected by means of a ventral incision along the posterior two-thirds of the body (Martins & Gordo, 1993) in order to obtain the following information: content of the digestive tract, and number of food items. A species was considered specialized when one type of prey represented 75% or more of the total number of registered prey (see Martins *et al.,* 2001). To detect possible diet and activity differences between juveniles and adults, reproductive maturity was assessed through gonad examination. The snout-vent length of the smallest mature male and smallest mature female of each species served to differentiate immature individuals from adult individuals (see criteria in Shine, 1977 and Marques, 1996).

To evaluate the seasonal activity pattern of the snakes we isolated the factors that can interfere in the abundance of snakes at different times of the year: difference in sampling effort; seasonal difference in the number of snakes (mainly with regard to recruitment); and seasonal difference in snake activity (Henderson *et al.,* 1987). A similar sampling effort every month was considered and the monthly abundance was analyzed in two ways: with all the individuals and only with adult individuals. With regard to the relative abundance of the species they were classified as dominant (when they represented 15% or more of the encounters), common (between 5 and 15% of the encounters), of intermediate abundance (between 1 and 4% of the encounters), and rare (less than 1% of the encounters). The diet, activity period and substrate use were characterized using complementary information taken from other studies about snakes in the Atlantic Forest (see Sazima & Haddad, 1992; Marques, 1998; Marques & Sazima, 2004; Marques *et al.,* 2004).

Sampling methods

Pitfall traps with drift fences (PT) – Eight 1 m high tarpaulin drift fences were installed, with eight 100 L buckets each at 10 m intervals (Cechin & Martins, 2000; Sawaya *et al.,* 2008). Each drift fence was subdivided into two groups of 40 m, each with four buckets and a 50 m gap between them. A total of 64 buckets were installed along 640 m of drift fences. The pitfall traps were installed from October to December 2001 and were considered to be functioning from January to December 2002. The traps were kept open from eight to 11 consecutive days every month. The pitfall traps had remained open for 102 non-consecutive days or 6,120 bucket days.

Time constrained search (TCS) – We hiked along trails at a slow pace (about 100-120 m/h), searching the environment visually for snakes, for two to four hours each time (see Cechin & Martins, 2000; Sawaya *et al.,* 2008). Fifty to 70 men-hours per month of time constrained search were carried out. In total, throughout the 15 sampling months (October 2001 to December 2002), 795 men-hours of time constrained search were sampled.

Sampling by car (SC) – We drove slowly (about 30-40 km/h) through the area searching for snakes (Sawaya *et al.,* 2008). We covered 16 km daily along the highway that cuts through the park in both directions. Additionally we also drove through secondary, unpaved roads that cut through the park. Every month, from October 2001 to December 2002, we drove about 300 to 415 km which gives a total of 5,173 km throughout the 15 months.

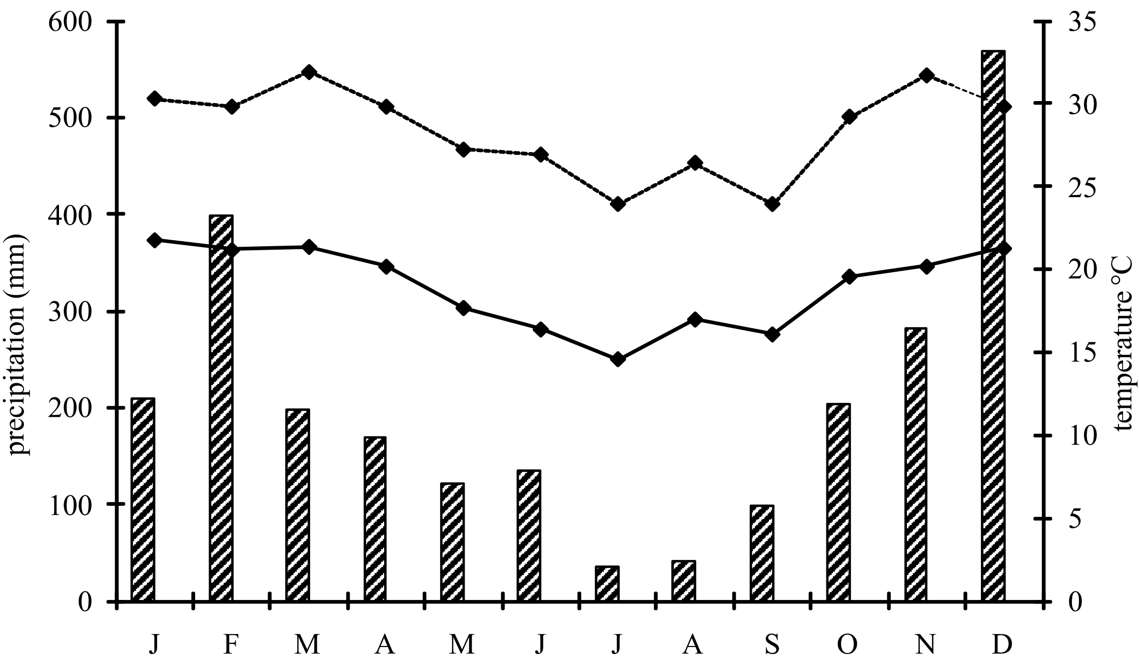

FIGURE 1: Precipitation (mm, bars) and minimum and maximum temperatures (°C; lines) from January to December 2002 at Núcleo Picinguaba, Serra do Mar State Park. Data obtained from the Instituto Nacional de Metereologia, from the meteorological station of the Instituto Agronômico de Campinas, in the Ubatuba headquarters (23°27'S, 45°04'W).

Local collectors (LC) – We distributed 20 L containers with 15% formaldehyde at the headquarters of the Núcleo Picinguaba and to the neighbouring villagers for them to deposit snakes that they regularly kill (see Cechin, 1999; Sawaya *et al.,* 2008). Cards were also given to the villagers for them to record information such as time and site of encounter. Three containers were distributed in November 2001. If we consider the monthly sample as a container-month, the sampling effort until December 2002 was 42 container-months.

Opportunistic encounters (OE) – Individuals found during activities that were not part of the sampling methods were considered OE (see Cechin & Martins, 2000; Sawaya *et al.,* 2008). For example, when moving between the pitfall traps, we covered 8 km daily and in the 12 months we covered a total of 756 km. We also considered as OE the snakes found in the preliminary data collection.

The taxonomy on the level of subfamily and family used herein is that proposed by Zaher *et al.* (2009).

RESULTS AND DISCUSSION

Diversity

We found 24 species of snakes, belonging to 16 genera and four families in the study site. We included in the list two species, *Echinanthera undulata,* found after the fieldwork, and *Siphlophis pulcher,* not found in this study but with confirmed occurrence in the region (see Marques *et al.,* 2001). Therefore, we list 26 snake species for the region of the Núcleo Picinguaba (Table 1). Nevertheless, it is possible that other species occur at the study site. *Tropidodryas serra* was registered in a neighboring area (see Sazima & Puorto, 1993), and *Philodryas patagoniensis,* a species found in open areas (Hartmann, 2001), was found about 50 km away from the study site which suggests that its distribution may be expanding due to the increase of deforestation in the region.

The number of species obtained by first order Jackknife richness estimator, using all methods, was between 25 and 28 species in the Núcleo Picinguaba ($N_{(J1)} = 26.8 \pm 1.49$). Two species were dominant: *Bothrops jararaca* and *B. jararacussu* (more than 30 individuals found). Three species were common (19-29 individuals); 11 were of intermediate abundance (3-13 individuals), and eight species were rare (1-2 individuals, Table 1). As in other Neotropical snake assemblages, the most abundant species were viperids (see Martins, 1994; Marques, 1998; Cechin, 1999; Sawaya *et al.,* 2008). Together, both species of *Bothrops* represent more than 40% of the snakes found. This dominance is apparent when we compare it to the abundance of species from other genera. For example, even with five species, all with more than ten individuals found in the area, the genus *Chironius* represents only 29% of the assemblage.

TABLE 1: Snakes recorded at Núcleo Picinguaba, Parque Estadual da Serra do Mar, from January 2001 to December 2002. Number of individuals found (N) and percentage of the total number of individuals (%).

Family/Species	N	(%)
Colubridae		
Chironius bicarinatus (Wied, 1820)	12	4,26
Chironius exoletus (Linnaeus, 1758)	19	6,74
Chironius fuscus (Linnaeus, 1758)	29	10,28
Chironius foveatus (Bailey, 1955)	12	4,26
Chironius laevicollis (Wied, 1824)	9	3,19
Spilotes pullatus (Linnaeus, 1758)	13	4,61
Dipsadidade		
Clelia plumbea (Wied, 1820)	1	0,35
Dipsas indica Laurenti, 1768	2	0,71
Dipsas sp.	2	0,71
Echinanthera cephalostriata (Di-Bernardo, 1996)	3	1,06
Echinanthera undulata (Wied, 1824)[1]	—	—
Helicops carinicaudus (Wied, 1825)	1	0,35
Imantodes cenchoa (Linnaeus, 1758)	4	1,42
Liophis miliaris (Linnaeus, 1758)	20	7,09
Oxyrhopus clathratus Duméril, Bribon & Duméril, 1854	10	3,55
Philodryas olfersii (Lichtenstein, 1823)	4	1,42
Sibynomorphus neuwiedi (Ihering, 1911)	2	0,71
Siphlophis pulcher (Raddi, 1820)[2]	—	—
Taeniophallus affinis (Günther, 1858)	4	1,42
Taeniophallus bilineatus (Fischer, 1885)	2	0,71
Thamnodynastes cf. *nattereri* Mikan, 1828	5	1,77
Uromacerina ricardinii (Peracca, 1897)	1	0,35
Xenodon neuwiedii Günther, 1863	2	0,71
Elapidae		
Micrurus corallinus (Merren, 1820)	7	2,48
Viperidae		
Bothrops jararaca (Wied,1824)	71	25,18
Bothrops jararacussu Lacerda, 1884	47	16,67
Total	282	100

[1] Species found after the fieldwork.
[2] Species not found in this study, but with confirmed occurrence in the region (see Marques *et al.,* 2001).

