Trophic ecology and foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil

Leonardo B. Ribeiro[1,2] & Eliza M. X. Freire[1]

1. Laboratório de Herpetologia, Departamento de Botânica, Ecologia e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, 59072-970, Natal, Rio Grande do Norte, Brazil.
2. Corresponding author. Current address: Universidade Federal do Vale do São Francisco - UNIVASF, Campus Ciências Agrárias, Colegiado de Ciências Biológicas, 56300-990, Petrolina, Pernambuco, Brazil. (leonardo.ribeiro@univasf.edu.br)

ABSTRACT. This study aimed to analyze the seasonal variation in diet composition and foraging behavior of *Tropidurus hispidus* (Spix, 1825) and *T. semitaeniatus* (Spix, 1825), as well as measurement of the foraging intensity (number of moves, time spent stationary, distance traveled and number of attacks on prey items) in a caatinga patch on the state of Rio Grande do Norte, Brazil. Hymenoptera/Formicidae and Isoptera predominated in the diet of both species during the dry season. Opportunistic predation on lepidopteran larvae, coleopteran larvae and adults, and orthopteran nymphs and adults occurred in the wet season; however, hymenopterans/Formicidae were the most important prey items. The number of food items was similar between lizard species in both seasons; however the overlap for number of prey was smaller in the wet season. Preys ingested by *T. hispidus* during the wet season were also larger than those consumed by *T. semitaeniatus*. Seasonal comparisons of foraging intensity between the two species differed, mainly in the wet season, when *T. hispidus* exhibited less movement and fewer attacks on prey, and more time spent stationary if compared to *T. semitaeniatus*. Although both lizards are sit-and-wait foragers, *T. semitaeniatus* is more active than *T. hispidus*. The diet and foraging behavior of *T. hispidus* and *T. semitaeniatus* overlap under limiting conditions during the dry season, and are segregative factors that may contribute to the coexistence of these species in the wet season.

KEYWORDS. Diet, foraging strategies, lizards, semiarid, sympatric species.

RESUMO. Ecologia trófica e comportamanto de forrageamento de *Tropidurus hispidus* e *Tropidurus semitaeniatus* (Squamata, Tropiduridae) em uma área de caatinga do nordeste do Brasil. Este estudo objetivou analisar a variação sazonal na composição da dieta e no comportamento de forrageamento de *Tropidurus hispidus* (Spix, 1825) e *T. semitaeniatus* (Spix, 1825) e medir a intensidade de forrageamento (número de movimentos, tempo gasto parado, distância percorrida e número de ataques sobre itens-presa) destas espécies em uma área do bioma caatinga no estado do Rio Grande do Norte, Brasil. Hymenoptera/Formicidae e Isoptera predominaram na dieta de ambas as espécies durante a estação seca. A predação oportunística de larvas de Lepidoptera, larvas/adultos de Coleoptera e ninfas/adultos de Orthoptera ocorreu na estação chuvosa, contudo as formigas foram os itens-presa mais importantes. O número de itens alimentares foi similar entre as espécies de lagartos em ambas as estações; no entanto a sobreposição para o número de presas foi menor na estação chuvosa. As presas ingeridas durante a estação chuvosa por *T. hispidus* foram maiores do que aquelas de *T. semitaeniatus*. As comparações sazonais da intensidade de forrageamento entre as duas espécies mostraram diferenças, principalmente na estação chuvosa, quando *T. hispidus* apresentou menos movimentos e ataques sobre presas, e mais tempo gasto parado comparado a *T. semitaeniatus*. Embora ambos os lagartos sejam forrageadores senta-e-espera, *T. semitaeniatus* é mais ativo do que *T. hispidus*. A dieta e o comportamento de forrageamento de *T. hispidus* e *T. semitaeniatus* mostram sobreposição sob condições limitantes durante a estação seca, e são fatores segregativos que podem contribuir para a coexistência dessas espécies na estação chuvosa.

PALAVRAS-CHAVE. Dieta, estratégias de forrageamento, lagartos, semiárido, espécies simpátricas.

The ecological and behavioral interactions of lizards are directly related to their foraging mode (Huey & Pianka, 1981; Rocha, 1994; Werneck *et al*., 2009). In a broader context, factors related to lizards' trophic ecology include prey availability in the environment and selectivity by the forager (Vrcibradic & Rocha, 1995; Rocha & Anjos, 2007). Diets are therefore an important and dynamic component of the interaction of a lizard with its environment and with other co-existing species (Duffield & Bull, 1998). Lizard species may differ in their diets as competition-reducing mechanisms (Dunham, 1983; Vitt & Zani, 1996), as a result of morphological differences (Colli *et al*., 1992; Mesquita *et al*., 2006), as well as related to different availability of food types (Stamps *et al.*, 1981; Durtsche, 1995; Sousa & Cruz, 2008). An additional source of variation in diet may result from different foraging behaviors, especially among phylogenetically related species (Magnusson *et al*., 1985; Duffield & Bull, 1998).

The tropidurid lizards *Tropidurus hispidus* (Spix, 1825) and *T. semitaeniatus* (Spix, 1825) are found in sympatry in rocky outcrops in the caatinga of northeastern Brazil. Studies on the diet of these species were previously conducted in one caatinga area in the state of Pernambuco (Vitt, 1995), and on *T. hispidus* in the Amazon Forest (Vitt *et al*., 1996) and rocky meadows in the state of Minas Gerais (Van Sluys *et al*., 2004). Ants, insect larvae, termites and beetles were the most frequent items in the diet of both species. In relation to behavior, the only study addressing foraging was carried out in the Amazon region of Brazil for *T. hispidus* (Vitt *et al*., 1996). In addition, the role of *T. semitaeniatus* as a seed disperser (Ribeiro *et al*., 2008), drinking and thermoregulatory behaviors (Ribeiro & Freire, 2009a; Ribeiro & Freire, 2010), as well as the reproductive cycle of this species (Ribeiro *et al*., 2010) were described in the caatinga.

Given that tropidurid lizards are traditionally considered sit-and-wait foragers (Schoener, 1971; Rocha, 1994), our initial prediction was that *T. hispidus* and *T. semitaeniatus* would have generalized diets, and that preys would be captured according to their availability in the environment. Furthermore, we expected little variation between the foraging behaviors of these species. In this study, we analyse the diet composition and foraging behavior of *T. hispidus* and *T. semitaeniatus* in an area of the Caatinga Biome in northeast Brazil.

