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Patterns of space, time and trophic resource use by *Tropidurus hispidus* and *T. semitaeniatus* in an area of Caatinga, northeastern Brazil

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This study examines how two species of diurnal lizards (*Tropidurus semitaeniatus* and *T. hispidus*, Tropiduridae) use spatial, trophic and temporal resources in the Conservation Unit of Monumento Natural Grota do Angico, Poço Redondo, Sergipe (Brazil). Both species were mostly active during sunny days, with a reduction in activity during the hottest hours, and showed a preference for rocks, using rock crevices as main shelter. *Tropidurus hispidus* is the larger species as measured with SVL, and the species did not markedly differ in overall body shape. Both species mostly predated ants, insect larvae and termites. The head morphologies of *T. semitaeniatus* and *T. hispidus* are better adapted for the ingestion of larger and longer prey, respectively. *Tropidurus semitaeniatus* individuals modified their food intake during periods of higher rainfall, possibly to avoid competition with *T. hispidus.* Despite the high overlap in the use of space, time and diet, the coexistence of the two species is facilitated through resources strategies that minimise the negative effects of competition.

Key words: dry forest, ecology, lizards, resource partitioning, sympatry

INTRODUCTION

Organisms coexist by sharing available resources (Toft, 1985), and interspecific competition is one of the main factors responsible for community structure (Milstead, 1965; Janzen & Schoener, 1968; Schoener, 1975; Huey & Pianka, 1977; Ribeiro & Freire, 2009, 2011). Competition can result in competitive exclusion and habitat shifts (Hutchinson, 1957; Schoener, 1975), or may enable co-occurrence through character displacement (Pianka, 1973). Lizards are considered to be excellent models for ecological studies about coexistence (Araújo, 1987; Rodrigues, 1987; Colli et al., 1992; Vitt & Pianka, 1994; Carvalho et al., 2005). The presence of lizards in given environments is strongly connected with the availability of resources such as food, shelter and sites for thermoregulation (Vitt, 1991, 1993; Bergallo & Rocha, 1993). The degree of resource sharing can be quantified using differences in morphology, spatial resources and foraging modes (M'Closkey & Hecnar, 1994; Vitt & Zani, 1998; Faria & Araujo, 2004). Morphology may be linked to structural characteristics of habitats (Ricklefs et al., 1981; Losos, 1990; Colli et al., 1992), and head as well as jaw size are associated to diet preferences (Vitt, 1995; Silva & Araújo, 2008).

Tropidurus hispidus (Spix, 1825) and *T. semitaenitus* (Spix, 1825) are members of the *torquatus* and *semitaeniatus* groups within the family Tropiduridae, respectively (Frost et al., 2001; Bérnils & Costa, 2012). *Tropidurus hispidus* is considered the largest species of the genus, and occupies a wide distribution that extends into the Caatinga area (Rodrigues, 1987); it is a habitat generalist which can often be observed on rocky substrates (Vitt et al., 1996; 1997; VanSluys et al., 2004). *Tropidurus semitaeniatus* is exclusively saxicolous, with a flattened head and body to allow the use of rocky crevices as shelters, and is found throughout the Caatinga of northeastern Brazil (Rodrigues, 2005; Freitas & Silva, 2007; Carvalho et al., 2013). Species of the genus *Tropidurus* are characterised by phylogenetic inertia associated with foraging modes (VanSluys, 1993; Faria & Araújo, 2004; Cooper, 1994; Pianka & Vitt, 2003), which should lead to intense competitive interactions (Webb et al., 2002; Losos, 2008). In this study, we investigated how *T. hispidus* and *T. semitaeniatus* use and share spatial, trophic and temporal resources.

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MATERIALS AND METHODS

The Caatinga has an estimated area of 800,000 km^2 in northeastern Brazil, extending from 2°54’ to 17°21’S (Prado, 2005). Shallow flagstones, crystalline soils and irregular rainfall contribute to xeromorphic vegetation (Chiang & Koutavas, 2004; Krol et al., 2001; Prado, 2005). Annual precipitation ranges from 240–1,500 mm (Sampaio, 1995; Prado, 2005). Despite high annual variation, long periods of drought are common (Nimer, 1972; Reis et al., 2006). Populations of *T. hispidus* and *T. semitaeniatus* were studied in the State Conservation Unit of Monumento Natural Grota do Angico, located in the semi-arid region of Sergipe state (Brazil, 9°41’S and 38°31’W), between the municipalities of Poço Redondo and Canindé de São Francisco (Fig. 1). The Conservation Unit has an area of 2.183 ha and its vegetation is typical of the Caatinga biome. The average annual precipitation is 500 mm and the altitude ranges from 10 to 200 m (Ruiz-Esparza et al., 2011).

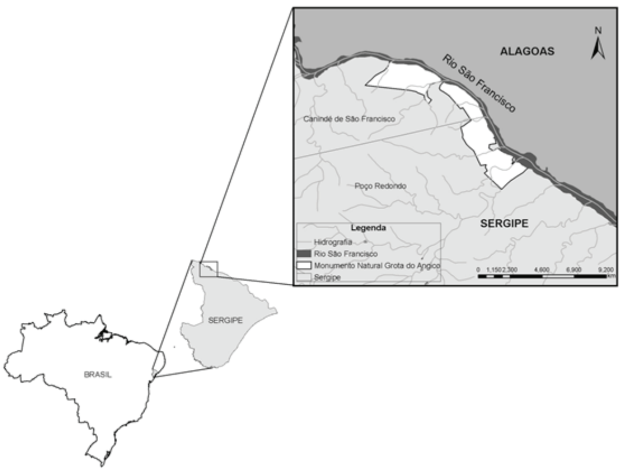

Fig. 1. Location of the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo - SE. (Image: Sidney Feitosa Gouveia)

The study was undertaken between December 2008 and November 2009. Data collections were made on three consecutive days in each month, between 0600 and 1730 hours each day. Three flat areas measuring 450×20 m (2.7 ha) were demarcated with a 50-m tape measure in the bedrocks of dry streams. Active searches were employed to achieve systematic surveys. Lizards were captured with nylon ties attached to fishing rods (2.5 m). Observations were undertaken over one day in each area. For each captured lizard we recorded time of capture, substrate when located (1) and after (2) the approach of the observer (rock, tree, rock crevice, litter, bromeliad, lair, excreta and cactus), activity when located (1) and after (2) the approach of the observer (motionless, walking, running, agonism, foraging, interacted with lace), sun exposure (sun, shadow or mosaic), perch height and weather conditions (sunny, cloudy, drizzle or rainy). We measured snout–vent length (SVL); tail length; body length and width, head length, width and height; and length of both limbs (right side of the body) using a digital caliper with an accuracy of 0.01 mm (Faria & Araújo, 2004). Mass was also recorded using a Pesola® balance (accuracy 0.5 g). Captured lizards were marked with Corrector water-based white colour to prevent recapture. After measurements animals were released at the site of capture.