Natural history

Information on natural history of each species, especially with regard to their abundance, habitat use, activity period, and feeding habit are presented below.

Family Colubridae

Chironius bicarinatus: A species of intermediate abundance (see Table 1), it was found in the forest (N = 2), on the forest edge (N = 4), and in open areas (N = 6). It used the ground more frequently (N = 10) than the vegetation (N = 2). With a semi-arboreal habit (Sazima & Haddad, 1992; Dixon *et al.,* 1993; Marques & Sazima, 2004), its slender body and green coloration make it difficult to detect on the branches in the forest. It was recorded during all seasons. The individuals encountered during the day were active (N = 6) and the only one found at night was resting on the vegetation. These data confirm that *C. bicarinatus* is mainly diurnal, as are the other species in the genus (Marques *et al.,* 2000).

The diet is composed mainly by anurans, although *C. bicarinatus* can also occasionally capture lizards and birds (Sazima & Haddad, 1992; Carvalho-Silva & Fernandes, 1994; Marques & Sazima, 2004). In the specimens examined (N = 11), only anurans were found (N = 4), and it was possible to identify two of them: *Leptodactylus ocellatus* and *Haddadus binotatus* (Leptodactylidae). In order to find its prey, *C. bicarinatus* moves along the ground or on the vegetation, searching for anurans. One individual was found on the ground of an open area, ingesting an adult *Leptodactylus ocellatus* and another was found trying to capture a non-identified anuran on the forest edge, also on the ground. The encounter of individuals foraging on the ground and the incidence of leptodactylids in the diet indicate that this species hunts more frequently on the ground.

Chironius exoletus: A common species in the Núcleo Picinguaba region, it was found mainly associated to forested areas (15 individuals on the forest edge and three within the forest). It was found on the ground (N = 15) and on the vegetation (N = 4). Of the individuals found on the vegetation, one was found at 21:00 h resting on branches over a marsh about 1.5 m high. The other three were active during the day, moving along thin branches within the forest. The habit of *C. exoletus* is semi-arboreal (Dixon *et al.,* 1993; Marques *et al.,* 2004), and this species seems to rest on trees and shrubs during the night, using the branches and trees as a perch (Dixon *et al.,* 1993; Marques *et al.,* 2004). It seems to be more active during the rainy season, when most of the individuals were found (N = 11). All the specimens found during the day were active (N = 6), indicating mainly a diurnal habit (Sazima & Haddad, 1992; Marques & Sazima, 2004).

The diet of *C. exoletus* is composed mainly of anurans (Sazima & Haddad, 1992; Dixon *et al.,* 1993; Marques & Sazima, 2004). In the examined specimens (N = 14), one had anuran remains in its digestive tract. The species seems to exhibit active foraging, frequently whilst on the vegetation (Marques & Sazima, 2004). Three individuals found on the vegetation were moving on thin branches during the day, apparently in foraging activity. One adult was found ingesting an anuran on the forest floor (*Leptodactylus ocellatus*).

Chironius fuscus: A common species, it was the third most abundant species recorded in the study. It was found mainly within the forest or on the forest edge (N = 28). It has a semi-arboreal habit and was found both on the ground (N = 19) and on the vegetation (N = 10), which it seemed to use mainly for resting (Dixon *et al.,* 1993; Marques & Sazima, 2004). Of the individuals found on the vegetation, eight were resting at night at heights ranging from 0.5 to 3 m (mean = 1.62 ± 0.73 m). Apparently, *C. fuscus* may use the same nocturnal perch more than once. Two individuals were found using the same perch at the previous night after being absent from the site during the day. Adults of *Chironius fuscus* were found throughout the year and young were found mainly from February to April (N = 6). The activity of *C. fuscus* is mainly diurnal (Dixon *et al.,* 1993). All individuals encountered during the day were moving along the forest floor (N = 12) or on low vegetation (less than 0.5 m high; N = 2). Nevertheless, this species may show crepuscular activity because one young (CRC = 241 mm) was found foraging along the forest edge at night (20:00 h), where anurans were calling (*Thoropa taophora, Scinax hayii,* and *Leptodactylus ocellatus*).

The diet of *C. fuscus* is composed of anurans, mainly of the family Leptodactylidae (Dixon *et al.,* 1993; Martins & Oliveira, 1999; Marques & Sazima, 2004). To capture their prey, individuals of this species move along the forest floor and on low vegetation searching for anurans. Five amphibians were found in the gut of five individuals, and we were able to identify *Haddadus binotatus* (Craugastoridae) and *Thoropa taophora* (Cycloramphidae), species normally found on the forest floor or on rock ledges. On two occasions, adult individuals of *C. fuscus* (CRC = 710 and 738 mm) shook their tails strongly when handled, and one of them lost its tail when it was held up by it. One adult (CRC = 720) was found with an amputated tail. Marques & Sazima (2004), also state that an individual vibrated its tail when ambushed.

Chironius laevicollis: This species showed intermediate abundance and was always found associated to forested areas (N = 9). With a terrestrial habit, it was found mainly on the ground (N = 6), but it can also use low vegetation (less than 1 m high; N = 3). One adult was seen moving on vegetation in the forest and another was seen moving on shrubs on the edge of a temporary pond. Individuals were also found moving on the forest floor (N = 4), on the low vegetation (N = 1), and on the forest edge (N = 2). Among the species of *Chironius, C. laevicollis* is the most robust (Marques, 1998), what may reflect its primary terrestrial habit. The species has diurnal habits (Dixon *et al.,* 1993), and most of the individuals of *C. laevicollis* found were active during the day (N = 7). The diet is composed primarily of anurans (Dixon *et al.,* 1993). Anuran remains were found in the stomach of four individuals (two *Leptodactylus ocellatus* and two non-identified anurans). Apparently *C. laevicollis* forages by moving over the forest floor or on low vegetation, searching the environment for anurans. Young individuals were green, and achieved a darker color pattern as they grew; as adults they have a black dorsum. Marques & Sazima (2003) suggest that the green color of the offspring of *C. laevicollis* is related to the more frequent use of the vegetation. Alternatively, the green colored young of *C. laevicolis* and *C. scurrulus* may be related to a possible mimicry of species of *Philodryas* (see Martins & Oliveira, 1999; Marques & Sazima 2003). At the Núcleo Picinguaba, young individuals of *C. laevicollis* were found on the ground but they were crossing the highway between two forested areas.

Chironius foveatus: Of intermediate abundance, this species was found in forested areas (N = 6) and on the forest edge (N = 6). It is a semi-arboreal species and was found moving on the forest floor (N = 5) or on low vegetation (N = 1). Two individuals were seen lying on the ground on the forest edge. This species may use the vegetation to rest at night, like its close relative, *C. multiventris,* in the Amazon (Dixon *et al.,* 1993; Martins & Oliveira, 1999). It was found during all the seasons of the year. It is a diurnal species and most individuals were seen in activity in the morning (N = 8). *Chironius foveatus* feeds on anurans (Dixon *et al.,* 1993; Marques, 1998). In the specimens examined we found an individual of *Hypsiboas faber* and another of *Bokermannohyla* aff. *circumdata* (Hylidae). Rocha *et al.,* (1999) found two anurans, *Bokermannohyla* aff. *circumdata* (Hylidae) and *Proceratophrys appendiculata* (Cycloramphidae), in the gut of one individual. Apparently *C. foveatus* preys mainly on hylids without disregarding other anurans that it encounters whilst foraging. One individual observed in foraging activity on the vegetation, searched the surrounding environment, until finding a treefrog and eating it (*Hypsiboas faber;* I. Sazima, pers. comm.). An adult was found moving over the forest floor whilst ingesting an anuran (*Hypsiboas faber*). Records of this species moving on the higher part of trees or bushes are rare. Thus, it seems that *C. foveatus* has at least part of its foraging activity concentrated on the ground and on the lower vegetation strata.

Spilotes pullatus: A common species, it may be found in forested areas (N = 4), forest edges (N = 7), and open areas (N = 1). It has a semi-arboreal habit (Vanzolini *et al.,* 1980; Marques & Sazima, 2004). Individuals were found mainly on the ground (N = 12). One individual was observed on the vegetation, moving between tree branches at the edge of the forest. Individuals that were captured then let loose climbed the vegetation (N = 3), and one reached a height greater than 10 m. The species was more abundant in the rainy season from October to March (N = 9), but was also found in the months of July and August (both N = 1). A female found in December had eggs in its oviducts (N = 7, length greater than 56 mm). *Spilotes pullatus* has diurnal activity (Vanzolini *et al.,* 1980; Marques & Sazima, 2004) and individuals were found active in the morning (N = 3) and in the beginning of the afternoon (N = 4; see also Sazima & Haddad, 1992). *Spilotes pullatus* has a generalist diet and feeds mainly on endothermic prey such as rodents, bats, and birds (Wehekind, 1995; Marques & Sazima, 2004), that it finds by active foraging on the forest floor and on the vegetation (N = 3). Mammal fur was found in the gut of one adult specimen. To subjugate its prey, it can press it against the substrate with one or more of its body loops (N = 1; Marques & Sazima, 2004).