MATERIAL AND METHODS

Study area. The study was conducted at the Seridó Ecological Station (ESEC Seridó, 06°34'36.2"S, 37°15'20.7"W, datum: WGS84; altitude: 192 m), which encompasses a Caatinga area of 1,166.38 hectares located in the municipality of Serra Negra do Norte, Rio Grande do Norte, Brazil. The climate is semiarid (Ab'Sáber, 1974), with a short wet season between March and May and rainfall ranging between 500 and 700 mm/year. Mean annual temperatures vary from 28ºC to 30ºC, but can exceed 40ºC; the minimum ranges between 17ºC and 20ºC. Relative air humidity oscillates around 30-50% in the dry season, but reaches 80-90% in the wet season (Nimer, 1972). The vegetation of the study area is arboreal-bushy hyperxerophilous (Varela-Freire, 2002). Amidst this vegetation, various rocky extrusions are found that remain covered by the vegetation during the wet season, resulting in partially shaded areas. During the dry season these rocky outcrops become exposed after leaf fall (Velloso *et al*., 2002).

Trophic ecology. Fieldwork was conducted on monthly excursions, each lasting three consecutive days, from October 2007 to May 2008. The dry season was from October 2007 through January 2008, and the wet season lasted from February to May 2008. Although the wet season is concentrated between March and May, rainfall is irregular in the semiarid region. Indeed, February 2008 was considered rainy at ESEC Seridó due to recorded rainfall of about 90 mm. Mean monthly rainfall during the study period was 8.0 mm for the dry season and 236.7 mm for the wet season.

Lizards were captured on five rocky outcrops between 07:00 and 18:00 h, using air rifles. At the end of each collection day, the animals were dissected for stomach removal and these were stored in 70% alcohol for subsequent analysis. Animal items were identified to order level, except for hymenopterans, for which the family Formicidae was identified. For Coleoptera and Lepidoptera, the development stage of the individual (larva or adult) was also considered. Arthropod fragments were categorized as arthropod remains. Plant items were classified into the following categories: leaves, flowers and seeds; those that could not be identified, were categorized as nonidentified.

Monthly samplings of arthropods were conducted at the same time as lizard collections, to determine their availability (possible food item; Strüsmann *et al*., 1984; Vrcibradic & Rocha, 1995; Rocha & Anjos, 2007). Thirty traps consisting of plastic trays (50.0 x 25.0 x 5.5 cm) containing water and soap were used. They were placed 2 m apart, covering the rocky surface and leaf litter around the rocky outcrops that make up the study area. The trap system in the leaf litter was set up, buried in the soil, analogous to pitfall traps. Trays were exposed from 07:00 to 17:00 h and the arthropods that fell into the traps were collected. Ten traps consisting of cardboard boxes (5.0 x 5.0 x 5.5 cm) containing canned sardines in oil were also used daily during one hour of exposure for ant collection. All arthropods found in the traps were fixed in 70% alcohol for later identification.

The following measurements were taken for all lizards collected using a manual caliper (to the nearest 0.1 mm): snout-vent length (SVL); head length (HL); jaw length (JL) and head width (HW). Classification of *T. semitaeniatus* individuals into adult and juvenile categories considered females with SVL ≥ 58 mm and males with SVL ≥ 64 mm (Vitt, 1995). For *T. hispidus*, size ranges were defined according to Ribeiro & Freire (2009b), adult females had SVL ≥ 65 mm and adult males had SVL ≥ 68 mm. All lizards were deposited in the Herpetological Collection of the Departamento de Botânica, Ecologia e Zoologia (CHBEZ), Universidade Federal do Rio Grande do Norte.

The frequency of occurrence (number of lizards) and the number and volume of prey were estimated for each prey type. The volume of prey was estimated using the ellipsoid formula (*e.g.*, Vitt *et al*., 1996): $V = 4/3\pi (length/2) \times (width/2)^2$. The index of relative importance (I) was calculated for each food category, adding occurrence, numerical and volumetric percentages and dividing by three (Mesquita *et al*., 2006).

The overlap in the number of food items in the diets of *T. hispidus* and *T. semitaeniatus* was determined using Pianka's Symmetric Overlap Index (O_{jk}) (Pianka, 1973). Values approaching zero indicate no similarity in diets, whereas values near one indicate diet overlap. Niche overlap was calculated using Ecological Methodology software (Kenney & Krebs, 2000).

A t-test was used to evaluate intra and interspecific differences in SVL of males and females. Differences in the mean number and volume of food items found in the stomachs of *T. hispidus* and *T. semitaeniatus* in each season, and in the diets of each species between seasons, were evaluated using the Mann-Whitney U test (Zar, 1999). It was also applied to ascertain whether the mean size of food items ingested by *T. hispidus* and *T. semitaeniatus* differed in general, as well as in each season and between sexes of each species. The same test was applied to assess intraspecific differences between seasons for food item size. In order to analyze the effect of body size on prey size, we tested the relationship between jaw width and mean length of the five largest food items found in each stomach, using Linear Regression Analysis (Zar, 1999).

The diets of the *Tropidurus* species were compared with arthropod availability in the environment, by number of prey, using Spearman's correlation (Zar, 1999). Nonidentified arthropod and plant parts were not considered in the statistical tests and when calculating item sizes. Statistical analyses were conducted using SPSS 13.0 and the significance level adopted was 0.05.

Foraging behavior. For behavioral observations, five rocky outcrops surrounded by vegetation and distant 500 m from the lizard collection area were established. Observations were made from October to December 2006 (dry season 2006; mean monthly rainfall: 1.6 mm), October to December 2007 (dry season 2007; mean monthly rainfall: 1.2 mm) as part of the dry season, with the wet season represented between April and June 2007 (wet season 2007; mean monthly rainfall: 68.7 mm) and April and June 2008 (wet season 2008; mean monthly rainfall: 141.7 mm).

Foraging intensity is a measure of predator activity when hunting and capturing prey (Rocha *et al*., 2000). Behavioral data were collected on three consecutive days, from 07:00 to 10:00 h and from 14:00 to 17:00 h, divided into 6 one-hour intervals to obtain a homogeneous sample. These time intervals were selected based on periods of the highest lizard activity (Vitt, 1995). During these intervals, 10-min focal sampling sessions were carried out (Altmann, 1974), alternating the species observed whenever possible, using a voice recorder and digital watch. As each animal was observed only once, at 10-minute intervals, each observation was independent of the others. Observation was initiated 5 minutes after the lizard was sighted to minimize observer interference. Because foraging intensity is expressed mainly in terms of movement, we have applied the following indices to assess the foraging intensity of *T. hispidus* and *T. semitaeniatus*: number of moves (NM), time spent stationary (TS, in seconds), distance travelled (DT, in cm; linear distance between the initial location of the lizard to the most distant point reached, using a tape measure) and number of attacks on prey items (NAP). We also discussed the foraging site characteristics and hunting strategies of both lizard species during the dry and wet seasons.