Five specimens of each species per month were sacrificed using a lidocaine solution for diet analysis. Specimens were fixed in 10% formalin and preserved in 70% ethanol, and deposited in the Coleção Herpetológica da Universidade Federal de Sergipe (CHUFS). Ingested items were identified to the lowest possible taxonomic level. Whole specimens were counted and their length and width was measured with a digital caliper (accuracy: 0.01 mm). Prey volume was estimated using the formula for an ellipsoid (volume=(π*length*width²)/6, Magnusson et al., 2003), or through measurement in a water column using a graduated cylinder (plant material). Prey availability was estimated using monthly collections. Fifteen pitfall traps (250 ml plastic pots) were placed in each area at a minimum distance of 5 m from each other for three consecutive days. Each trap contained a solution of water, salt and detergent for conserving invertebrates until they were transferred to 70% ethanol.

The data were analysed using Systat v.12.0 and BioEstat v.5.0 for Windows. A 5% significance level was applied. Normality of the samples was tested using a Shapiro–Wilk’s test in order to determine whether parametric or nonparametric analysis should be used. Before analysis, all morphometric variables were $\log_{10}$-transformed in order to convert the sample to a normal distribution and reduce scale effects. For animals with broken or regenerated tails, the original length was estimated using a regression model (SVLxtail length, Faria & Araújo, 2004). Body size was defined as an isometric variable following the protocol of Somers (1986), by which the scores of an isometric vector initially set at p<0.5 were obtained by multiplication of the matrix n x p of the $\log_{10}$-transformed data, where n is the number of observations and p the isometric eigenvector (Jolicoeur, 1963; Somers, 1986). The residuals of the regressions of each $\log_{10}$-transformed variable with body size was used. A principal component analysis (PCA) of size-adjusted morphological variables served to examine possible differences in morphology between species. To test if the differences in form between the species were significant, we undertook a multivariate analysis of variance (MANOVA) on the first five factors of the PCA. The body size and mass of the two species were also compared by variance analysis (ANOVA).

The numerical and volumetric compositions of the prey categories consumed by the two species were compared using a Kolmogorov–Smirnov test on a monthly basis. The widths of food niches (number and volume of prey), spatial niches (substrates and perch height) and temporal niches (time of activity: period in which the animal remains exposed) were calculated using the inverse of Simpson’s (1949) diversity index:

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where *p* is the proportion of resource category (trophic, spatial or temporal) used, and n is the number of resource categories adopted. *B* ranges between 1 (exclusive use of a resource type) and 0 (homogeneous use of all types of resources). The estimated availability (total and monthly) of food resources was also measured using this method.

The overlap between the food, spatial and temporal niches were calculated using the formula for symmetrical overlap (Pianka, 1973):

$$\phi_{jk} = \frac{\sum_{n=1} p_j \, p_k}{\sqrt{\sum_{i=1}^{n} p_j^{\,2} \sum_{i=1}^{n} p_k^{\,2}}}$$

where *j* and *k* represent different species. Values close to zero indicate no similarity in resource use, and values close to one indicate the similar use of such resources. This index was also adopted to compare prey categories ingested with those available in the environments. A canonical correlation between two set of variables (maximum length and maximum width of prey versus length, width and height of the head) was used to investigate the relationship between the prey dimensions and head measurements.

RESULTS

In total, 1,760 observations were made (422 for *T. hispidus* and 1,338 for *T. semitaeniatus*). Morphometric and diet analyses were performed using a total of 102 specimens, comprising 51 *T. hispidus* (9 males, 9 females and 33 young) and 51 *T. semitaeniatus* (12 males, 9 females and 30 young).

No significant differences were observed between both species with respect to substrate use (G=9.3421; g.l.=7; p=0.229; $n_{T.\ hispidus}$=421; $n_{T.\ semitaeniatus}$=1,333). In total, 83.13% and 93.17% of *T. hispidus* and *T. semitaeniatus* were found on rocks (Fig. 2A), and niche space width (*B*) was 1.42 and 1.15, respectively. Overlap in use of microhabitats was high (φ_{jk}=0.99). The average perch height was 63.22±66.07 cm (n=300) for *T. hispidus* and 56.36±51.30 cm (n=912) for *T. semitaeniatus* (including animals found on the ground, Fig. 2B), without significant differences (Mann–Whitney, U=42.50; p=0.5708; n=1,212). Niche widths (*B*) of perch height were 2.89 for *T. hispidus* and 2.73 for *T. semitaeniatus*, with a high overlap between species (φ_{jk}=0.99).

Both *T. hispidus* (78.67%) and *T. semitaeniatus* (83.03%) preferred sunny days (Fig. 2C) without differences between them (G=1.4534; g.l.=3; p=0.6931;