Family Dipsadidae

Clelia plumbea: This species is rare in the Núcleo Picinguaba region. The only individual found was run over in a road near the forested area. Its habit is terrestrial (Marques *et al.,* 2001), which seems to be characteristic for the genus (*e.g.,* Martins & Oliveira, 1999). It was found in April. It seems to be mainly nocturnal, as are other members of the tribe Pseudoboini (Marques, 1998; Martins & Oliveira, 1999). No food items were found in the individual from Picinguaba; however, there are records of snakes and lizards in the diet of this species (Marques *et al.,* 2004). It uses constriction as its main prey subjugation strategy (Marques *et al.,* 2004).

Dipsas indica: A rare species at Núcleo Picinguaba (N = 2) with a semi-arboreal habit (Marques *et al.,* 2004). Individuals of *Dipsas indica* were found either moving on branches, at a height of about 1 m, during the night (N = 1) or run over in a road between forested areas (N = 1). This species is more frequently found in the more humid months, from October to March (Sazima, 1989). At Núcleo Picinguaba it was found in March and in October. Its activity is crepuscular and nocturnal (N = 1; see also Sazima, 1989). It feeds upon mollusks; a slug (Veronicellidae) was found in the digestive tract of one of the specimens examined. *Dipsas indica* forages by moving slowly along the substrate (ground or vegetation), flicking its tongue searching for mucous trails left by the molluscs (Sazima, 1989).

Dipsas sp.: This is a rare species in the Núcleo Picinguaba region, found in the area of preserved forest (N = 2). One individual was found moving on thin branches next to a stream (about 1.5 m high), during the night. An individual was found run over, which suggests that this species uses the ground to move from one forested area to another. It seems to be a nocturnal species as are the other species of this genus (Sazima, 1989; Martins & Oliveira, 1999; Marques & Sazima, 2004). Its diet is specialized on mollusks (Sazima, 1989), which it captures at night. We found the remains of a slug in the stomach of one individual.

Echinanthera cephalostriata: A species of intermediate abundance. As with the other two species of *Echinanthera* recorded in the study site, it is restricted to forested areas (N = 3). It was not found on the coastal plain and seems to occur at altitudes greater than 200 m. It is terrestrial and was found moving on the forest floor (N = 2). One individual was found dead, at the edge of a trail within the forest, with marks possibly caused by a predator on its dorsal region, close to its head. Active individuals were found during the day (N = 2). It feeds mainly on anurans (Marques *et al.,* 2004). No food items were found in the specimens examined.

Echinanthera undulata: Only one individual was found at the end of the study. Its diet is composed of anurans (Marques *et al.,* 2004).

Helicops carinicaudus: A rare species at Núcleo Picinguaba, it was found near the forest edge of an altered area (N = 1). Its habit is aquatic (Dixon & Soini, 1977), and it was observed swimming in a temporary pond (N = 1). It seems to have nocturnal (N = 1) and diurnal (Marques & Sazima, 2004) activity. Its diet is composed mainly of fish but it may also capture anurans (Marques & Sazima, 2004).

Imantodes cenchoa: This species of intermediate abundance is restricted to forested areas (N = 4). It is arboreal and was found moving on the vegetation near streams (N = 4). However, Marques & Sazima (2004), encountered individuals of *I. cenchoa* on the forest floor, indicating that they may descend to the ground when foraging or changing sites (Henderson & Nickerson, 1976). All the individuals encountered were active at night (N = 4), confirming its nocturnal activity (Martins & Oliveira, 1999; Marques & Sazima, 2004). The diet of this species is composed of lizards and anurans. In the digestive tract of two individuals we found vestiges of anurans (one hylid and one non-identified specimen). The presence of hylids, arboreal lizards (Sazima & Argolo, 1994; Martins & Oliveira, 1999) and the encounter of active individuals on branches, indicates that this species forages mainly on the vegetation where it can find active nocturnal anurans and resting diurnal lizards and anurans.

Liophis miliaris: A common species, it was found in forested areas (N = 14), forest edges (N = 4), and open areas (N = 2). Its habit is semi-aquatic and it moves frequently over the ground as indicated by the number of encounters of this species in the pitfall traps (N = 14). Additionally, it was found close to water bodies (N = 2), swimming in a temporary pond (N = 1), and run over (N = 3). It was more abundant in the rainy months, from October to March (N = 15). Its activity is both nocturnal and diurnal (Sazima & Haddad, 1992; Marques & Sazima, 2004). It was found active during the day (N = 3), at sunset (N = 1) and at night (N = 1). It has a generalist diet, which includes anurans, which seem to be the main prey type (Sazima & Haddad, 1992; Marques & Sazima, 2004), fish (Marques & Souza, 1993), and lizards (Machado *et al.,* 1998). One individual was found ingesting eggs of the frog *Bokermannohyla* aff. *circumdata* deposited on the bank of a stream. Another individual was ingesting a frog (*Leptodactylus ocellatus*) close to a marsh. One of the individuals captured in a pitfall trap regurgitated several frogs (a *Rhinella ornata,* six *Chiasmoclei carvalhoi* and two *Physalaemus atlanticus*), probably ingested within the trap. Apparently this species actively searches for active prey. However, it can also search for inactive prey in shelters, on the forest floor or in bromeliads (Rocha & Vrcibradic, 1998). *Liophis miliaris* was captured mainly in the pitfall traps close to water bodies (N = 13) and on rainy days (N = 11), when many frogs also fell into the traps. A high concentration of snakes in places with great food availability was registered for genera such as *Liophis, Helicops* (Martins & Oliveira, 1999), *Leptodeira* (Duellman, 1978), and *Thamnodynastes* (Bernarde *et al.,* 2000a, 2000b). In the Atlantic Forest, *Liophis miliaris* apparently uses an opportunistic foraging strategy: it seems to increase its foraging activity during or just after rainfall and concentrates in places with a high availability of prey.

Oxyrhopus clathratus: A species with intermediate abundance, it was found within the forest (N = 1), on the edge of the forest (N = 5) and in open areas (N = 4). With a terrestrial habit (Marques & Sazima, 2004), it was always found on the ground (N = 10). One individual was found moving on the forest floor close to a stream and another in the restinga forest. Individuals found run over on roads of different physiognomies (N = 6) indicate that this species may occupy altered areas and has a high capacity for migrating between areas. Five additional individuals were found in streams in the Picinguaba region after the field sampling (from 2006 to 2008), all of them active, apparently foraging, at night; three were moving over rocks on the stream bank, one was moving on the ground amidst loose pebbles, and one was moving on a fern, about 1 m above the ground (M. Martins, pers. obs.). *Oxyrhopus clathratus* did not show any noticeable activity peaks throughout the year. Its activity seems to be mainly nocturnal, but it can also be found active during the day (N = 1). Its diet is composed mainly of rodents and lizards (Marques & Sazima, 2004).

Philodryas olfersii: A species of intermediate abundance, it was found in the forest (N = 1), on the forest edge (N = 1), and in open areas (N = 2). With a semi-arboreal habit (Hartmann, 2001; Hartmann & Marques, 2005), it was found on the vegetation (N = 1) and on the ground (N = 3). This species is slender and agile and moves quickly on both substrates. One individual of *P. olfersii* was seen in the restinga forest at 15:00 h, moving over the ground and climbing the vegetation. When resting, it remains on the vegetation in protected sites or on the ground, under fallen logs or in holes (Hartmann, 2001). It is diurnal (N = 3), being active mainly in the warmest hours of the day (Sazima & Haddad, 1992; Hartmann & Marques, 2005). Its diet is composed mainly of anurans, but it can capture and ingest small mammals, lizards, and bird nestlings (Hartmann, 2001). No food items were found in the specimens examined. *Philodryas Olfersii* searches actively for food, and to subjugate its prey it uses constriction and poison (Hartmann & Marques, 2005).

Sibynomorphus neuwiedi: A rare species in the region of the Núcleo Picinguaba, it was found in the forest (N = 1), moving on thin branches at 1.5 m above the ground, and on the forest edge, run over in roads (N = 1). Its habit is semi-arboreal, and it can descend to the ground frequently (Oliveira, 2001; Marques & Sazima, 2004). Its activity is nocturnal (N = 2; see also Peters, 1960; Marques & Sazima, 2004). When resting during the day it remains on branches and on tree trunks. It is specialized in eating molluscs, mainly slugs (Oliveira, 2001; Marques & Sazima, 2004), of which it forages actively on the vegetation. No food items were found in the specimens examined.

Siphlophis pulcher: This species was recorded by Marques *et al.* (2001) for Núcleo Picinguaba, but it was not found in the region throughout the field sampling. *Siphlophis pulcher* feeds mainly lizards (Sazima & Argolo, 1994; Prudente *et al.,* 1998; Marques & Sazima, 2004). Sazima & Argolo (1994) recorded mainly lizards (*Gymnodactylus darwinii, Placosoma glabellum* and *Hemidactylus mabouia*), as the food items of individuals from the northern coast of the state of São Paulo, Brazil.

Taeniophallus affinis: A species of intermediate abundance (N = 4). All the individuals were found in the forest, moving on the ground (N = 3) and inside a pitfall trap (N = 1). All the active individuals were captured during the day (N = 3), indicating diurnal activity. *Taeniophallus affinis* feeds primarily on anurans, but may also capture small lizards and amphisbaenians (Barbo & Marques, 2003; Marques *et al.,* 2004). In the specimens examined we found only anuran remains (N = 2). The species seems to forage actively. One individual was observed moving slowly over the forest floor, flicking its tongue and searching through the leaf litter.

Taeniophallus bilineatus: A rare species at Núcleo Picinguaba. It has a terrestrial habit and was found moving over the forest floor during the day (N = 1) and inside a pitfall trap (N = 1), in the forest. It was found in January and July. Its activity is mainly diurnal, but it can also be active at sunset (N = 1). Its diet is composed of anurans and small lizards (Di-Bernardo, 1990; Sazima *et al.,* 1992; Marques & Sazima, 2004). One of the captured individuals had remains of anurans in its digestive tract. It is likely that this species is an active forager, searching for its prey amongst the leaf litter.