The foraging indices (NM, TS, DT, NAP) were estimated for each lizard using the arithmetic mean by species and season, following methodology adapted from Strüssman *et al*. (1984), Magnusson *et al*. (1985) and Gasnier *et al*. (1994). The Mann-Whitney U test (Zar, 1999) was used to evaluate whether foraging differed between *T. hispidus* and *T. semitaeniatus*. Descriptive statistics are represented in the text as mean ± 1 standard error.

RESULTS

Trophic ecology. Thirty seven specimens of *T. hispidus* were collected: 36 adults (24 females and 12 males) and one juvenile female. Adult males were significantly larger (mean SVL = 116.3 ± 15.0 mm) than adult females (92.8 ± 12.0 mm; t_{34} = -5.120, P = 0.0001). For *T. semitaeniatus*, 50 specimens were collected: 45 adults (24 females and 21 males) and five juveniles (two females and three males). Adult males were significantly larger (mean SVL = 77.6 ± 5.0 mm) than adult females (66.0 ± 2.3 mm; t_{43} = -10.358, P = 0.0001). Male and female *T. hispidus* were significantly larger than the respective adult *T. semitaeniatus* (males: t_{31} = -8.651, P = 0.0001; females: t_{46} = -10.854, P = 0.0001).

The most important animal food items for *T. hispidus* (Tab. I) during the dry season were ants (45.5%) and isopterans (26.4%). Leaves were the plant items with the highest index of importance (12.4%). In the wet season, the most important prey items were ants (48.1%) and lepidopteran larvae (37.8%), whereas leaves were the most important plant items (32.3%). One adult female *T. hispidus* consumed an adult of the hylid frog *Scinax x-signatus* (Spix, 1824) during the wet season. For *T. semitaeniatus* (Tab. II), in the dry season, the most important food items were isopterans (30.3%) and ants (28.2%); in the wet season, ants (46.1%) and lepidopteran larvae (38.0%). Leaves were the most important plant items in both seasons (Tab. II).

The diets of both lizard species overlapped considerably, especially during the dry season (dry season: O_{jk} = 0.91; wet season: O_{jk} = 0.76). During the dry season, the diets of *T. hispidus* and *T. semitaeniatus* did not differ in number (Mann-Whitney U test, z = -1.811, P = 0.074) nor volume of the items consumed (Mann-Whitney U test, z = -1.953, P = 0.052). The number of items consumed by both species was also not different during the wet season (Mann-Whitney U test, z = -1.585, P = 0.113). However, *T. hispidus* ingested a larger volume of items (Mann-Whitney U test, z = -4.082, P = 0.0001).

The diet of *T. hispidus* did not differ significantly in number of items (Mann-Whitney U test, z = -0.732, P = 0.479) between the dry and wet seasons, whereas the mean volume of items ingested was significantly higher during the wet season (Mann-Whitney U test, z = -3.181, P = 0.001). The same occurred for *T. semitaeniatus* in the number of items (Mann-Whitney U test, z = -1.735, P = 0.083) and in mean volume (Mann-Whitney U test, z = -3.822, P = 0.0001) between the dry and wet seasons.

In total, 6,049 arthropod specimens were collected during sampling prey availability in the environment, with 21 prey categories recognized (Figs. 1, 2). There was no significant correlation between the diet composition of *T. hispidus* and food availability (number of items) in the dry season (r_s = 0.339, P = 0.133). During the dry months some arthropod recorded in the environment (*e.g.*, Araneae and Embioptera) were absent in the stomach contents of *T. hispidus*. However, in the wet season this correlation was significant (r_s = 0.032, P = 0.035). For *T. semitaeniatus*, there was a significant correlation between diet composition and prey availability, in both the dry (r_s = 0.473, P = 0.017), and wet seasons (r_s = 0.546, P = 0.005).

The linear regression analysis indicated no relationship between jaw width and prey size for *T. hispidus* (R = 0.198, $F_{1,36}$ = 1.434, P = 0.239). However,

Tab. I. Frequency of occurrence (F), number (#), volume (mm^3) and index of importance (I) of prey types in the diet of *Tropidurus hispidus*, during the dry (October 2007 through January 2008) and wet (from February to May 2008) seasons in ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil (dry, n = 19; wet, n = 18).

Prey types	F (%)		# (%)		Volume (%)		I	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Araneae	—	3 (16.7)	—	3 (0.3)	—	1510.8 (2.6)	—	6.5
Blattaria	—	2 (11.1)	—	2 (0.2)	—	168.5 (0.3)	—	3.8
Coleoptera	3 (15.7)	11 (61.1)	5 (0.5)	26 (2.8)	443.8 (4.2)	3059.7 (5.4)	6.8	23.1
Diplopoda	—	3 (16.6)	—	5 (0.5)	—	395.7 (0.7)	—	6.0
Embioptera	—	1 (5.6)	—	1 (0.1)	—	3.7 (~0)	—	2.0
Gastropoda	—	2 (11.1)	—	3 (0.3)	—	158.5 (0.3)	—	4.0
Hemiptera	1 (5.2)	—	1 (0.1)	—	1329.8 (12.5)	—	6.0	—
Hymenoptera								
Formicidae	11 (58.0)	18 (100.0)	479 (53.0)	312 (33.5)	2753.0 (26.0)	6175.1 (11.0)	45.6	48.1
Non ants	1 (5.2)	6 (33.4)	1 (0.1)	10 (1.0)	33.0 (0.3)	965.8 (1.7)	1.8	12.0
Isoptera	5 (26.3)	5 (27.8)	396 (43.8)	393 (42.2)	979.4 (9.2)	1362.0 (2.4)	26.4	24.1
Larvae								
Coleoptera	—	2 (11.1)	—	2 (0.2)	—	119.0 (0.2)	—	3.8
Lepidoptera	—	17 (94.5)	—	79 (8.4)	—	5838.5 (10.3)	—	37.8
Lepidoptera	—	2 (11.1)	—	9 (1.0)	—	582.0 (1.0)	—	4.4
Orthoptera	—	4 (22.2)	—	4 (0.4)	—	1260.2 (2.2)	—	8.3
Arthropod remains	6 (31.5)	9 (50.0)	—	—	433.6 (4.1)	187.6 (0.3)	—	—
Plants								
Leaves	6 (31.5)	8 (44.4)	21 (2.3)	74 (8.0)	376.3 (3.5)	25008.0 (44.3)	12.4	32.3
Nonidentified	11 (58.0)	9 (50.0)	—	—	4220.4 (40.0)	3094.0 (5.4)	—	—
Seeds	1 (5.2)	2 (11.1)	1 (0.1)	7 (0.7)	6.3 (~0)	250.1 (0.4)	1.7	4.1
Vertebrate								
Anura	—	1 (5.6)	—	1 (0.1)	—	6280.0 (11.1)	—	5.6
Total			904	931	10575.6	56419.2		

Tab. II. Frequency of occurrence (F), number (#), volume (mm^3) and index of importance (I) of prey types in the diet of *Tropidurus semitaeniatus*, during the dry (October 2007 through January 2008) and wet (from February to May 2008) seasons in ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil (dry, n = 25; wet, n = 25).