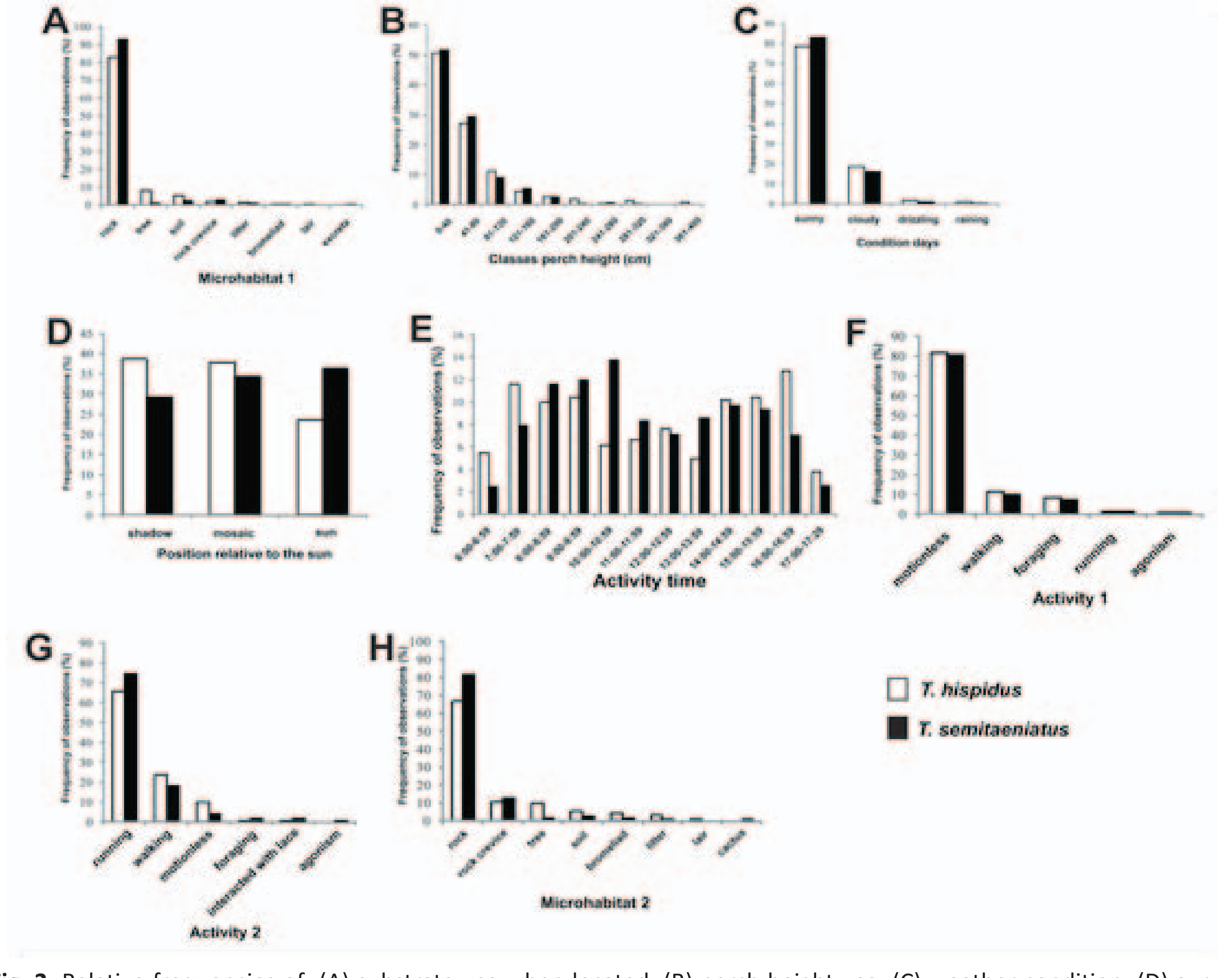

Fig. 2. Relative frequencies of: (A) substrate use when located, (B) perch height use, (C) weather condition, (D) sun exposure, (E) activity levels across the day, (F) behaviour when sighted, (G) behaviour when escaping from the observer, (H) substrate use after the approach of the observer of *T. hispidus* and *T. semitaeniatus* in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo – SE.

Table 1. Descriptive data for morphological characteristics of reproductive individuals of *T. hispidus* and *T. semitaeniatus* in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo - SE. Linear measurements are in millimetres, the weight is in grams and values in parentheses refer to size-adjusted variables.

	Tropidurus semitaeniatus				*Tropidurus hispidus*			
Variables	Females (*n*=9)		Males (*n*=12)		Females (*n*=9)		Males (*n*=9)	
	Average±sd	Min.–Max.	Average±sd	Min.–Max.	Average±sd	Min.–Max.	Average±sd	Min.–Max.
Body size	3.52±0.53	2.68–4.25	6.48±1.34	3.48–8.33	10.50±2.19	7.81–13.58	15.55±6.34	2.09–23.99
Mass	6.99±1.00	5.85–9.00	14.69±3.91	8.00–20.25	23.48±5.53	16.50–31.00	31.22±14.17	14.25–52.00
	(0.052±0.110)	(-0.068–0.242)	(-0.094±0.268)	(-0.846–0.160)	(0.075±0.127)	(-0.085–0.327)	(0.004±0.061)	(-0.100–0.081)
SVL	65.16±3.67	59.69-71.99	79.68±4.56	73.17–87.32	84.05±7.90	74.16-96.11	95.54±13.64	71.19–114.08
	(0.047±0.020)	(0.017–0.073)	(0.073±0.014)	(0.049–0.095)	(0.017±0.015)	(-0.010–0.043)	(-0.028±0.065)	(-0.125–0.110)
Body width	20.25±1.54	17.61–22.37	23.08±4.14	15.23–29.83	25.00±2.06	19.74-28.21	24.82±4.04	16.42–31.06
	(0.097±0.030)	(0.043–0.133)	(0.086±0.061)	(-0.062–0.176)	(0.046±0.039)	(-0.015–0.101)	(-0.062±0.056)	(-0.148–0.032)
Body height	7.45±1.11	5.36–9.10	8.48±1.09	6.64–9.93	14.07±1.46	11.22–16.39	15.64±4.39	4.39–22.09
	(0.015±0.060)	(-0.100–0.097)	(-0.021±0.054)	(-0.167–0.048)	(0.077±0.055)	(-0.007–0.162)	(-0.055±0.101)	(-0.226–0.073)
Head width	12.03±0.73	11.04–13.50	15.61±1.72	11.25–18.00	17.19±1.71	15.21–19.74	19.93±3.95	11.62–23.99
	(0.011±0.020)	(-0.017–0.049)	(0.057±0.037)	(-0.020–0.102)	(0.016±0.020)	(-0.018–0.049)	(-0.032±0.047)	(-0.109–0.045)
Head length	17.16±1.64	12.57–18.84	21.44±1.81	17.24–24.80	23.64±2.39	20.85–26.86	32.61±18.45	16.81–91.82
	(0.008±0.044)	(-0.112–0.043)	(0.044±0.019)	(0.014–0.079)	(0.002±0.013)	(-0.017–0.033)	(-0.001±0.177)	(-0.153–0.562)
Head height	5.80±0.37	4.97–6.37	7.17±0.76	5.44–8.40	10.31±1.00	9.23–12.40	12.02±3.30	4.18–17.77
	(-0.026±0.022)	(-0.067–0.002)	(-0.010±0.029)	(-0.069–0.030)	(0.042±0.025)	(0.002–0.076)	(-0.042±0.061)	(-0.127–0.084)
Tail length	98.60 ±6.75	89.72–116.87	131.55±12.51	104.87–149.18	122.44±17.16	88.72–141.31	144.13±19.02	111.62–171.36
	(-0.004±0.028)	(-0.036–0.070)	(0.078±0.042)	(-0.010–0.148)	(-0.111±0.056)	(-0.111–0.056)	(-0.014±0.055)	(-0.082–0.080)
Foreleg length	32.66±1.64	29.99–35.00	39.83±3.039	32.55–44.43	40.41±2.56	36.13–43.83	46.05±7.62	33.27–56.40
	(0.044±0.018)	(0.006–0.063)	(0.073±0.019)	(0.040–0.106)	(0.009±0.023)	(-0.042–0.042)	(-0.029±0.053)	(-0.114–0.074)
Hind limb length	45.25±2.62	40.21–48.89	57.05±3.82	49.61–62.94	57.64±3.65	50.50–62.82	68.15±9.79	50.56–80.72
	(0.022±0.020)	(-0.012–0.043)	(0.066±0.011)	(0.050–0.085)	(0.001±0.023)	(-0.042–0.034)	(-0.018±0.051)	(-0.097–0.090)