Thamnodynastes cf. *nattereri:* A species of intermediate abundance, it occurred in forested areas (N = 5). It is semi-arboreal and moves over the ground (N = 3), and on the vegetation (N = 2), frequently close to swamps (N = 4). One of the individuals found on the vegetation was active on the edge of a marsh and the other was coiled, resting on thin branches (1.2 m above the ground); both encountered at night. As with other species of the genus, *T.* cf. *nattereri* probably uses the vegetation as a resting place and for foraging (Strüssmann, 1992; Bernarde *et al.,* 2000a, 2000b; Marques & Sazima, 2004). It was found only during rainy months, from October to March. Its activity seems to be crepuscular and nocturnal (Marques & Sazima, 2004), however, it can be found active during the day, from the middle to the end of the afternoon (N = 4). The diet of species of *Thamnodynastes* seems to be composed mainly by frogs, although it can also consume other types of prey (Strüssmann, 1992; Rocha & Vrcibradic, 1998; Bernarde *et al.,* 2000a; Marques & Sazima, 2004). Frog vestiges were found in the gut of one individual. *Thamnodynastes* cf. *nattereri* seems to forage mainly in the afternoon and evening. It forages actively moving along the ground or vegetation, searching for flooded sites where calling frogs are abundant.

Uromacerina ricardinii: A rare species at Núcleo Picinguaba, with only one individual encountered during the study period. It seems to be restricted to forested areas and their surroundings. It has a slender body and cryptic coloration, being difficult to find when on vegetation. The few records (Amaral, 1978; Marques, 1998; Hartmann, 2006) and its body-shape indicate an arboreal habit. It was found during the day, moving on low vegetation (about 30 cm above the ground), at the edge of a forest cut by a road. It was found in May and it seems to be diurnal. Its diet is composed mainly of frogs (Marques *et al.,* 2004), although there are also records of lizards in its diet (Amaral, 1978).

Xenodon neuwiedii: A rare species in the region of the Núcleo Picinguaba, it was found on the ground of forested areas (N = 2). It was found in February and April. Its diet is composed of frogs, mainly species of the genus *Rhinella* (Sazima & Haddad, 1992; Jordão, 1996; Marques & Sazima, 2004).

Family Elapidae

Micrurus corallinus: A species of intermediate abundance, it occupies mainly forested areas (N = 2) and forest edges (N = 5). It was found moving on the forest floor or surrounding areas (N = 4) and in pitfall traps (N = 2). It was found active mainly in rainy months (N = 6). Its diet is composed of elongate vertebrates such as amphisbaenians, caecilians, and snakes. In the gut of one individual we found the remains of a caecilian. *Micrurus corallinus* seems to search actively for its prey (N = 2), capturing them on the surface of the ground or in subterranean galleries (Marques & Sazima, 1997).

Family Viperidae

Bothrops jararaca: A dominant species, it had the largest number of records in this study. It was found mainly in forested areas and its surroundings. Adults are primarily terrestrial whereas juveniles are frequently found on the vegetation (Sazima, 1992; Hartmann *et al.,* 2003). Adults were found moving over the forest floor (N = 6) and coiled, in an ambush posture (N = 1). Only two adult individuals were found resting on the vegetation; one was in the forest and the other on the edge of a swamp. Of the 63 young individuals encountered, 13 were on the vegetation inside the forest. The juveniles of *B. jararaca* were found mainly close to streams within the forest (N = 47). During the day, they were found coiled on the rocks on the edge of a stream (N = 32), and in two occasions they were using tail luring (Hartmann & Almeida, 2001). At night, individuals were found on the vegetation (N = 8), coiled on thin branches of small trees at the edge of streams or on the ground (N = 6). Four individuals were found moving at night, apparently searching for prey on the rocks at the edge of the streams. Adults were found throughout the year and juveniles at the beginning (N = 22) and the end (N = 27) of the rainy season. Adults of *B. jararaca* were found active mainly at night or at sunset (N = 5). The young were found active during the day (N = 18) and at night (N = 17). *Bothrops jararaca* forages mainly by ambush, within the forest or on the edge of swamps and streams. The diet of juveniles is composed mainly of frogs while adults feed mainly on small mammals (Sazima, 1992; Marques & Sazima, 2004). The individuals examined, which were all young, we found the remains of frogs (N = 12; eight *Hylodes* sp.; one *Physalaemus* sp. and one non-identified hylid).

Bothrops jararacussu: A dominant species, it was found within the forest (N = 18), on the forest edge (N = 25) and in open areas (N = 3). Its habit is terrestrial and all individuals were found on the ground. However, one adult individual escaped by climbing the vegetation (about 2.5 m high). Individuals were found coiled on the forest floor, in an ambush posture (N = 8), and moving along the edge of a swamp (N = 2). Three adults were found moving at night under heavy rain. One adult individual was found ingesting a rodent in the first hours of the morning. A gravid female was found coiled on the edge of the forest during the day, probably basking. As *B. jararaca,* young of *B. jararacussu* can also use streams as a foraging site (Hartmann *et al.,* 2003). On 14 occasions we found individuals of this species on rocks at the edges of streams, during the day, close to active frogs (individuals of *Hylodes asper* and *H. phyllodes*). Adults were found throughout the year and juveniles mainly during the rainy season, from October to March (N = 24). Individuals were found active during the day (N = 20) and night (N = 16), indicating that they can be active during both periods. This species shows ontogenetic variation in diet, with juveniles preying on ectothermic animals, mainly anurans (N = 8), and adults preying on small mammals (N = 3; see also Martins *et al.,* 2002). The most common foraging strategy is ambush, although they can also search actively for prey alongside swamps and streams. Young individuals can use tail luring, exposing and slowly moving the white tip of their tail to attract their prey (N = 2; see also Sazima, 1991).

Sampling methods

The five sampling methods together enabled the encounter of 282 snakes belonging to 24 species (Table 2). None of the methods provided the capture of more than 80% of the species. Of the five methods used, three enabled us to capture species that were not recorded by other methods, and four species were found only by one method. The use of several methods for sampling snakes seems to be the best way for achieving results that are closest to the actual composition of a given area (see Martins, 1994; Melo *et al.,* 2003; Sawaya *et al.,* 2008) in less time.

The time constrained search at Núcleo Picinguaba resulted in the largest number of encounters amongst the different methods (N = 91; about 32% of the snakes). However, the richness obtained was only 11 species, or 45% of the registered species. The method seems to be limited with regard to richness estimates because there is a tendency for the observer to find more conspicuous and/or larger species. The species most found by this method were *Bothrops jararaca* and *B. jararacussu* (N = 49 and 21, respectively). The average encounter rate was 0.11 snakes per man-hour of time constrained search (or 8.73 man-hours of search for each snake found). The number of encounters did not differ significantly between the seasons ($\chi^2 = 0.18$, g.l. = 1, p = 0.67). Four variables can affect results obtained by the time constrained search method. The time of the year: the activity of many species is influenced by temperature (Gibbons & Semlitsch, 1987), and in colder seasons snakes may look for shelter and/or reduce their activity (see Cechin, 1999; Marques *et al.,* 2000). The structural complexity of the environment: environments with denser vegetation lower the viewing depth of the observer. The faunistic composition of the region: conspicuous and/or large species are easier to find (see Martins 1994; Sawaya *et al.,* 2008; Bernarde, 2004; present study). And, finally, the experience of the observers. An advantage of the time constrained search is the possibility of obtaining valuable ecological and behavioral data for each snake found (see Martins, 1994; Hartmann *et al.* 2003; Sawaya *et al.,* 2008).

Amongst the different sampling methods, opportunistic encounters allowed us to attain the biggest richness values (19 species, N = 82). The large distances covered while checking the pitfall traps, through different vegetation physiognomies, certainly contributed toward this result. However, the limitation of this method is the difficulty in standardizing sampling effort.

The sampling by car method enabled us to find more than 60% of the species registered for the region. It was the third best method in number of individuals (N = 54) and the second best in terms of richness (15 species). On average, one snake was found every 106 km covered. There was no difference in encounter rate throughout the year (average of one snake every 101 km from October to March and 111 km from April to September; $\chi^2 = 1.4$ g.l. = 1, p = 0.26). The capture of larger species and of those with great capacity for displacement (*e.g. Chironius* spp., *Philodryas olfersii* and *Liophis miliaris*) was high-

TABLE 2: Species and number (N) of the snakes recorded for each sampling method at Núcleo Picinguaba, Parque Estadual da Serra do Mar, from January to December 2002. PT, pitfall traps with drift fences; TCS, time constrained search; SC, sampling by car; OE, opportunistic encounters; and LC, local collectors.

Family/Species	N	Method				
		PT	TCS	SC	OE	LC
Colubridae						
Chironius bicarinatus	12		1	8	3	
Chironius exoletus	19			11	5	3
Chironius fuscus	29	1	9	6	11	2
Chironius foveatus	12			2	9	1
Chironius laevicollis	9		1	3	4	1
Spilotes pullatus	13			2	7	4
Dipsadidae						
Clelia plumbea	1			1		
Dipsas sp.	2		1		1	
Dipsas indica	2		1	1		
Echinanthera cephalostriata	3				1	2
Helicops carinicaudus	1				1	
Imantodes cenchoa	4		3		1	
Liophis miliaris	20	14		3	2	1
Oxyrhopus clathratus	10		1	6		3
Philodryas olfersii	4			3	1	
Sibynomorphus neuwiedi	2		1	1		
Taeniophallus affinis	4	1			3	
Taeniophallus bilineatus	2	1			1	
Thamnodynastes cf. *nattereri*	5		3		2	
Uromacerina ricardinii	1				1	
Xenodon neuwiedii	2					2
Elapidae						
Micrurus corallinus	7	2		1	2	2
Viperidae						
Bothrops jararaca	71		49	3	14	5
Bothrops jararacussu	47		21	3	13	10
Number of individuals	282	19	91	54	82	36
Number of species	24	5	11	15	19	12
Percentage of the species recorded for each sampling method	—	20%	45%	62%	79%	50%

est. The low speed allows one to pay more attention to the road and increases the possibilities of visualizing snakes on the curb. This method is extremely useful for recording the richness in areas that are cut by roads.