Prey types	F (%)		# (%)		Volume (%)		I	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Araneae	2 (8.0)	5 (20.0)	2 (0.4)	7 (1.3)	477.2 (15.3)	59.1 (0.2)	8.0	7.2
Blattaria	—	1 (4.0)	—	2 (0.3)	—	18.8 (0.1)	—	1.5
Coleoptera	5 (20.0)	13 (52.0)	5 (1.0)	21 (4.0)	55.1 (1.7)	1265.6 (6.1)	7.6	20.7
Diplopoda	1 (4.0)	2 (8.0)	2 (0.4)	3 (0.5)	39.6 (1.2)	61.2 (0.3)	1.9	3.0
Diptera	—	2 (8.0)	—	3 (0.5)	—	19.6 (0.1)	—	2.8
Embioptera	7 (28.0)	2 (8.0)	21 (4.2)	6 (1.1)	53.3 (1.7)	34.0 (0.1)	11.3	3.1
Shed skin	2 (8.0)	1 (4.0)	4 (0.8)	1 (0.2)	257.0 (8.2)	14.6 (~0)	5.6	1.4
Hemiptera	—	2 (8.0)	—	2 (0.3)	—	14.1 (~0)	—	2.7
Homoptera	—	2 (8.0)	—	7 (1.3)	—	1701.2 (8.2)	—	5.8
Hymenoptera								
Formicidae	11 (44.0)	19 (76.0)	147 (30.0)	288 (55.7)	331.4 (10.6)	1369.0 (6.6)	28.2	46.1
Non ants	5 (20.0)	8 (32.0)	6 (1.2)	12 (2.3)	75.8 (2.4)	533.0 (2.5)	7.8	12.3
Isoptera	3 (12.0)	5 (20.0)	287 (58.4)	57 (11.0)	639.3 (20.5)	206.3 (1.0)	30.3	10.7
Larvae								
Coleoptera	—	4 (16.0)	—	9 (1.7)	—	116.3 (0.5)	—	6.1
Lepidoptera	—	21 (84.0)	—	59 (11.4)	—	3776.5 (18.3)	—	38.0
Lepidoptera	—	3 (12.0)	—	4 (0.7)	—	241.2 (1.1)	—	4.6
Mantodea	—	1 (4.0)	—	1 (0.2)	—	261.6 (1.2)	—	1.8
Orthoptera	—	7 (28.0)	—	12 (2.3)	—	653.3 (3.1)	—	11.1
Arthropod remains	10 (40.0)	12 (48.0)	—	—	208.3 (6.7)	186.0 (1.0)	—	—
Plants								
Leaves	7 (28.0)	3 (12.0)	17 (3.4)	23 (4.4)	539.6 (17.3)	7261.7 (35.2)	16.2	17.2
Nonidentified	11 (44.0)	14 (56.0)	—	—	434.7 (14.0)	2825.6 (13.7)	—	—
Total			491	517	3111.3	20618.7		

for *T. semitaeniatus* this analysis showed significant association ($R = 0.401$; $F_{1,48} = 9.009$, $P = 0.004$).

With respect to mean item size, when comparing only adults, *T. hispidus* consumed larger items (10.6 ± 6.0 mm, n = 36) than *T. semitaeniatus* (6.2 ± 3.2 mm, n = 44; Mann-Whitney U test, z = -3.448, P = 0.001). Furthermore, *T. hispidus* adult males consumed larger items (14.7 ± 5.4 mm, n = 12) than adult males of *T. semitaeniatus* (7.0 ± 4.2

Tab. III. Measures of foraging intensity during ten-minute focal observations of *Tropidurus hispidus* (Th) and *Tropidurus semitaeniatus* (Ts), in the dry (October to December 2006-2007) and wet (April to June 2007-2008) seasons at ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil [NM, number of moves; TS, time spent stationary (seconds); DT, distance travelled (cm); NAP, number of attacks on prey items; n, sample size]. Data are represented as mean ± 1 SE (range) and P values are based on the Mann-Whitney U test. Significant differences are highlighted with an asterisk.

Index	Dry season				Wet season			
	Year	Th	Ts	P	Year	Th	Ts	P
NM	2006	10.1 ± 1.4 (3 – 28)	12.5 ± 1.4 (0 – 41)	0.374	2007	3.0 ± 0.8 (0 – 11)	9.8 ± 1.2 (1 – 38)	0.0001*
	2007	6.2 ± 1.3 (0 – 17)	11.5 ± 1.5 (0 – 27)	0.031*	2008	7.5 ± 1.5 (2 – 17)	15.0 ± 2.1 (3 – 43)	0.009*
TS	2006	585.5 ± 2.9 (541 – 598)	580.0 ± 3.4 (497 – 600)	0.528	2007	596.6 ± 1.0 (585 – 600)	587.0 ± 2.1 (549 – 599)	0.0001*
	2007	591.1 ± 2.1 (573 – 600)	579.3 ± 3.4 (534 – 600)	0.050	2008	587.2 ± 3.0 (570 – 598)	575.1 ± 3.0 (545 – 594)	0.018*
DT	2006	252.5 ± 48.1 (10 – 1000)	212.7 ± 23.9 (0 – 805)	0.792	2007	144.3 ± 45.6 (0 – 620)	185.0 ± 22.1 (12 – 650)	0.082
	2007	154.2 ± 38.4 (0 – 495)	201.2 ± 30.0 (0 – 600)	0.220	2008	263.7 ± 50.0 (50 – 580)	221.0 ± 22.5 (90 – 380)	0.685
NAP	2006	1.8 ± 0.4 (0 – 8)	1.3 ± 0.2 (0 – 6)	0.245	2007	0.3 ± 0.1 (0 – 2)	1.7 ± 0.3 (0 – 9)	0.003*
	2007	0.5 ± 0.2 (0 – 3)	1.0 ± 0.2 (0 – 3)	0.076	2008	1.2 ± 0.6 (0 – 7)	3.0 ± 0.5 (0 – 10)	0.007*
n	2006	22	43		2007	16	41	
	2007	13	24		2008	12	19	

mm, n = 21; Mann-Whitney U test, z = -3.518, P = 0.0001). The same occurred between adult females of *T. hispidus* (8.5 ± 5.1 mm, n = 24) and *T. semitaeniatus* (5.5 ± 1.7 mm, n = 23; Mann-Whitney U test, z = -2.054, P = 0.040).