Table 2. Descriptive data for morphological characteristics of non-reproductive individuals of *T. hispidus* and *T. semitaeniatus* in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo - SE. Linear measurements are in millimetres, the weight is in grams and values in parentheses refer to size-adjusted variables.

	Tropidurus semitaeniatus				*Tropidurus hispidus*			
Variables	Females (*n*=13)		Males (*n*=17)		Females (*n*=15)		Males (*n*=18)	
	Average±sd	Min.–Max.	Average±sd	Min.–Max.	Average±sd	Min.– Max.	Average±sd	Min.–Max.
Body size	1.00±0.49	0.25–2.01	2.95±1.60	0.75–6.17	3.88±1.78	1.37–6.84	3.95±1.71	1.15–6.44
Mass	1.96±0.88	0.75–3.50	5.62±3.84	1.10–13.00	7.77±3.78	2.00–15.25	8.07±3.38	2.50–12.50
	(-0.009±0.063)	(-0.140–0.072)	(-0.015±0.074)	(-0.159–0.112)	(-0.029±0.111)	(-0.264–0.068)	(0.035±0.040)	(-0.024–0.104)
SVL	44.22±7.82	26.96–56.84	59.65±10.67	41.67–72.76	57.42±10.99	39.91–72.71	57.91±8.72	38.82–69.36
	(-0.094±0.072)	(-0.276–-0.008)	(0.010±0.054)	(-0.098–0.075)	(-0.025±0.061)	(-0.167–0.031)	(-0.020±0.040)	(-0.135–0.022)
Body width	11.72±2.21	6.93–14.68	16.45±3.76	10.87–22.66	15.38±3.30	11.26–21.02	15.44±3.044	10.50–19.44
	(-0.105±0.086)	(-0.306–-0.006)	(0.005±0.073)	(-0.122–0.092)	(-0.041±0.060)	(-0.120–0.045)	(-0.040±0.058)	(-0.143–0.035)
Body height	4.65±1.15	3.37–7.69	6.26±14.80	3.51–8.73	8.89±2.16	5.38–12.30	8.97±2.32	5.57–12.19
	(-0.113±0.089)	(-0.256–0.078)	(-0.053±0.079)	(-0.224–0.046)	(0.071±0.068)	(-0.058–0.143)	(0.072±0.074)	(-0.036–0.173)
Head width	9.07±1.80	6.06–11.94	11.91±2.43	7.62–15.72	12.05±1.71	9.33–14.50	12.28±1.80	9.20–15.14
	(-0.082±0.074)	(-0.221–0.019)	(0.007±0.062)	(-0.134–0.075)	(-0.002±0.031)	(-0.057–0.053)	(0.004±0.034)	(-0.059–0.070)
Head length	12.96±1.89	9.33–15.55	15.94±3.12	9.45–20.22	17.57±2.60	13.14–22.23	17.63±2.46	12.55–21.52
	(-0.070±0.057)	(-0.185–0.010)	(-0.018±0.075)	(-0.248–0.047)	(0.010±0.031)	(-0.062–0.058)	(0.010±0.033)	(-0.075–0.053)
Head height	4.02±0.55	2.99–4.97	5.62±0.98	3.99–7.20	7.44±1.09	5.71–8.73	7.73±1.22	5.69–9.55
	(-0.120±0.054)	(-0.224–-0.049)	(-0.027±0.044)	(-0.112–0.030)	(0.072±0.030)	(0.028–0.132)	(0.086±0.035)	(0.027–0.161)
Tail length	81.15±16.38	53.34–102.45	107.03±20.98	76.87–150.90	97.02±11.84	75.06–112.87	97.32±11.92	69.96–119.44
	(-0.072±0.089)	(-0.231–0.046)	(0.033±0.065)	(-0.073–0.144)	(-0.019±0.043)	(-0.091–0.056)	(-0.018±0.046)	(-0.118–0.058)
Foreleg length	23.24±4.24	13.97–29.37	30.57±5.72	19.46–37.79	29.40±4.77	21.03–35.87	28.47±4.14	19.72–35.55
	(-0.081±0.077)	(-0.270–0.013)	(0.015±0.063)	(-0.135–0.102)	(-0.017±0.047)	(-0.112–0.041)	(-0.031±0.040)	(-0.136–0.026)
Hind limb length	34.37±5.55	22.80–43.44	44.36±7.55	31.15–53.59	43.45±5.95	32.67–50.38	43.08±6.35	31.08–52.01
	(-0.075±0.064)	(-0.224–-0.008)	(0.012±0.055)	(-0.097–0.077)	(-0.011±0.039)	(-0.087–0.024)	(-0.016±0.043)	(-0.105–0.040)

Both *T. hispidus* (78.67%) and *T. semitaeniatus* (83.03%) preferred sunny days (Fig. 2C) without differences between them (G=1.4534; g.l.=3; p=0.6931; $n_{T.\ hispidus}$=422 and $n_{T.\ semitaeniatus}$=1,338). *Tropidurus hispidus* was most often observed in shaded (38.71%) and mosaic sites (37.76%), whereas *T. semitaeniatus* was most often found at sites exposed to the sun (36.38%) followed by mosaic sites (34.43%) (Fig. 2D). The difference between species was significant (T=8.597; df=3.64; p<0.001; $n_{T.\ hispidus}$=421 and $n_{T.\ semitaeniatus}$=1,333).