The local collectors recorded 36 individuals belonging to 12 species (50% of the richness). The snakes captured by this method are amongst the most common in the region (Table 2). However, *Xenodon neuwiedii* was only recorded using this method. This method shows a trend for sampling more conspicuous species, less inclined to escape, and with at least part of their activity during the day (Sawaya *et al.,* 2008). In short-term samplings, local collectors facilitate the sampling of the most common species. In studies along longer periods, they increase the records of rare species or of species that occupy the margins of the studied area (see Cechin, 1999).

The pitfall traps captured 19 individuals belonging to five species. Of these, 14 were *Liophis miliaris.* No species was recorded exclusively by this method. Pitfall traps capture snakes that have a smaller total length than the height of the bucket (Semlitsch & Gibbons, 1982). In fact, the buckets used were 70 cm tall and all the captured snakes were smaller than this. One of the advantages of pitfall traps is the capture of fossorial or cryptozoic species which are rarely found with visually-based methods (Cechin, 1999). However, no fossorial species were recorded in our study area and only one can be considered cryptozoic (*Micrurus corallinus*). The only species that uses the vegetation and was captured in the traps was a juvenile *Chironius* *fuscus,* with total length of about 45 cm. This method seems to be more adequate for open areas, such as fields and open pasture, where the snakes move mainly on the ground (see Cechin, 1999; Cechin & Martins, 2000; Sawaya *et al.,* 2008). Perhaps drift fences are more effective to capture snakes in open areas, since the higher structural complexity of forests may allow its avoidance by climbing the vegetation.

Seasonal activity

More active (*i.e.,* not resting) snakes were found in the rainy/warmer season (October to March) than in the dry/colder season (April to September; Fig. 2). The months with lower abundance were July and September. However, there was no significant difference between the number of snakes captured in the

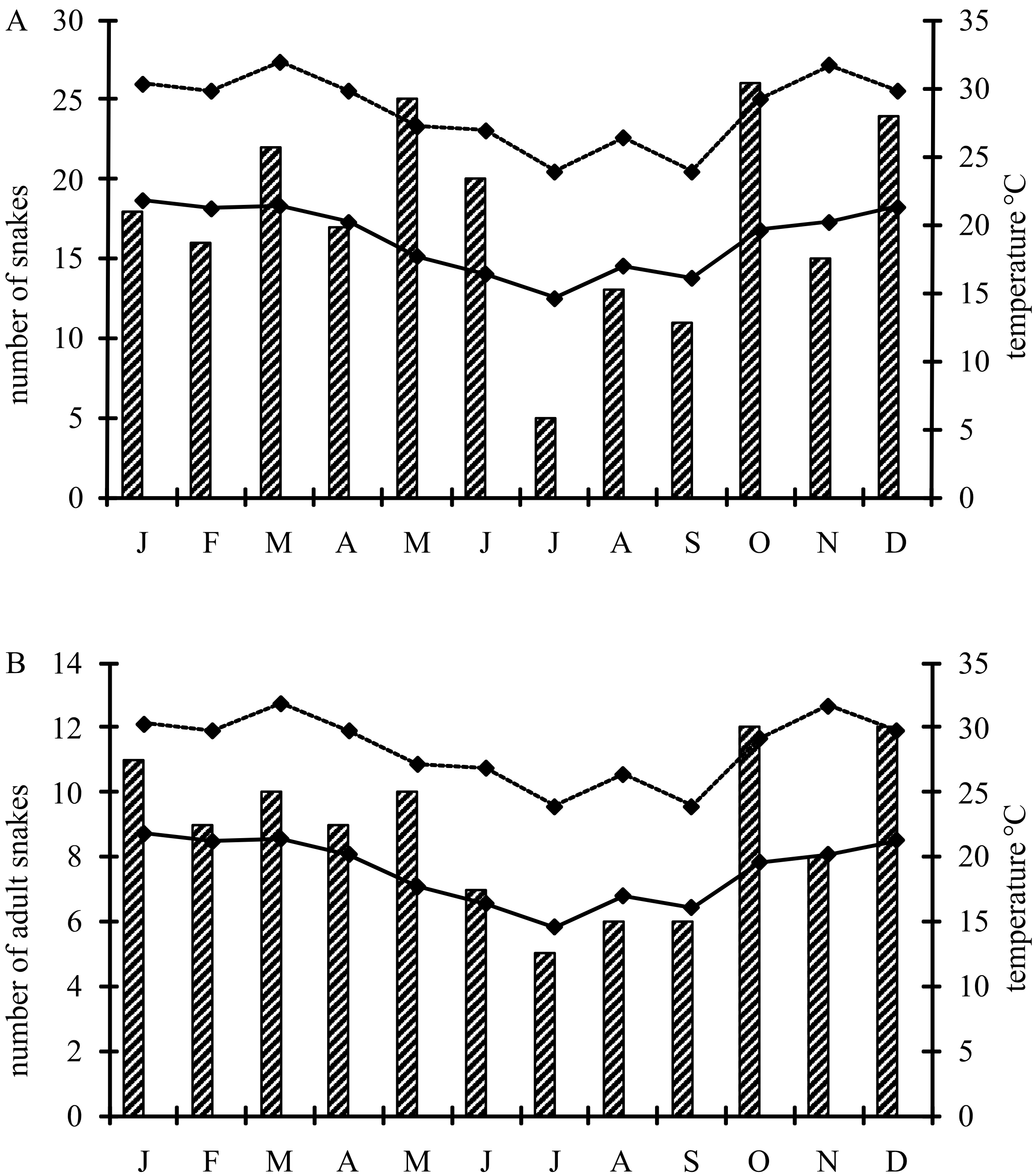

FIGURE 2: Number of snakes (A, bars, N = 212), only adult snakes (B, bars, N = 105) and minimum and maximum temperatures (°C; lines) from January to December 2002 at Núcleo Picinguaba, Parque Estadual da Serra do Mar.

dry/colder and rainy/warmer seasons considering juveniles and adults ($\chi^2 = 0.71$, g.l. = 1, p = 0.41) or considering only adults ($\chi^2 = 1{,}03$, g.l. = 1, p = 0.31). The main variable related to abundance of snakes was minimum temperature (Multiple Regression, Rp = 0.84; p << 0.001; N = 105). The abundance of adult snakes was also related to rainfall (Multiple Regression, Rp = 0.80; p = 0.002; N = 105) as well as to maximum temperature (Multiple Regression, Rp = 0.76; p = 0.003; N = 105). Low temperatures seem to be a limiting factor for the activity of most snakes (Gibbons & Semlitsch, 1987; Sawaya *et al.,* 2008), because this can reduce their metabolic rate (Lillywhite, 1987).

Rainfall is also suggested as being an important factor in the determination of the seasonal activity in tropical snakes, mainly in regions where a well defined dry season occurs (Henderson *et al.,* 1978; Martins & Oliveira, 1999; Sazima, 1992; Strüssmann & Sazima, 1993). The influence of rainfall on the activity of some species of snakes may be indirect, affecting the availability of prey (Martins & Oliveira, 1999; Marques *et al.,* 2000). In the Atlantic Forest, Marques *et al.* (2000) noticed that some frog-eating species were captured more often in the rainy season, when the availability of frogs increases. However, other frog-eating species did not show a seasonal shift in activity. In the present study, we also found more snakes when frogs (main food source in the studied assemblage) were more active and this pattern is common in other Neotropical localities (*e.g.,* Martins & Oliveira, 1999; Marques *et al.,* 2000; Sawaya *et al.,* 2008). At Nucleo Picinguaba, only four of the 13 frog-eating species (*Chironius exoletus, Liophis miliaris, Taeniophallus affinis* and *Thamnodynastes* cf. *nattereri*) showed an increase in activity during the rainy season. Alternatively to food availability, tolerance to extreme climatic conditions, reproductive cycle, and phylogenetic constraints may also affect patterns of snake activity throughout the year (Martins & Oliveira, 1999, Marques *et al.,* 2000).

TABLE 3: Diet, daily activity and substrate use for each species recorded, from January 2001 to December 2002 at Núcleo Picinguaba, Parque Estadual da Serra do Mar. In parenthesis are the sporadic observations. An, anurans; Amp, amphisbaenians; Bi, birds; Li, lizards; Ma, mammals; Mo, molluscs; Fi, fish; Sn, snakes; D, diurnal; N, nocturnal; C, crepuscular; Sa, semi-arboreal; Ar, arboreal; Aq, aquatic; Fo, fossorial; Te, terrestrial.