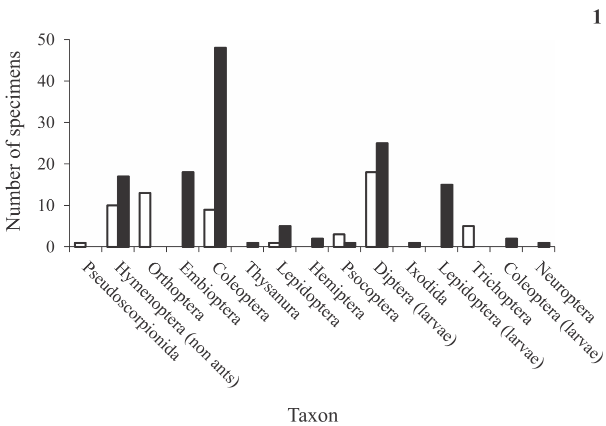
Tropidurus hispidus ingested significantly larger preys during the wet season (12.1 ± 5.4 mm, n = 18) than during the dry season (7.2 ± 5.8 mm, n = 19; Mann-Whitney U test, z = -2.768, P = 0.006). For *T. semitaeniatus*, preys consumed were similar in size (wet season = 7.1 ± 3.3 mm, n = 25; dry season = 4.0 ± 1.6 mm, n = 25; Mann-Whitney U test, z = -3.468, P = 0.001). Finally, food item size was similar between the species during the dry season (Mann-Whitney U test, z = -1.268, P = 0.20) and larger for *T. hispidus* in the wet season (Mann-Whitney U test, *z* = -3.534, P = 0.0001).

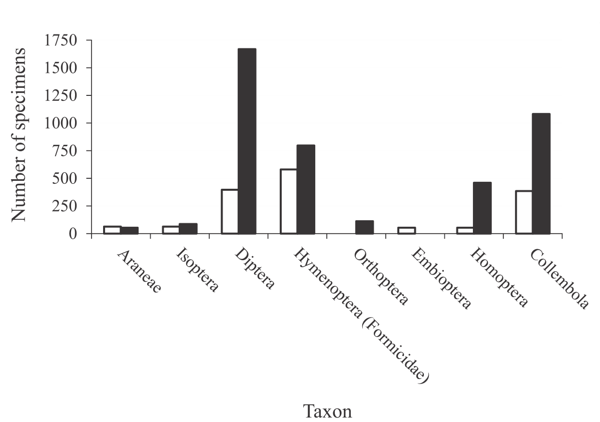
Foraging Behavior. A total of 122 focal observations were carried out for foraging behavior in the dry and wet seasons of 2006-2007: 38 for *T. hispidus* and 84 for *T. semitaeniatus*. In the dry and wet seasons of 2007-2008, there were 68 focal samplings: 25 for *T. hispidus* and 43 for *T. semitaeniatus*. During the dry season, foraging intensity did not differ (P > 0.05) between *T. hispidus* and *T. semitaeniatus*, in either year (Tab. III). The only exception was that the number of moves was greater for *T. semitaeniatus* (Tab. III) in 2007. However, during the wet season only the distance travelled was similar for both species (Tab. III). The number of moves and attacks on prey was significantly (P < 0.05) higher for *T. semitaeniatus*, while time spent stationary was comparatively longer for *T. hispidus* (Tab. III).

DISCUSSION

Tropidurus hispidus and *T. semitaeniatus* are consumers of plant matter and various arthropods, although being predominantly insectivores. This diet composition is similar to that of other Tropidurids (Colli *et al*., 1992; Van Sluys, 1993; Teixeira & Giovanelli, 1999; Fialho *et al*., 2000; Faria & Araújo, 2004; Meira *et al*., 2007). Nevertheless, seasonal variations in diet are expected in species that live in habitats in which local productivity is subject to humidity (Janzen & Schoener, 1968; Ballinger & Ballinger, 1979) and rainfall cycles (Rocha, 1994; Van Sluys, 1995) like the Caatingas (Ab'Sáber, 1974). The diet composition of *T. hispidus* and *T. semitaeniatus* during the dry season, with ants and termites as the most important items, resembled that recorded for the respective species in another caatinga area (Vitt, 1995), and for *T. hispidus* in rocky outcrops in the Amazon region (Vitt *et al*., 1996) and the Atlantic Forest domain (Van Sluys *et al*., 2004).

Sedentary prey items such as termites, unpredictably distributed and grouped in the environment, are considered typical of active foraging lizard diets (Huey & Pianka, 1981; Magnusson *et al*., 1985). However, many lizard species with low movement





Figs. 1, 2. Estimates of arthropod availability in the environment during the dry (white bars) and wet (black bars) seasons at ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil: 1, up to 50 specimens collected; 2, more than 50 specimens collected.

rates also consumed termites in high frequencies (SCHOENER, 1967; VITT & CARVALHO, 1995; VRCIBRADIC & ROCHA, 1998; FIALHO *et al*., 2000). According to TEIXEIRA & GIOVANELLI (1999), the species saves energy by investing in small, numerically abundant prey, such as ants and termites. Furthermore, availability and ease of capture may account for the large amount of these preys in the lizard diet (FLOYD & JENSSEN, 1983). The high proportion of ants in the diet of both *Tropidurus* species seems to be related to their high density in the area and reinforces a well-known pattern of item consumption among tropidurids [e.g. *T. spinulosus* (Cope, 1862): COLLI *et al*., 1992; *T. etheridgei* Cei, 1982: CRUZ *et al*., 1998; *T. itambere* Rodrigues, 1987: FARIA & ARAÚJO, 2004; *T. oreadicus* Rodrigues, 1987: ROCHA & SIQUEIRA, 2008; *T. torquatus* (Wied, 1820): CARVALHO *et al*., 2007]. In addition, the high termite consumption by these lizards, as well as characterizing predation on insects with clumped distribution, also identifies them as important sources of water (NAGY *et al*., 1984).