Tropidurus hispidus and *T. semitaeniatus* showed the same temporal activity patterns (G=8.2992; g.l.=11; p=0.6863; $n_{T.\ hispidus}$=422 and $n_{T.\ semitaeniatus}$=1,356). Both species were bi-modally active. *Tropidurus hispidus* activity was highest between 0800 and 1100 hours, declining at midday and rising again between 1400 and 1600 (Fig. 2E). For *T. semitaeniatus*, the highest peaks occurred between 0700 and 1000 and between 1400 and 1700 (Fig. 2E). The niche widths for activity times were 10.78 and 10.41 for *T. hispidus* and *T. semitaeniatus*

Table 3. Summary of prey availability and diets of *Tropidurus hispidus* and *T. semitaeniatus* in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo - SE. *n* – number of prey; *n*% – percentage of prey; F – frequency of prey; V – volume; V% – percentage of volume.

Taxon	Availability		*Tropidurus semitaeniatus* (*n*=60)						*Tropidurus hispidus* (*n*=60)					
	n	*n*%	F	F%	*n*	*n*%	V (mm³)	V%	F	F%	*n*	*n*%	V (mm³)	V%
Acarina	268	0.74	2	3.33	2	0.14	0.39	0.00	4	6.67	14	0.49	711.76	2.31
Araneae	523	1.45	20	33.33	35	2.36	272.19	2.27	16	26.67	26	0.90	698.93	2.26
Blattaria	272	0.76			1	0.07			5	8.33	5	0.17	98.11	0.32
Chilopoda	8	0.02	1	1.67	1	0.07	12.2	0.10	1	1.67	1	0.03	570.09	1.85
Coleoptera	3497	9.71	19	31.67	32	2.16	131.21	1.09	36	60.00	98	3.41	1488.96	4.82
Dermaptera	3	0.01												
Diplopoda	92	0.26							1	1.67	1	0.03	29.25	0.09
Diplura	1	0.00												
Diptera	5386	14.95	15	25.00	33	2.23	244.58	2.04	10	16.67	12	0.42	100.33	0.33
Embioptera	1	0.00												
Ephemeoptera	6	0.02												
Gastropoda	24	0.07	2	3.33	4	0.27	37.54	0.31	1	1.67	1	0.03	3.47	0.01
Hemiptera	20	0.06							2	3.33	2	0.07	309.19	1.00
Homoptera	56	0.16	2	3.33	5	0.34	17.39	0.14	3	5.00	10	0.35	27.31	0.09
Hymenoptera	24908	69.16	54	90.00	989	66.82	2776.34	23.13	56	93.33	2088	72.65	8675.13	28.11
Isopoda	9	0.02							1	1.67	1	0.03	20.28	0.07
Isoptera	72	0.20	7	11.67	39	2.64	45.05	0.38	8	13.33	412	14.34	1141.57	3.70
Insect larvae	118	0.33	30	50.00	309	20.88	7670.65	63.90	30	50.00	175	6.09	13420.30	43.48
Lepidoptera	693	1.92	15	25.00	21	1.42	325.76	2.71	15	25.00	22	0.77	395.60	1.28
Mantodea	1	<0.01												
Organic material			5	8.33			0.55	0.0046	17	28.33			1730	5.60
Mecoptera	1	<0.01												
Neuroptera	6	0.02												
Odonata	3	0.01												
Opilionidae	13	0.04												
Orthoptera			4	6.67	4	0.27	453.71	3.78	4	6.67	4	0.14	1443.51	4.68
Protura	2	0.01				0.00								
Pseudoscorpionida	14	0.04	2	3.33	4	0.27	4.61	0.04	1	1.67	2	0.07	1.87	0.01
Pscoptera	1	<0.01				0.00								
Scorpionida	12	0.03	1	1.67	1	0.07	12.99	0.11						
Siphonoptera	1	<0.01												
Strepsitera	1	<0.01												
Thrichoptera	1	<0.01												
Thysanura	2	0.01												
TOTAL	36015	100			1480	100	12005.16	100			2874	100	30865.66	100
B					2.02		2.96				2.06		2.26	

respectively, with a high overlap of these schedules (φ_{jk}=0.92).

The two species were indiscernible with regard to activity when sighted (*G*=0.4808; g.l.=4; *p*=0.9753; $n_{T.\ hispidus}$=461 and $n_{T.\ semitaeniatus}$=1,338). A standing position dominated for both *T. hispidus* (81.78%) and *T. semitaeniatus* (80.79%) (Fig. 2F). Running for shelter was the main activity after having been encountered for both species (*Tropidurus hispidus*: 65.80%, *T. semitaeniatus*: 74.27%) (Fig. 2G), without statistical differences (*G*=7.2499; g.l.=6; *p*=0.2984; $n_{T.\ hispidus}$=421 and $n_{T.\ semitaeniatus}$=1,337). Similar shelters were chosen by the two species (*G*=13.3158; g.l.=7; *p*=0.0648; $n_{T.\ hispidus}$=421 and $n_{T.\ semitaeniatus}$=1,331). Rocks were used most frequently (*T. hispidus* 66.74% and *T. semitaeniatus* 81.36%), followed by crevices (*T. hispidus* 10.69% and *T. semitaeniatus* 12.54%) (Fig. 2H). Niche width for shelters use was 2.11 and 1.47 for *T. hispidus* and *T. semitaeniatus*, respectively, with a high overlap (φ_{jk} = 0.99).

Adult *T. hispidus* were larger than *T. semitaeniatus* (ANOVA, $F_{1,36}$=42.119; *p*<0.001; *n*=382, Table 1). Average SVL of *T. hispidus* was 92.68±13.58 mm for adults and 63.91±14.13 mm for juveniles; average SVL of *T. semitaeniatus* adults and young was 73.66±9.04 mm and 55.55±13.03 mm, respectively. The size-adjusted masses (adults) were similar between the species (ANOVA, $F_{1,28}$=1.283; *p*=0.267; *n*=30; Table 1). Adults and young of *T. hispidus* had masses of 32.08±11.51 g and 10.95±6.46 g; *T. semitaeniatus* weighed 12.19±5.06 g and 5.07±3.81 g, respectively (Tables 1 and 2).

The first and second principal components of a PCA together explained 70% of the variation in morphology of the two species. The first principal component was related to SVL, anterior and posterior limb length, and head width. The two species did not significantly differ in shape (MANOVA, Wilk's Lambda=0.893; *p*=0.566), although *T. hispidus* is slightly larger than *T. semitaeniatus*, with a larger and higher head, longer limbs and a higher body.