Family/Species	Diet	Daily activity	Substrate use
Colubridae			
Chironius bicarinatus	An (Li, Bi)	D(C)	Sa
Chironius exoletus	An	D(C)	Sa
Chironius fuscus	An	D(C)	Sa
Chironius foveatus	An	D(C)	Sa
Chironius laevicollis	An	D(C)	Te
Spilotes pullatus	Ma, Bi	D	Sa
Dipsadidae			
Clelia plumbea	Sn, Li	N	Te
Dipsas sp.	Mo	N	Ar
Dipsas indica	Mo	N	Ar
Echinanthera cephalostriata	An	D	Te
Echinanthera undulata	An	D	Te
Helicops carinicaudus	Fi, An	N	Aq
Imantodes cenchoa	Li, An	N	Ar
Liophis miliaris	An (Fi, Li, Ma, eggs An)	DN	Aq, Te
Oxyrhopus clathratus	Ma, Li	N	Te
Philodryas olfersii	An, (Ma, Li, Bi)	D	Sa
Sibynomorphus neuwiedi	Mo	N	Sa
Siphlophis pulcher	Li (Sn)	N(C)	Sa
Taeniophallus affinis	An (Li)	D	Te
Taeniophallus bilineatus	An	D	Te
Thamnodynastes cf. *nattereri*	An (Ma, Li)	DN	Sa
Uromacerina ricardinii	An, Li	D	Ar
Xenodon neuwiedii	An	D	Te
Elapidae			
Micrurus corallinus	Amp (Sn)	D(C)	Te, Fo
Viperidae			
Bothrops jararaca	Ma (An, Li)	DN	Te
Bothrops jararacussu	Ma (An, Li)	DN	Te

Diel activity and substrate use

A little more than half of the snakes at Picinguaba are predominantly diurnal (14 species, 54%; Table 3). Six species are predominantly diurnal, but can also be active at sunset. Amongst these are the five species of *Chironius* that can be active at sunset, possibly to search for anurans at the beginning of their activity; the other diurnal species (*Micrurus corallinus*) that can be active at sunset preys on nocturnal snakes. *Siphlophis pulcher,* which is nocturnal, can also be active at sunset and also preys on nocturnal snakes. Eight species have nocturnal habits (31%), and four species can be active during both periods (15%) although adults of *Bothrops jararaca* and *B. jararacussu* seem to be more active at night.

The most frequent condition of substrate use is the terrestrial habit (12 species, 46%). Two of the terrestrial species can also frequently use other habitats: *Micrurus corallinus* can be considered partially fossorial and *Liophis miliaris* is partially aquatic. Nine species were considered semi-arboreal (35%). The arboreal habit is characteristic of four species (15%). Only one species (4%) can be considered aquatic (Table 3).

Individuals of 20 species were found on the ground (76%). In three species, individuals were found resting; two of these during the day (*Bothrops* spp.) and two at night (*Bothrops jararaca* and *Oxyrhopus clathratus*). The low encounter rate for resting snakes during the day may be related to the fact that nocturnal snakes rest in shelters to prevent visually-oriented predators from finding them (Martins, 1994). Individuals of 14 species were found on the vegetation (53%). Of these, eight species were active during the day and six at night. In four species, individuals were found resting on the vegetation during the night. Individuals of only one species (*Bothrops jararaca;* see Hartmann *et al.,* 2003) were found resting on the vegetation during the day. It is likely that the five species of *Chironius* found in this study use the vegetation to rest during the night, at least while young. In the same way, juveniles of *Bothrops jararaca* were found resting in the low vegetation. The use of vegetation during the night for resting may be related to protection against nocturnal predators, mainly small marsupials (*e.g. Lutreolina crassicaudata, Philander opossum* and *Didelphis marsupialis*) as these predators generally move along the ground whilst foraging (Emmons, 1990). Alternatively, invertebrates may be important potential predators of snakes resting on the ground (Martins, 1993).

Diet

Most snakes from Picinguaba had specialized diets (Table 3). Frogs were the most frequent food item; 19 species (73%) may capture this item at some stage of their life. Frogs were the main food item in the diet of thirteen species (50%). The large proportion of species that feed on anurans shows the importance of this kind of prey as a food resource for the Atlantic Forest snakes. Anurans are common prey in the diet of South American snakes, possibly due to their abundance and great capacity of occupying different habitats (*e.g.* Vitt & Vangilder, 1983; Duellman, 1990; Strüssmann & Sazima, 1993; Martins & Oliveira, 1999; Marques, 1998; Cechin, 1999; Di-Bernardo, 1999; Bernarde *et al.,* 2000a; Marques & Sazima, 2004; Marques *et al.,* 2004). At Picinguaba there are about 40 species of anurans (Hartmann, 2004). Many environments where snakes are found can be associated to environments occupied by anurans. This seems to be the pattern for Neotropical snake assemblages (see Strüssmann 1992, Martins, 1994, Marques, 1998, Cechin, 1999, Sawaya, 2004, Bernarde, 2004).

Frog-eating snakes capture their prey in several ways. The species of *Chironius,* as well as *Philodryas olfersii* seem to capture anurans using active search, either on the ground or on the vegetation (Martins, 1994; Marques, 1998; Hartmann, 2001). The species of *Echinanthera* and *Taeniophallus* are restricted to capturing small anurans on the forest floor (Marques & Sazima, 2004). Species associated to aquatic habitats (*Helicops carinicaudus* and *Liophis miliaris*) capture anurans and their egg clutches on the edges of water bodies or inside the water. The arboreal species (*Imantodes cenchoa* and *Uromacerina ricardinii*) seem to capture anurans, mainly hylids, on the vegetation, in their resting place. *Thamnodynastes* cf. *nattereri* capture anurans in activity on the vegetation at the edge of ponds during sunset and at night. The diet of *Xenodon neuwiedii* is mostly, but not exclusively, made up of anurans of the genus *Rhinella* that it captures actively on the forest floor (Jordão, 1996; Marques & Sazima, 2004). Juveniles of *Bothrops jararaca* and *B. jararacussu* capture diurnal anurans (*Hylodes* spp.) on the banks of Atlantic Forest streams (Hartmann *et al.,* 2003), or temporary ponds.

Thirteen species of snakes can consume lizards in some phase of their life. However, only four seem to capture them frequently (*Clelia plumbea, Imantodes cenchoa, Oxyrhopus clathratus* and *Siphlophis pulcher*). Seven species can capture mammals and in three of these (11%) this may be considered the main food item. The vipers *Bothrops jararaca* and *B. jararacussu* and the dipsadid *Oxyrhopus clathratus* capture mammals mainly in their adult phase. The capture of mammals is habitually restricted to the species that have an efficient subjugation mechanism, such as poisoning and/or constriction, as the prey can strike back when they are captured (Sazima, 1992; Cadle & Greene, 1993). Two species that capture mammals frequently use venom as a subjugation tactic (*B. jararaca, B. jararacussu*) and one species (*Oxyrhopus clathratus*), uses constriction, which makes it possible to safely capture mammals. The other species that include mammals in the diet sporadically may also use constriction (*e.g. Spilotes pullatus*) or poisoning and constriction (*e.g. Philodryas olfersii* and *Thamnodynastes* cf. *nattereri*).

Three species feed on elongated vertebrates such as snakes, amphisbaenians and caecilians, and in two these may be considered the main food item (8%). *Micrurus corallinus* and *Clelia plumbea* seem to capture other snakes with frequency. The use of constriction, poisoning or both, are tactics frequently used by ophiophagous snakes to subjugate their prey (Greene, 1976; Gans, 1978; Roze, 1982).

Two species can capture fish, and in one of them (*Helicops carinicaudus*) fish can be considered a frequently consumed item. Two species (8%) can consume birds, but none seems to capture birds frequently. Shine *et al.* (1996) comment that birds are rare in the diet of snakes, as they are difficult to capture, and Hayes (1992) demonstrated for rattlesnakes birds are more difficult to subjugate than small mammals. Birds are voluminous prey and snakes that include them in their diet need a bigger gape than those that feed on mammals or lizards of similar mass (Greene, 1983), which indicates that only the larger individuals eat birds (Rodrígues-Robles *et al.,* 1999). It is likely that these species feed mainly on nestlings as they are easier to capture and subjugate (Hartmann & Marques, 2005). Only three species (11%) consumed exclusively invertebrates, all belonging to the Dipsadinae.

Community structure

According to Cadle & Greene (1993), the composition of Neotropical snake assemblages reflects the probability that different lineages have of colonizing the area. As a result, the structure of assemblages reflects, to a large extent, the contribution of the different lineages. For example, the amount of species that feed on invertebrates is much larger in Central America and the Amazon than in the Atlantic Forest and southern Brazil, due to the high representation of the subfamily Dipsadinae in these assemblages. Recent studies show that this hypothesis is proven in several assemblages of Neotropical snakes (see Cadle & Greene, 1993; Martins & Oliveira, 1999; Marques, 1998; Sawaya *et al.,* 2008). Thus, a large number of species of the same lineage in one given region can cause an extensive overlap in the resource use. The assemblage at Núcleo Picinguaba fits into this condition.

According to the characterization of main food items, substrate use and period of activity, we can identify six groups (or pairs) of species, or guilds, that use the same types of resources. Species that feed mainly on anurans, are diurnal and/or crepuscular and semi-arboreal: *Chironius bicarinatus, C. exoletus, C. fuscus, C. foveatus, C. laevicollis* and *Thamnodynastes* cf. *nattereri.* Species that consume mainly anurans, are diurnal and terrestrial: *Echinanthera cephalostriata, E. undulata, Taeniophallus affinis, T. bilineatus* and *Xenodon neuwiedii.* Species with a generalist diet, are diurnal and/or crepuscular and semi-arboreal: *Philodryas olfersii* and *Spilotes pullatus.* Species with a malacophagous diet, nocturnal activity and are semi-arboreal: *Dipsas* sp., *Dipsas indica* and *Sibynomorphus neuwiedi.* Species that feed mainly on mammals, are nocturnal and terrestrial: *Bothrops jararaca, Bothrops jararacussu* and *Oxyrhopus clathratus.* And, finally, species that consume fish, have nocturnal activity and are aquatic: *Helicops carinicaudus* and *Liophis miliaris.*

TABLE 4: Number and percentage of the species recorded at Núcleo Picinguaba, Parque Estadual da Serra do Mar, for each colubroid lineage (cf. Zaher *et al.,* 2009).