The significant correlation between the diet composition of the two *Tropidurus* species and arthropod availability indicates that individuals captured prey according to their occurrence in the environment. This was confirmed for other lizard species (VAN SLUYS, 1993; VITT, 1993; ROCHA, 1996; ROCHA & ANJOS, 2007). In contrast to the *T. semitaeniatus*, the absence in the diet of *T. hispidus* of some arthropod taxa recorded in the environment, such as spiders and webspinners (Embioptera), may have favored the non-significance of correlations between prey availability and diet composition of this species during the dry months.

During the wet period, even though ants were predominant in the diet of both lizard species, a considerable volume of lepidopterans, coleopterans and orthopterans was also consumed, characterizing opportunistic predation on arthropods with reproductive cycles concentrated in the rainy months. We can therefore suppose that *T. hispidus* and *T. semitaeniatus* consumed fewer of these prey in the dry season owing to their lower availability in the environment. Our data on arthropod availability in the ESEC Seridó support these predictions, since such preys (e.g. larvae and adult lepidopterans, orthopterans and coleopterans) were significantly represented during the wet season.

Both species consumed a considerable volume of plant material, characterising them as omnivorous species, since more than 10% of plant material was ingested (COOPER & VITT, 2002). In Exu, another area of caatinga in Pernambuco, plant matter constituted nearly 30% by volume of the diet of *T. semitaeniatus* and more than 63% of *T. hispidus* (VITT, 1995). *Tropidurus torquatus* is also known for its consumption of plant matter, mainly fruits (FIALHO *et al*., 2000). The fact that plant parts (leaves, flowers, fruits and seeds) account for a sizable portion of the total volume ingested in the diet of *Tropidurus* species (CARVALHO *et al*., 2007; ROCHA & SIQUEIRA, 2008), suggests that ingestion is not accidental, and that plants are indeed a common food item for these lizards. At ESEC Seridó, in addition to invertebrates and plant material, the stomach contents of an adult female included an adult hylid frog *Scinax x-signatus* (6,280 mm^3 in volume) (RIBEIRO & FREIRE, 2009c). Published diets of *T. hispidus* include small vertebrates, such as frogs (VITT *et al*., 1996) and other lizards (VITT, 1995; COSTA *et al*., 2010) and reinforce the opportunistic habits of these lizards.

Tropidurus hispidus generally feeds on significantly larger prey than *T. semitaeniatus*, which may reflect their difference in body size. The two species represent opposite extremes in body size, *T. semitaeniatus* being one of the smallest species of *Tropidurus*, and *T. hispidus* the largest species of the genus (RODRIGUES, 1987). The difference in body size between the syntopic lizards *T. spinulosus* and *T. oreadicus* in the cerrado characterized the difference between the sizes of their ingested prey (COLLI *et al*., 1992). In contrast, similar sized species *T. itambere* and *T. oreadicus* in another cerrado area in central Brazil ingested similar sized prey (FARIA & ARAÚJO, 2004).

Although in *T. hispidus* significant result was not found in the regression of mean prey size on jaw width, in *T. semitaeniatus* the prey size varied significantly with jaw width. Significant associations between lizard body size, including head measurements, and prey dimensions have been reported in *Tropidurus*, as in *T. hispidus* and *T. montanus* Rodrigues, 1987 (Van Sluys *et al*., 2004), and *T. itambere* and *T. oreadicus* (Van Sluys, 1993; Faria & Araújo, 2004). Conversely, for *T. torquatus* (Carvalho *et al*., 2007) and for another population of *T. oreadicus* (Rocha & Siqueira, 2008) the authors failed to find an effect of lizard size on prey dimensions. Thus, factors other than lizard body size or head measurements may also be important in determining the size of prey consumed by these lizards.

Foraging in *Tropidurus* reflects a history of sit-and-wait foraging involving a set of associated characteristics in the family Tropiduridae and most of the Iguania (Cooper, 1994). In spite of the fact that there is a strong phylogenetic effect on lizards' foraging mode (Cooper, 1995), species can adjust their hunting strategies according to pressures imposed by the environment, such as seasonality (Huey & Pianka, 1981; Rocha, 1994). In this sense, during the dry season, the vegetation of the Caatinga becomes completely dry, reducing foraging sites of *T. hispidus* and *T. semitaeniatus* to rocky formations that serve as observation points (waiting sites), which are visited alternately during displacements. The lizards wait at these sites with their heads pointing downward and quickly jump onto potential preys sighted moving through the leaf litter accumulated in the rock crevices or around the rocks. On the other hand, during the wet season, the Caatinga vegetation is invigorated and produces an abundance of flowers, acting as insect baits for lizards that remain motionless near them. Furthermore, when foraging during the wet season, *T. hispidus*, a habitat generalist, benefits from including the flowers on the trees above the rocky surfaces for foraging. In contrast, *T. semitaeniatus*, typically saxicolous, does not climb to the highest parts of the trees and limits itself to capturing prey items in the flowers of plants at the level of the rock surfaces. *Tropidurus semitaeniatus* also uses rapid movements to attack highly mobile prey such as flies (Muscidae) and leaf hoppers (Cicadellidae) when they land on rocky surfaces. This behavior was not observed for *T. hispidus*. These differences support the idea that foraging intensity may vary between species, even when they exhibit the same foraging mode (Gasnier *et al*., 1994).

Lizards have traditionally been classified into two categories according to foraging mode: active foragers and sit-and-wait foragers (Vitt & Congdon, 1978; Huey & Pianka, 1981). Nevertheless, the generalized diet composition of the two *Tropidurus* species, consisting of low (termites and insect larvae) and high-mobility (ants and orthopterans) prey, the foraging behavior described here and the indices of foraging intensity, such as the low number of movements and short distances traveled (Huey & Pianka, 1981), are consistent with the categorisation of *T. hispidus* and *T. semitaeniatus* as sit-and-wait foragers. This is similar to all other Tropidurids studied (e.g. Rocha & Bergallo, 1990; Vitt, 1991; Colli *et al.*, 1992; Vitt & Carvalho, 1995). Nonetheless, focal observations, especially in the wet season, revealed differences in the foraging intensity between *T. hispidus* and *T. semitaeniatus* for most indices evaluated, indicating that *T. semitaeniatus* is more active than *T. hispidus*. Furthermore, we found a similar mean number of moves and attacks on prey for *T. hispidus* in the caatinga, particularly during the wet season, as was observed in a population of *T. hispidus* studied in the Amazon region (Vitt *et al*., 1996).