A total of 60 stomachs were analysed for *T. semitaeniatus* and *T. hispidus* each. Eighteen prey categories were used by *T. hispidus* and 15 were used by *T. semitaeniatus*. The most frequent prey categories for *T. hispidus* were Hymenoptera, Coleoptera, insect larvae, Araneae and Lepidoptera. The corresponding groups for *T. semitaeniatus* were Hymenoptera, insect larvae, Araneae, Coleoptera, Diptera and Lepidoptera. The most abundant prey types were Hymenoptera and Isoptera for *T. hispidus*, and Hymenoptera and insect larvae for *T. semitaeniatus*. Highest prey volumes were represented by insect larvae and Hymenoptera for *T. hispidus* and insect larvae and Hymenoptera for *T. semitaeniatus* (Table 3). Formicidae represented 99.95% of the Hymenoptera ingested by the two species (Table 3). Both species also consumed plant material (28% of *T. hispidus* individuals, representing 60% of the volume of food consumed, and 8.33% of *T. semitaeniatus*, representing 0.0046% of food volume.

The trophic niche widths estimated for *T. hispidus* and *T. semitaeniatus* were 2.06 and 2.02 for prey number, and 2.26 and 2.96 for prey volume, respectively. Overlap was higher with regards to prey number (φ_{jk}=0.96, prey volume: φ_{jk}=0.97), but prey number and prey volume were significantly different from each other (prey number: Kolmogorov–Smirnov, D_{max}=0.1584; *p*<0.01; prey volume: Kolmogorov–Smirnov, D_{max}=0.1816; *p*<0.01, Table 3). A total of 36,015 invertebrates, distributed into 33 categories, were used to estimate prey availability in the environment. The distribution of available prey differed from the consumed prey for both species (*T. hispidus*: D_{max}=0.2267; *p*<0.01; *T. semitaeniatus*: D_{max}=0.2294; *p*<0.01).

The mean number of prey categories consumed for each species was seven (*T. semitaeniatus*: 5–11, *T. hispidus*: 4–11). Five categories comprised more than 10% in at least one monthly sample for *T. hispidus* (Hymenoptera, insect larvae, Isoptera, Coleoptera and Lepidoptera), and four of these also comprised more than 10% in at least one monthly sample for *T. semitaeniatus* (all except Lepidoptera). The largest niche widths (*B*) were observed in February (2.54), June (2.48), April (2.45) and May (2.04) for *T. hispidus* and in July (3.10), February (2.89), June (2.84) and May (2.21) for *T. semitaeniatus*. Diet overlap was high (Ø>0.50) in all months except April (0.11) and December (0.20). However, significant differences between the diets were found in December, February, April, May and August (Table 4).

The proportion of items most used in the diets was similar to available prey in January, April, September and October for *T. hispidus* and in December, January, September and October for *T. semitaeniatus* (Table 4). The prey availability occurred between December 2008 and March 2009 and between October and November 2009 (Table 4). The numbers of available prey categories ranged from eight (August) to 19 (February). The highest diversity of available prey was observed in May (3.78) (Table 4).

Focusing on the two most common food items, Hymenoptera were most abundantly available in December 2008 and January 2009 and between September and November 2009 (Table 4). *Tropidurus semitaeniatus* largely consumed Hymenoptera (over 50% of diet) in the months of December 2008, January, March and July to November 2009, whereas insect larvae were more consumed in February, April, May and June. For *T. hispidus,* Hymenoptera comprised >50% of the diet in all month except December and February (Table 4). Insect larvae never exceeded 50% of the number of prey consumed.

A strong relationship was seen when comparing the morphology of the head of each species *Tropidurus* with the dimensions of prey actually consumed by them (Table 5). The first canonical variable for *T. semitaeniatus* showed an inverse relationship in which animals with narrower heads were related to larger prey (Table 5). Already *T. hispidus* for the first canonical variable was significantly positive for the relation between animals with large heads and longer prey (Table 5).

Table 4. Monthly distribution of food availabilty (D) and of the stomach contents of *T. hispidus* (Th) and *T. semitaeniatus* (Ts) in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo - SE (Brazil). The values in parentheses refer to the number of invertebrates per sample.

	December			January			February			March			April			May		
	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D
	(126)	(451)	(4072)	(90)	(505)	(14185)	(73)	(83)	(4308)	(107)	(151)	(3895)	(178)	(45)	(799)	(108)	(267)	(826)
Acarina			1.65		0.59	0.57			0.07			0.03			0.75			0.36
Araneae	1.59	0.44	0.61	2.25	0.20	0.73	1.37	1.20	1.18	3.74	0.63	1.82			6.13	3.70	0.75	
Blattaria		0.44	0.10	1.12	0.20	0.48			0.26			0.10			0.38		0.37	0.12
Chilopoda		0.22				0.01						0.03						0.48
Coleoptera	3.17	0.44	4.47	5.62	0.79	8.51	2.74	3.61	4.74	0.93	1.25	13.76	2.25	24.44	16.02	0.93	4.87	18.52
Dermaptera												0.08						
Diplopoda									0.09						1.38		0.37	7.63
Diplura									0.02									
Diptera	14.29		1.92	2.25	0.59	2.87		4.82	47.47	1.87	1.88	44.72			15.77			37.77
Embioptera															0.13			
Ephemeoptera															0.75			
Gastropoda															1.00			1.09
Hemiptera						0.01			0.02			0.03					0.37	1.21
Homoptera			0.07			0.01					0.63					0.93	0.37	0.73
Hymenoptera	79.37	16.41	90.84	80.90	90.69	86.75	39.73	46.99	38.97	84.11	80.00	28.11	3.37	57.78	52.44	31.48	65.17	28.45
Isopoda			0.22															
Isoptera	0.79	81.82	0.02	1.12	6.34		42.47		0.91	1.87			0.56	2.22	0.63		1.12	0.61
Insect larva	0.79	0.22		3.37		0.01	6.85	40.96	0.42	0.93	9.38	0.36	93.26	4.44	3.75	59.26	25.09	1.94
Lepidoptera				2.25	0.59		2.74	2.41	5.64	6.54	6.25	10.94	0.56	11.11	0.50	1.85	1.12	0.85
Mantodea			0.02															
Mecoptera									0.02									
Neuroptera																		
Odonata									0.05									
Opilionidae												0.03						
Orthoptera				1.12												1.85	0.37	
Protura						0.01			0.02									
Pseudoscorpionida						0.02	4.11								0.25			0.24
Pscóptera			0.02															
Scorpionida			0.05			0.02			0.05						0.13			
Siphonoptera									0.02									
Strepsitera									0.02									
Thrichoptera									0.02									
Thysanura						0.01												
B	1.53	1.43	1.21	1.51	1.21	1.31	2.89	2.54	2.61	1.40	1.53	3.22	1.15	2.45	3.02	2.21	2.04	3.78
	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*
Ts x Disp	0.99	0.10	>0.05	1.00	0.08	>0.05	0.44	0.50	<0.01	0.54	0.54	<0.01	0.10	0.89	<0.01	0.30	0.63	<0.01
Th x Disp	0.20	0.82	<0.01	0.99	0.11	>0.05	0.54	0.44	<0.01	0.54	0.57	<0.01	0.94	0.18	>0.05	0.55	0.61	<0.01
Ts x Th	0.20	0.80	<0.01	0.99	0.09	>0.05	0.59	0.30	<0.01	0.99	0.08	>0.05	0.11	0.78	<0.01	0.75	0.36	<0.01