Family/Subfamily	Number of species and percentage of recorded species
Colubridae	
Colubrinae	06 (23%)
Dipsadidae	
Dipsadidade incertae sedis	01 (04%)
Dipsadinae	04 (15%)
Xenodontinae	12 (46%)
Elapidae	01 (04%)
Viperidae	02 (08%)

The lack of species using some food resources are expected to be a consequence of the scarcity of food or of the absence of lineages that typically consume these resources in the regional species pool. This is clearly the case of the scarcity of snakes that feed on insects in Neotropical snake assemblages, in comparison with those of the American deserts (see Cadle & Greene, 1993). In the Picinguaba assemblage, amongst the 26 recorded species, only three consumed exclusively invertebrates (molluscs), all belonging to the tribe Dipsadini. Indeed, the invertebrate trophic resource is rare in this assemblage. This common pattern in Neotropical snake assemblages probably reflects the faunistic composition of this region, that is strongly influenced by the Dipsadidae, within which just a few lineages feed on invertebrates (Table 4, Cadle & Greene, 1993). In conclusion, our results indicate that the structure of the Picinguaba snake assemblage reflects mainly the phylogenetic constraints of each of its lineages, as predicted by Cadle & Greene (1993) for Neotropical assemblages in general.

RESUMO

O principal objetivo deste estudo foi obter informações sobre a história natural e a ecologia das espécies que compõem uma taxocenoses de serpentes da Mata Atlântica, no Núcleo Picinguaba do Parque Estadual da Serra do Mar, localizado no litoral norte do estado no Estado de São Paulo, sudeste do Brasil. Os principais aspectos estudados foram: riqueza, abundância relativa de espécies, padrões *de atividade diária e sazonal, utilização do ambiente e dieta. Um total de 282 serpentes, distribuídas em 24 espécies, pertencentes a 16 gêneros e quatro famílias, foi encontrado dentro dos limites do Núcleo Picinguaba. As espécies mais frequentemente encontradas foram* Bothrops jararaca *e* B. jararacussu. *Os métodos que proporcionaram maior retorno foram: procura limitada por tempo e encontros eventuais. Dentre os fatores abióticos analisados para a área de estudo, o mais relacionado à abundância das serpentes foi a temperatura mínima, seguido da temperatura média e da pluviosidade. A maioria das espécies encontradas apresenta dieta concentrada em uma categoria de presa ou restrita a poucos tipos de itens alimentares. A grande proporção de serpentes que se alimentam de anuros evidencia a importância deste tipo de presa como recurso alimentar nas espécies de serpentes da Mata Atlântica. Nossos resultados indicam que a estrutura da taxocenose de serpentes do Núcleo Picinguaba reflete principalmente as limitações filogenéticas inerentes às linhagens que a compõem.*

PALAVRAS-CHAVE: Taxocenose; Serpente; Dieta; Uso do ambiente; Atividade.

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REFERENCES

AMARAL, A. 1978. *Serpentes do Brasil:* Iconografia colorida. 2. ed. Melhoramentos/Editora da Universidade de São Paulo, São Paulo.

ARGÔLO, A.J.S. 2004. *Serpentes dos cacauais do sudeste da Bahia.* Editus, Ilhéus.

BARBO, F.E. & MARQUES, O.A.V. 2003. Do aglyphous colubrid snakes prey on live amphisbaenids able to bite? *Phyllomedusa,* 2:113-114.

BEGON, M.; HARPER, J.L. & TOWNSEND, C.R. 1996. *Ecology:* individuals, populations and communities. Blackwell Science, Cambridge.

BERNARDE, P.S. 2004. *Composição faunística, ecologia e história natural de serpentes em uma região no sudoeste da Amazônia, Rondônia, Brasil.* (Tese de doutorado). Universidade Estadual Paulista, Rio Claro.

BERNARDE, P.S.; KOKUBUM, M.N.C. & MARQUES, O.A.V. 2000a. Utilização de habitat e atividade em_*Thamnodynastes strigatus* (Günther, 1858) no sul do Brasil (Serpentes, Colubridae). *Boletim do Museu Nacional,* Nova Série Zoologia, 428:1-8.

BERNARDE, P.S.; MOURA-LEITE, J.C.; MACHADO, R.A. & KOKUBUM, M.N.C. 2000b. Diet of the colubrid snake, *Thamnodynastes strigatus* (Günther, 1858) from Paraná state, Brazil, with fields notes on anuram predation. *Revista Brasileira de Biologia,* 60:695-699.

CADLE, J.E. & GREENE, H.W. 1993. Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblage. In: Ricklefs, R.E. & Schulter, D. (Eds.), *Species Diversity in Ecological Communities – Historical and geographical perspectives.* University Chicago Press, Chicago, p. 281-293.

CARVALHO-SILVA, S.P. & FERNANDES, R. 1994. *Chironius bicarinatus. Herpetological Review,* 25:28.

CECHIN, S.T.Z. & MARTINS, M.R.C. 2000. Eficiência de armadilhas de queda (pitfall traps) em amostragens de anfíbios e répteis no Brasil. *Revista Brasileira de Zoologia,* 17:729-740.

CECHIN, S.T.Z. 1999. *História Natural de uma comunidade de Serpentes na Região da Depressão Central (Santa Maria), Rio Grande do Sul, Brasil.* (Tese de doutorado). Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre.

DI-BERNARDO, M. 1990. O gênero *Rhadinea* Cope, 1963 no Brasil meridional IV. *Rhadinea bilineata* (Fisher, 1885) (Serpentes, Colubridae). *Acta Biologica Leopoldensia,* 12:359-392.

DI-BERNARDO, M. 1999. *História natural de uma Comunidade de Serpentes da Borda Oriental do Planalto das Araucárias, Rio Grande do Sul, Brasil.* (Tese de doutorado). Universidade Estadual de Paulista, Rio Claro.

DIXON, J.R. & SOINI, P. 1977. The reptiles of the upper Amazon basin, Iquitos region, Peru. II. Crocodilians, turtles, and snakes. *Milwaukee Public Museum. Contributions in Biology and Geology,* 12:1-71.

DIXON, J.R. & SOINI, P. 1986. *The Reptilies of the upper Amazon Basin, Iquitos region, Peru.* Milwauke Public Museum, Milwauke.

DIXON, J.R. 1979. Origin and distribution of reptiles in lowland tropical; rain forest os South America. In: Duellman, W.E. (Ed.), *The South America herpetofauna:* its origin, evolution, and dispersion. Monograph of the Museum of Natural History, Kansas, 7:217-240.

DIXON, J.R.; WIEST, J.A. & CEI, J.M. 1993. Revision of the tropical snake *Chironius* Fitzinger (Serpentes, Colubridae). *Monogafie Museo Regionale di Scienze Naturali,* XIII:1-279.

DUELLMAN, W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Equador. *Miscellaneous Publications. Museum of Natural History of the University of Kansas,* 65:1-352.

Duellman, W.E. 1990. Herpetofaunas in neotropical rainforests: Comparative composition, history, and resource use. In: Gentry, A.H. (Ed.), *Four neotropical rainforests.* Yale University Press, New Haven, p. 455-505.

Emmons, L.H. 1990. *Neotropical Rainforest Mammals.* The University of Chicago Press, Chicago.

Gans, C. 1978. Reptiliam venoms: some evolutionary considerations. In: Gans, C. & Gans, K.A. (Ed.), *Biology of the Reptilia.* Academic Press, London, 8:1-42.

Gibbons, J.W. & Semlitsch, R.D. 1987. Activity patterns. In: Seigel R.A., Collins J.T. & Novak S.S. (Eds.), *Snakes: Ecology and Evolutionary Biology,* McGraw-Hill, New York, p. 396-421.

Greene, H.W. 1976. Scale overlap as a directional sign stimulus for prey ingestion by ophiophagous snakes. *Zeitschrift fur Tierpsychologie,* 46:113-120.

Greene, H.W. 1983. Dietary correlates of the origin and radiation of snakes. *American Zoologist,* 23:431-441.

Hartmann, M.T. 2004. *Biologia reprodutiva de uma comunidade de anuros (Amphibia) na Mata Atlântica (Picinguaba, Ubatuba, SP).* (Tese de doutorado). Universidade Estadual Paulista, Rio Claro.

Hartmann, P.A. & Almeida, M.T. 2001. *Bothrops jararaca. Herpetological Review,* 32: 45.

Hartmann, P.A. & Marques, O.A.V. 2005. Diet and habitat use of two sympatric species of *Philodryas* (Colubridae), in south Brazil. *Amphibia-Reptilia,* 26:25-31.

Hartmann, P.A. 2001. *Hábito alimentar e utilização do ambiente em duas espécies simpátricas de* Philodryas, *no sul do Brasil.* (Dissertação de mestrado). Universidade Estadual Paulista, Rio Claro.

Hartmann, P.A. 2006. *Uromacerina ricardinii. Herpetological Review,* 37:95.

Hartmann, P.A.; Hartmann, M.T. & Giasson, L.O.M. 2003. Uso do hábitat e alimentação em juvenis de Jararaca, *Bothrops jararaca* (Serpentes, Viperidae), na Mata Atlântica. *Phyllomedusa,* 2:35-41.

Hayes, W.K. 1992. Prey-handling and envenomation strategies of prairie rattlesnakes (*Crotalus v. viridis*) feeding on mice and sparrows. *Journal of Herpetology,* 26:496-499.

Henderson, R.W. & Nickerson, M.A. 1976. Observations on the behavior ecology of three specie of *Imantodes cenchoa* (Reptilia, Serpentes, Colubridae). *Journal of Herpetology,* 10:205-210.

Henderson, R.W.; Dixon, J. & Soini, P. 1979. Resource partitioning in Amazonian snake communities. *Milwaukee Public Museum. Contributions in Biology and Geology,* 22:1-11.