We conclude that the feeding behavior and diet composition of *T. hispidus* and *T. semitaeniatus* are affected by the marked rainfall seasonality in the Caatinga. Both species are opportunistic and generalist predators that prey upon arthropods and consume plant material. In summary, the more adverse conditions in the dry season constrain both species to similar hunting strategies, but in the wet season, the different vegetation characteristics and higher food availability result in different hunting strategies.

Acknowledgements. This study was carried out within the Programa de Pós-graduação em Psicobiologia of the Departamento de Fisiologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte. We thank the Programa PELD/CNPq – Caatinga: Estrutura e Funcionamento for logistic support and Hugo W. B. Almeida for field assistance. Carlos F. D. Rocha, Sandra M. Hartz and an anonymous reviewer provided insightful criticisms on the manuscript. L.B. Ribeiro and E.M.X. Freire received research grants from CNPq (141993/2006-5 and 304077/2008-9, respectively), and IBAMA issued the required permit (Permit 206/2006, Process 02001.004294/03-15).

REFERENCES

Ab'Sáber, A. N. 1974. O domínio morfoclimático semiárido das Caatingas brasileiras. **Geomorfologia 43**:1-139.

Altmann, J. 1974. Observational study of behaviour: sampling methods. **Behaviour 49**:227-267.

Ballinger, R. E. & Ballinger, R. A. 1979. Food resource utilization during periods of low and high food availability in *Sceloporus jarrevui* (Sauria: Iguanidae). **Southwestern Naturalist 24**:347-363.

Carvalho, A. L. G.; Silva, H. R.; Araújo, A. F. B.; Alves-Silva, R. & Silva-Leite, R. R. 2007. Feeding ecology of *Tropidurus torquatus* (Wied) (Squamata, Tropiduridae) in two areas with different degrees of conservation in Marambaia Island, Rio de Janeiro, southeastern, Brazil. **Revista Brasileira de Zoologia 24**(1):222-227.

Colli, G. R.; Araújo, A. F. B.; Silveira, R. & Roma, F. 1992. Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. **Journal of Herpetology 26**(1):66-69.

Cooper Jr., W. E. 1994. Prey chemical discrimination, foraging mode, and phylogeny. *In*: Vitt L. J. & Pianka E. R. eds. **Lizard ecology: historical and experimental perspectives**. New Jersey, Princeton University Press. p. 95-116.

___. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. **Animal Behaviour 50**:973-985.

Cooper Jr., W. E. & Vitt, L. J. 2002. Distribution, extent, and evolution of plant consumption by lizards. **Journal of Zoology 257**:487-517.

Costa, J. C. L.; Manzani, P. R.; Brito, M. P. L. & Maciel A. O. 2010. *Tropidurus hispidus* (Calango). Prey. **Herpetological Review 41**(1):87.

Cruz, F. B.; Silva, S. & Scrocchi, G. J. 1998. Ecology of the lizard *Tropidurus etheridgei* (Squamata: Tropiduridae) from the dry Chaco of Salta, Argentina. **Herpetological Natural History 6**(1):23-31.

Duffield, G. A. & Bull, C. M. 1998. Seasonal and ontogenetic changes in the diet of the Australian skink *Egernia stokesii*. **Herpetologica 54**(3):414-419.

Dunham, A. E. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition. *In*: Huey R. B.; Pianka E. R. & Schoener T. W. eds. **Lizard ecology: studies of a model organism**. Cambridge, Harvard University Press. p. 261-280.

DURTSCHE, R. D. 1995. Foraging ecology of the fringe-toed lizard, *Uma inornata*, during periods of high and low food abundance. **Copeia 1995**(4):915-926.

FARIA, R. G. & ARAÚJO, A. F. B. 2004. Sintopy of two *Tropidurus* lizard species (Squamata: Tropiduridae) in a rocky cerrado habitat in central Brazil. **Brazilian Journal of Biology 64**(4):775-786.

FIALHO, R. F.; ROCHA, C. F. D. & VRCIBRADIC, D. 2000. Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. **Journal of Herpetology 34**(2):325-330.

FLOYD, H. B. & JENSSEN, T. A. 1983. Food habits of the Jamaican lizard *Anolis opalinus:* resource partitioning and seasonal effects examined. **Copeia 1983**(2):319-331.

GASNIER, T. R.; MAGNUSSON, W. E. & LIMA, A. P. 1994. Foraging activity and diet of four sympatric lizard species in a tropical rainforest. **Journal of Herpetology 28**(2):187-192.

HUEY, R. B. & PIANKA, E. R. 1981. Ecological consequences of foraging mode. **Ecology 62**(4):991-999.

JANZEN, D. H. & SCHOENER, T. W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. **Ecology 49**(1):96-110.

KENNEY, A. J. & KREBS, C. J. 2000. **Programs for Ecological Methodology**. Version 5.2. Vancouver, University of British Columbia.

MAGNUSSON, W. E.; PAIVA, L. J.; ROCHA, R. M.; FRANKE, C. R.; KASPER, L. A. & LIMA, A. P. 1985. The correlates of foraging mode in a community of Brazilian lizards. **Herpetologica 41**(3):324-332.

MEIRA, K. T. R.; FARIA, R. G.; SILVA, M. D. M.; MIRANDA, V. T. & ZAHN-SILVA, W. 2007. História natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. **Biota Neotropica 7**(2):155-164.

MESQUITA, D. O.; COLLI, R. C.; FRANÇA, F. G. R. & VITT, L. J. 2006. Ecology of a cerrado lizard assemblage in the Jalapão region of Brazil. **Copeia 2006**(3):460-471.

NAGY, K. A.; HUEY, R. B. & BENNETT, A. F. 1984. Field energetics and foraging modes of Kalahari lacertid lizards. **Ecology 65**:588-596.

NIMER, E. 1972. Climatologia da região Nordeste do Brasil. Introdução à climatologia dinâmica. **Revista Brasileira de Geografia 34**: 3-51.

PIANKA, E. R. 1973. The structure of lizard communities. **Annual Review of Ecology and Systematics 4**:53-74.

RIBEIRO, L. B. & FREIRE, E. M. X. 2009a. *Tropidurus semitaeniatus* (NCN). Drinking behavior. **Herpetological Review 40**(2):228-229.

___. 2009b. *Tropidurus hispidus* (NCN). Minimum size at maturity; Maximum body size. **Herpetological Review 40**(3):350-351.

___. 2009c. *Tropidurus hispidus* (NCN). Frog predation. **Herpetological Review 40**(2):228.

___. 2010. Thermal ecology and thermoregulatory behaviour of *Tropidurus hispidus* and *T. semitaeniatus* in a caatinga area of northeastern Brazil. **Herpetological Journal 20**(3):201-208.