Table 4. *(Continued)*

	June			July			August			September			October			November		
	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D	Ts	Th	D
	(95)	(120)	(933)	(59)	(156)	(899)	(46)	(63)	(219)	(150)	(170)	(1023)	(240)	(564)	(2424)	(209)	(294)	(2432)
Acarina				1.69		0.11		3.17					0.42	1.60	2.23			2.14
Araneae	4.21	2.44	4.93	6.78		4.45			10.05	2.67	1.76	2.25	1.25	1.24	1.53	3.35	0.34	2.26
Blattaria			0.43		0.64	0.22						0.49			0.17			6.83
Chilopoda			0.11	1.69		0.11												
Coleoptera	4.21	7.32	20.26	3.39	6.41	26.59		4.76	16.89	3.33	12.35	18.18	0.42	1.42	5.90	1.44	4.08	12.05
Dermaptera																		
Diplopoda			1.50															
Diplura																		
Diptera	3.16	0.81	39.01	3.39		13.90	4.35		9.13	0.67	0.59	2.25	0.42		2.39	0.96		3.54
Embioptera																		
Ephemeoptera																		
Gastropoda				5.08					1.37		0.59	0.20			0.04	0.48		0.04
Hemiptera		0.81	0.32			0.11			0.46									0.08
Homoptera		0.81	0.96	3.39	0.64	1.45	4.35	3.17	1.83		2.35	0.29			0.62			0.08
Hymenoptera	42.11	56.10	29.26	52.54	85.26	52.50	65.22	74.60	58.45	90.67	79.41	74.29	96.67	93.79	86.10	90.43	94.90	72.20
Isopoda								1.59										
Isoptera				1.69				11.11		1.33		0.59			0.58			0.08
Insect larva	41.05	28.46	2.36	18.64	7.05	0.22	23.91	1.59		0.67	1.76	0.39		0.71	0.17	3.35	0.68	0.29
Lepidoptera	3.16	2.44	0.21	1.69		0.33	2.17		1.83		0.59	0.39	0.83	0.71				
Mantodea																		
Mecoptera																		
Neuroptera			0.64															
Odonata															0.04			
Opilionidae												0.39			0.12			0.21
Orthoptera	1.05	0.81									0.59			0.18				
Protura																		
Pseudoscorpionida	1.05													0.35	0.08			0.21
Pscóptera																		
Scorpionida										0.67		0.29			0.04			
Siphonoptera																		
Strepsitera																		
Thrichoptera																		
Thysanura																		
B	2.84	2.48	3.54	3.10	1.36	2.72	2.05	1.74	2.57	1.21	1.54	1.71	1.07	1.13	1.34	1.22	1.11	1.84
	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*	Ø	Dmax	*p*
Ts x Disp	0.49	0.56	<0.01	0.85	0.28	<0.01	0.89	0.01	<0.01	0.98	0.17	>0.05	1.00	0.10	>0.05	0.98	0.21	<0.05
Th x Disp	0.56	0.56	<0.01	0.56	0.39	<0.01	0.94	0.30	<0.01	1.00	0.08	>0.05	1.00	0.09	>0.05	0.99	0.23	<0.05
Ts x Th	0.95	0.15	>0.05	0.95	0.18	>0.05	0.93	0.25	<0.01	0.99	0.11	>0.05	1.00	0.02	>0.05	1.00	0.03	>0.05

DISCUSSION

The presence of a species in an environment may be related to specific physiological needs, improved access to food, availability of resources, presence of refuges, morphological adaptations, inter and intraspecific interactions, as well as historical factors (Pianka, 1973; Herfindal et al., 2005; Borger et al., 2006; Silva & Araújo, 2008). The habitat and microhabitat chosen by a species should meet their essential needs to allow viable populations (Silva & Araújo, 2008). In the study area, *T. hispidus* and *T. semitaeniatus* largely were active on rocky substrates. Such sites are able to maximise the uptake of heat necessary for thermoregulation, both through direct exposure and contact with heated surfaces (Rocha & Bergallo, 1990; VanSluys, 1992; Meira et al., 2007).

Tropidurus semitaeniatus is considered to be a saxicolous species, endemic of Caatinga environments, whereas *T. hispidus* occupies a generalist habitat in open formations of various biomes (Rodrigues, 1987). Despite this variation in the use of microhabitats, *T. hispidus* tends towards a saxicolous habit in places where rocks are abundant. Vitt et al. (1997) found that where *T. hispidus* use rocks, individuals displayed greater dorso-ventral flattening than when in habitat areas without rocks. This suggests that the flattening in these individuals could be adaptive to the use of cracks in rock outcrops. In the present study, no differences were established in body shape between the species.

The preference of these species for rocks has been recorded in other localities and environments. *Tropidurus hispidus* uses rocks in Caatinga environments (Vitt, 1981; Dias & Lira-da-Silva, 1998; Kolodiuk et al. 2009), in the Amazonian rainforest (Vitt & Carvalho, 1995; Vitt et al. 1996; Vitt & Zani, 1998), Amazonian savannahs (Mesquita et al., 2006) and fields in Minas Gerais (VanSluys et al., 2004); *T. semitaeniatus* uses rocky substrates in the Caatinga biome (Vitt, 1981; Kolodiuk et al., 2009; Ribeiro & Freire, 2010) and in Agreste, Sergipe (Fernandes & Oliveira, 1997; Ramos & Denisson, 1997). The use of rocks is common to others species of the *semitaeniatus* group (*T. helenae* and *T. pinima*, Rodrigues, 1984; Manzani & Abe, 1990; Rodrigues, 2005), as well as for several species of the *torquatus* group (*T. montanus, T. itambere* and *T. oreadicus,* Rodrigues, 1987; Faria & Araujo, 2004; VanSluys et al., 2004; Meira et al., 2007). Both species adopted vertical positions which were in most cases <40 cm above ground (50.64% and 51.78% of observations for *T. hispidus*: and *T. semitaeniatus*, respectively). Teixeira-Filho et al. (1996) suggest that layers close to the ground are heated up more quickly, with advantages for thermoregulation and a consequently lower risk of predation and more time for other activities such as foraging.