Henderson, R.W.; Dixon, J.R. & Soini, P. 1978. On The Seasonal Incidence of Tropical Snakes. *Milwaukee Public Museum. Contributions in Biology and Geology,* 17:1-15.

Henderson, R.W.; Noeske-Hallin, T.A.; Ottenwalder, J.A. & Schwartz, A. 1987. On the diet of Boa *Epicrates striatus* on Hispaniola, with notes on *E. fordi* and *E. gracilis. Amphibia-Reptilia,* 8:251-258.

Jordão, R.S. 1996. *Estudo comparativo da alimentação e da reprodução de Waglerophis merremii e Xenodon neuwiedii (Serpentes: Colubridae).* (Dissertação de mestrado). Universidade de São Paulo, São Paulo.

Köeppen, W. 1948. *Climatología:* Con un estudio de los climas de la tierra. Fondo de Cultura Economica, México.

Lillywhite, H.B. 1987. Temperature, energetics, and physiological ecology In: Seigel, R.A.; Collins, J.T. & Novak, S.S. (Eds.), *Snakes:* ecology and evolutionary biology. McGraw-Hill, New York, p. 422-477.

Machado, R.A.; Bernarde, P.S. & Morato, S.A.A. 1998. *Liophis miliaris. Herpetological Review,* 29:45.

Marques, O.A.V. & Sazima, I. 1997. Diet and feeding behavior of the coral snake, *Micrurus corallinus,* from the Atlantic forest of Brasil. *Herpetological Natural History,* 5:88-93.

Marques, O.A.V. & Sazima, I. 2003. Ontogenetic color changes may strengthen suggestion about systematic affinities between two species of *Chironius* (Serpentes, Colubridae). *Phyllomedusa,* 2: 65-67.

Marques, O.A.V. & Sazima, I. 2004. História natural dos répteis da estação ecológica Juréia-Itatins. In: Marques O.A.V & Duleba W. (Eds.), *Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna Holos.* Holos, Ribeirão Preto, p. 257-277.

Marques, O.A.V. & Souza, V.C. 1993. Nota sobre a atividade alimentar de *Liophis miliaris* no ambiente marinho (Serpentes, Colubridae). *Revista Brasileira de Biologia,* 53:645-648.

Marques, O.A.V. 1996. Biologia reprodutiva da cobra-coral *Erythrolamprus aesculapii,* Linnaeus (Colubridae), no sudeste do Brasil. *Revista Brasileira de Biologia,* 13:747-753.

Marques, O.A.V. 1998. *Composição faunística, história natural e ecologia de serpentes da Mata Atlântica, na região da estação ecológica Juréia-Itatins, São Paulo, SP.* (Tese de doutorado). Universidade de São Paulo, São Paulo.

Marques, O.A.V.; Eterovic, A. & Endo, W. 2000. Seasonal activity of snakes in the Atlantic Forest in southeastern Brazil. *Amphibia-Reptilia,* 22:103-101.

Marques, O.A.V.; Eterovic, A. & Sazima, I. 2001. *Serpentes da Mata Atlântica:* Guia Ilustrado para Serra do Mar. Holos, Ribeirão Preto.

Marques, O.A.V.; Eterovic, A. & Sazima, I. 2004. *Snakes of the Brazilian Atlantic Forest:* An Illustrated Field Guide for the Serra do Mar Range. Holos, Ribeirão Preto.

Martins, M. & Gordo, M. 1993. *Bothrops atrox. Herpetological Review,* 24:151-152.

Martins, M. & Oliveira, M.E. 1999. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History,* 6:78-150.

Martins, M. 1993. Why do snakes sleep on the vegetation in central Amazonia? *Herpetological Review,* 24:83-84.

Martins, M. 1994. *História Natural e Ecologia de uma Taxocenose de Serpentes de Mata na Região de Manaus, Amazônia Central, Brasil.* (Tese de doutorado). Universidade Estadual de Campinas, Campinas.

Martins, M.; Araújo, M.S.; Sawaya, R.J. & Nunes, R. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). *Journal of Zoology, London,* 254:529-538.

Martins, M.; Marques O.A.V. & Sazima I. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops.* In: Schuett G., Höggren M. e Greene H.W. (Eds.), *Biology of the Vipers.* Biological Sciences Press, Indiana, p. 307-328.

Melo, A.S.; Pereira, R.A.S.; Santos, A.J.; Shepherd, G.J.; Machado, G.; Medeiros, H.F. & Sawaya, R.J. 2003. Comparing species richness among assemblages using sample units: Why not use extrapolation methods to standardize different sample size? *Oikos,* 101: 398-410.

Oliveira, J.L. 2001. *Ecologia de três espécies de dormideira Sibynomorphus (Serpentes: Colubridae) na Mata Atlântica.* (Dissertação de mestrado). Universidade de São Paulo, São Paulo.

Peters, J.A. 1960. The snake of the subfamily Dipsadinae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan,* 114:1-224.

Prudente, A.L.C., Moura-Leite, J.C. & Morato, S.A.A. 1998. Alimentação das espécies de *Siphlophis* Fitzinger (Serpentes, Colubridae, Xenodontinae, Pseudoboini). *Revista Brasileira de Zoologia,* 15:375-383.

Rocha, C.F.D. & Vrcibradic, D. 1998. Reptiles as predators of vertebrates and as prey in a restinga habitat of southestern Brazil. *Ciência e Cultura,* 50:364-368.

Rocha, C.F.D.; Vrcibradic, D. & Sluys, M.V. 1999. *Chironius multiventris foveatus. Herpetological Review,* 30:99.

Rodrígues-Robles, J.A.; Bell, C.J. & Greene, H.W. 1999. Food habits of the glossy snake, *Arizona elegans,* with comparisons to the diet of simpatric long-nosed snakes, *Rhinocheilus lecontei. Jounal of Herpetology,* 33:87-92.

Roze, J.A. 1982. New World coral snakes (Elapidae): a taxonomic and biological summary. *Memórias do Instituto Butantan,* 46:305-338.

Sawaya, R.J. 2004. *História natural e ecologia das serpentes de cerrado da região de Itirapina, SP.* (Tese de Doutorado). Universidade Estadual de Campinas, Campinas.

Sawaya, R.J.; Marques, O.A.V. & Martins, M. 2008. Composition and natural history of a Cerrado snake assemblage at Itirapina, São Paulo state, southeastern Brazil. *Biota Neotropica,* 8(2):127-149. Available at: <http://www.biotaneotropica.org.br/v8n2/en/abstract?inventory+bn01308022008>

Sazima, I. & Argolo, A.J.S. 1994. *Siphlophis pulcher. Herpetological Review,* 25:126.

Sazima, I. & Haddad, C.F.B. 1992. Répteis da Serra do Japi: Notas sobre história natural. In: Morellato, L.P. (Ed.), *História natural da Serra do Japi:* Ecologia e preservação de uma área florestal no sudeste do Brasil. FAPESP, Campinas, p. 212-236.

Sazima, I. & Puorto, G. 1993. Feeding technique of juvenile *Tropidodryas striaticeps:* probable caudal luring in a colubrid snake. *Copeia,* 1993:222-226.

Sazima, I. 1989. Feeding behavior of the snail-eating snake *Dipsas indica. Journal of Herpetology,* 23:464-468.

Sazima, I. 1992. Natural History of Jararaca pitviper, *Bothrops jararaca* in southeastern Brazil. In: Campbell, J.A. & Brodie Jr., E.D. (Eds.), *Biology of the Pitvipers.* Selva, Tyler, p. 199-216.

Sazima, I.; Chini, S. & Souza, C.R.C. 1992. *Rhadinea biblineata. Herpetological Review,* 23:120.

Semlitsch, R.D. & Gibbons, J.W. 1982. Body size dimorphism and sexual selection in two species of water snakes. *Copeia,* 1982:974-976.

Shine, R. 1977. Habits, diet, and sympatry in snakes: a study of Australia. *Canadian Jounal of Zoolology,* 55:1118-1128.

Shine, R.; Harlow, P.S.; Branch, W.R. & Webb, J.K. 1996. Life on the lowest branch: Sexual dimorphism, diet, and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia,* 1996:290-299.

Strüssmann, C. & Sazima, I. 1993. The snake assemblage of the pantanal at Poconé, western Brazil: Faunal composition and ecological summary. *Studies on Neotropical Fauna and Environment,* 28:157-168.

Strüssmann, C. 1992. *Serpentes do Pantanal de Poconé, Mato Grosso: Composição Faunística, História Natural e Ecologia Comparada.* (Dissertação de mestrado). Universidade de Campinas, Campinas.

Vanzolini, P.E. 1948. Notas sobre os ofídios e lagartos de Emas, no município de Pirassununga, Estado de São Paulo. *Revista Brasileira de Biologia,* 8:377-400.

Vanzolini, P.E.; Ramos-Costa, A.M.M. & Vitt, L. 1980. *Répteis das Caatingas.* Academia Brasileira de Ciências, Rio de Janeiro.

Vitt, L.J. & Vangilder, L.D. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia,* 4:273-296.

Wehekind, L. 1995. Notes on the foods of the Trinidad snakes. *Jounal of Herpetology,* 2:9-13.

Zaher, H.; Grazziotin, F.G.; Cadle, J.E.; Murphy, R.W.; Moura-Leite, J.C. & Bonatto, S.L. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: A revised classification and description of new taxa. *Papéis Avulsos de Zoologia,* 49(11):115-153.

Zimmerman, B.L. & Rodrigues, M.T. 1990. Frogs, snakes, and lizards of the INPA/WWF reserves near Manaus, Brazil. In: Gentry, A.H. (Ed.), *Four Neotropical Rainforests.* Yale University Press, New Haven, p. 426-454.

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