RIBEIRO, L. B.; GOGLIATH, M. & FREIRE, E. M. X. 2008. *Tropidurus semitaeniatus* (Squamata: Tropiduridae) as a seed disperser of the plant *Commiphora leptophloeos* (Burseraceae) in the caatinga of northeastern Brazil. **Cuadernos de Herpetología 22**(2):91-94.

RIBEIRO, L. B.; KOLODIUK, M. F. & FREIRE, E. M. X. 2010. Ventral colored patches in *Tropidurus semitaeniatus* (Squamata, Tropiduridae): sexual dimorphism and association with reproductive cycle. **Journal of Herpetology 44**(1):177-182.

ROCHA, C. F. D. 1994. Introdução à ecologia de lagartos brasileiros. *In*: NASCIMENTO L. B.; BERNARDES A. T. & COTTA G. A. eds. **Herpetologia no Brasil I**. Minas Gerais, PUC/MG, Fundação Biodiversitas e Fundação Ezequiel Dias, MG, Brasil. p. 39-57.

___. 1996. Seasonal shift in lizard diet: the seasonality in food resources affecting the diet of *Liolaemus lutzae* (Tropiduridae). **Ciência e Cultura 48**(4):264-269.

ROCHA, C. F. D. & ANJOS, L. A. 2007. Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. **Brazilian Journal of Biology 67**(3):485-491.

ROCHA, C. F. D. & BERGALLO, H. G. 1990. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. **Ethology Ecology & Evolution 2**(3):263-268.

ROCHA, C. F. D. & SIQUEIRA, C. C. 2008. Feeding ecology of the lizard *Tropidurus oreadicus* Rodrigues 1987 (Tropiduridae) at Serra dos Carajás, Pará state, northern Brazil. **Brazilian Journal of Biology 68**(1):109-113.

ROCHA, C. F. D.; VRCIBRADIC, D. & ARAÚJO, A. F. B. 2000. Ecofisiologia de répteis de restingas brasileiras. *In*: ESTEVES, F. A. & LACERDA, L. D. eds. **Ecologia de restingas e lagoas costeiras**. Rio de Janeiro, Núcleo de Pesquisas Ecológicas de Macaé e Universidade Federal do Rio de Janeiro, RJ, Brasil. p. 117-149

RODRIGUES, M. T. 1987. Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao Sul do Rio Amazonas (Sauria, Iguanidae). **Arquivos de Zoologia do Estado de São Paulo 31**(3):105-230.

SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. **Science 155**:474-477.

___. 1971. Theory of feeding strategies. **Annual Review of Ecology and Systematics 2**:369-404.

SOUSA, B. M. & CRUZ, C. A. G. 2008. Hábitos alimentares de *Enyalius perditus* (Squamata, Leiosauridae) no Parque Estadual do Ibitipoca, Minas Gerais, Brasil. **Iheringia**, Série Zoologia **98**(2):260-265.

STAMPS, J. A.; TANAKA, S. & KRISHNAN, V. V. 1981. The relationship between selectivity and food abundance in a juvenile lizard. **Ecology 62**(4):1079-1092.

STRÜSMANN, C.; VALE, M. B. R.; MENEGHINI, M. H. & MAGNUSSON, W. E. 1984. Diet and foraging mode of *Bufo marinus* and *Leptodactylus ocellatus*. **Journal of Herpetology 18**(2):138-146.

TEIXEIRA, R. L. & GIOVANELLI, M. 1999. Ecologia de *Tropidurus torquatus* (Sauria: Tropiduridae) da restinga de Guriri, São Mateus, ES. **Revista Brasileira de Biologia 59**(1):11-18.

VAN SLUYS, M. 1993. Food habits of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. **Journal of Herpetology 27**(3):347-351.

VAN SLUYS, M. 1995. Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. **Ciência e Cultura 47**(1/2):61-65.

VAN SLUYS, M.; ROCHA, C. F. D.; VRCIBRADIC, D.; GALDINO, C. A. B. & FONTES, A. F. 2004. Diet, activity and microhabitat use of two syntopic *Tropidurus* species (Lacertilia: Tropiduridae) in Minas Gerais, Brazil. **Journal of Herpetology 38**(4):606-611.

VARELA-FREIRE, A. A. 2002. **A caatinga hiperxerófila Seridó: a sua caracterização e estratégias para sua conservação**. São Paulo, Academia de Ciências do estado de São Paulo. 39p.

VELLOSO, A. L.; EVERARDO, V. S. B.; SAMPAIO, E. V. S. B. & PAREYN, F. G. 2002. **Ecorregiões propostas para o Bioma Caatinga**. Recife, PNE, TNC. 76 p.

VITT, L. J. 1991. An introduction to the ecology of cerrado lizards. **Journal of Herpetology 25**(1):79-90.

___. 1993. Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. **Canadian Journal of Zoology 71**:2370-2390.

___. 1995. The ecology of tropical lizards in the caatinga of northeast Brazil. **Occasional Papers of the Oklahoma Museum of Natural History 1**:1-29.

VITT, L. J. & CARVALHO, C. M. 1995. Niche partitioning in a tropical wet season: lizards in the Lavrado area of Northern Brazil. **Copeia 1995**(2):305-329.

VITT, L. J. & CONGDON, J. D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. **American Naturalist 112**:595-608.

VITT, L. J. & ZANI, P. A. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. **Canadian Journal of Zoology 74**:1313-1335.

VITT, L. J.; ZANI, P. A. & CALDWELL, J. P. 1996. Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. **Journal of Tropical Ecology 12**(1):81-101.

VRCIBRADIC, D. & ROCHA, C. F. D. 1995. Variação sazonal na dieta de *Mabuya macrorhyncha* (Sauria, Scincidae) na restinga da Barra de Maricá, RJ. **Oecologia Brasiliensis 1**:143-153.

___. 1998. The ecology of the skink *Mabuya frenata* in an area of rock outcrops in Southeastern Brazil. **Journal of Herpetology 32**(2):229-237.

WERNECK, F. P.; COLLI, G. R. & VITT, L. J. 2009. Determinants of assemblage structure in Neotropical dry forest lizards. **Austral Ecology 34**:97-115.

ZAR, J. H. 1999. **Biostatistical analysis**. 4ed. New Jersey, Prentice-Hall. 663p.

Recebido em 2 de setembro, de 2010. Aceito em 15 de setembro de 2011. ISSN 0073-4721
Artigo disponível em: www.scielo.br/isz