Tropidurus individuals were active throughout the data collection period. Both species are sit-and-wait predators, implying a shorter time searching for prey and more energy invested in prey capture than is the case for more active foragers (Dias & Lira-da-Silva, 1998; Pianka & Vitt, 2003). Similar findings were already obtained for *T. hispidus* (Vitt, 1995; Vitt & Zani, 1998; VanSluys et al., 2004), *T. semitaeniatus* (Vitt, 1995), *T. torquatus* (Bergallo & Rocha, 1993; Teixeira-Filho et al., 1996; Hatano et al., 2001), *T. itambere* (VanSluys, 1992; Faria & Araujo, 2004), *T. montanus* (VanSluys et al., 2004) *and T. oreadicus* (Faria & Araujo, 2004; Meira et al., 2007). The observed bimodal patterns of activity have previously been found by VanSluys (1992) for *T. itambere* and by Vrcibradic & Rocha (1998) for *Mabuya frenata* during the wet season at high temperatures. The Caatinga biome is characterised by particularly hot temperatures (Prado, 2005), explaining the observed bimodal pattern for the present study species.

According to Huey & Slatkin (1976), thermoregulation in diurnal lizards involves a set of behavioural activities and options for microhabitat use. Displacement between environments with a differential exposure to sun will help to achieve the optimum temperature sought (Rocha & Bergallo, 1990; Vitt & Carvalho, 1995; Hatano et al., 2001). We observed a preference for sunny days, and exposure to sun was distributed between categories (sun, mosaic, shadow) for both species, with *T. semitaeniatus* having a preference for sun and *T. hispidus* having a preference for shadow. The difference in exposure adopted by each species may reflect their physiological needs. Vitt (1995) and Ribeiro & Freire (2010) verified that *T. semitaeniatus*

Table 5. Canonical correlation between the measurements of the head and the size of prey of *T. hispidus* and *T. semitaeniatus* in the Conservation Unit of the State Monumento Natural Grota do Angico, Poço Redondo – SE (Brazil).

	Tropidurus semitaeniatus			*Tropidurus hispidus*		
	Canonical coefficients			Canonical coefficients		
Head	1st Canonical Variable		2nd Canonical Variable	1st Canonical Variable		2nd Canonical Variable
Length	1,65		6,45	0,25		1,23
Height	-2,17		-6,86	1,36		0,28
Width	1,51		0,32	-0,64		-1,60
Prey						
Greater Length	0,38		1,39	1,29		-1,64
Greater Width	0,68		-1,27	-0,35		2,06
	Canonical Correlation	c^2	*p*	Canonical Correlation	c^2	*p*
I	0,95	136,34	<0,0001	0,53	14,437	0,0251
II	0,55	18,83	<0,0001	0,14	0,865	0,6488

presents a mean body temperature that is higher than *T. hispidus*. In the study area of the present work, *T. hispidus* may prefer shady places to avoid negative effects of high temperatures (Teixeira-Filho et al., 1996).

Ecological, historical and behavioural factors must be considered when evaluating the reasons why certain species consume particular types of prey (Vitt & Zani, 1998; Pianka & Vitt, 2003), and morphological limitations may further interfere with the type of food consumed (Toft, 1985; Magnusson & Silva, 1993). An opportunistic pattern in food use was observed for both species in this study, given the strong correlation between use and availability. The use of ants is widely observed in the diet of the genus *Tropidurus* and has been reported for several species (*T. hispidus*: Dias & Lira-da-Silva, 1998; *T. torquatus* group: Araújo, 1987; *T. itambere*: VanSluys, 1995; *T. oreadicus* and *T. spinulosos*: Colli et al., 1992; *T. torquatus*: Bergallo & Rocha, 1994; *T. hispidus T. oreadicus*, *T. semitaeniatus*: Vitt, 1993; *T. semitaeniatus* and *T. hispidus*: Ribeiro & Freire, 2011). Ants are abundant in the Caatinga (Santos et al., 1999). Insect larvae were mainly used in the rainy season, probably due to their higher availability during this period.

For lizards, prey composition is largely related to the type of foraging used and the habitat they occupy (Vitt, 1991; Toft, 1985). Diet overlap is common among sympatric species that hunt by stalking, since they have a preference for active prey (Zug et al., 2001; Silva & Araújo, 2008). In periods of higher rainfall both species became more selective, since the number of invertebrates in the environment was larger. *Tropidurus semitaeniatus* changed their diet towards insect larvae, which were not the most abundant prey category; *T. hispidus* continued to consume Hymenoptera as the main item in their diet. Considering the reduction in availability of Hymenoptera during the rainy season, it is likely that individuals of *Tropidurus* species broaden the diversity of food items to meet their daily nutritional needs. The seasonal change in food habits of *T. semitaeniatus* during the rainy season might be due to avoidance of competition during this period. Head morphology is reflected in the consumption of prey of different dimensions, it is expected that animals with larger heads consume larger prey (Pianka, 1969). However, this pattern was not observed for the target species of this study. Since, *T. semitaeniatus* that has a smaller width head was observed consuming relatively larger prey, whereas *T. hispidus* with larger heads prefers more elongated prey. Food availability in the environment probably best explains the observed pattern. Besides invertebrates, large quantities of plant material (flowers, leaves and seeds) were found in stomachs, and *T. hispidus* consumed more plants than *T. semitaeniatus*. Ingestion of plant material in *Tropidurus* and other lizards is relatively common, to provide energy as well as possibly water (Rocha & Bergallo, 1992; VanSluys, 1993; Dias & Lira-da-Silva, 1998). In our study area, the coexistence of *T. hispidus* and *T. semitaeniatus* on rocky outcrops is probably facilitated by small variations in spatial arrangement, the morphology of the trophic apparatus and temporary niche shifts in their diets depending on rather unpredictable rainfall patterns.

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