

Published by the British
Herpetological Society

Partition of trophic niche dimensions of a pair of syntopic lizard species (*Squamata, Tropidurus*)

Thiago Maia-Carneiro, Tatiana Motta-Tavares & Carlos Frederico Duarte Rocha

Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier 524, CEP 20550-013, Rio de Janeiro, Brazil

Here, we investigate influences of body sizes, ontogeny and body temperatures on components of trophic niche dimensions of syntopic *Tropidurus hispidus* and *T. semitaeniatus* lizards in northeastern Brazil. Divergences in body dimensions allowed differential food consumption between the species and within *T. semitaeniatus*, which may decrease overlaps in niche dimensions. Ants, termites, beetles and flowers were important food items for both species, as are typically found in *Tropidurus*. *Tropidurus semitaeniatus* consumed more plant material as lizards grew in body size, suggesting that consuming such food might be nutritionally and energetically advantageous. A relationship between total food volume and body temperature in *T. semitaeniatus* may have been associated with requirements for food acquisition and digestion.

Key words: body size, body temperature, diet, herbivory, niche segregation, ontogeny

INTRODUCTION

Body size is a variable trait among organisms within biological communities and relevant for different aspects of an organism's life (Pianka, 1973; Peters, 1983; Calder, 1996; Brown et al., 2004; Costa et al., 2008; Maia-Carneiro & Rocha, 2013). Differences in body dimensions might contribute to differential utilisation of trophic resources by syntopic species with consequent reduction of overlaps of ecological niche dimensions (Pianka, 1973; Colli et al., 1992; Costa et al., 2008; Ribeiro & Freire, 2011). Lizards of the genus *Tropidurus* typically have omnivorous feeding habits, eating mainly arthropods and plant material (e.g., Fialho et al., 2000; Vitt, 1991, 1995; Colli et al., 1992; Dutra et al., 2011; Siqueira et al., 2011, 2013; Dutra et al., 2013; Ribeiro & Freire, 2011). While juveniles are predominantly carnivores, adults have been reported to consume higher amounts of plant material (Fialho et al., 2000; Siqueira et al., 2011). Body temperature may influence the acquisition and processing of food in lizards (Tracy et al., 2005; Pafilis et al., 2007; Verwaijen & Van Damme, 2007).

Despite a substantial range of body sizes, species of the genus *Tropidurus* tend to consume similar food types, considerably overlapping in trophic niche dimensions (Vitt, 1991, 1993, 1995; Colli et al., 1992; Vitt & Carvalho, 1995; Rocha & Siqueira, 2008; Ribeiro & Freire, 2011; Siqueira et al., 2014). Therefore, although environmental conditions might influence the use of niche dimensions (Melville et al., 2006; Lopez-Darias et al., 2012; Maia-Carneiro et al., 2012; Sinervo et al., 2010), phylogeny

appears to predominate in determining ecological niches (Vitt et al., 1999; Gainsbury & Colli, 2003; Vitt & Pianka, 2005; Mesquita et al., 2006).

Tropidurus hispidus (Squamata, Tropiduridae) (Spix, 1825) is widely distributed across Colombia, Venezuela, French Guiana, Suriname, Guyana and Brazil, inhabiting environments ranging from Amazonian savannah enclaves and the Atlantic rainforest to Cerrado and Caatinga (Rodrigues, 1987, 1988; Avila-Pires, 1995; Carvalho, 2013). *Tropidurus semitaeniatus* (Squamata, Tropiduridae) (Spix, 1825) is a lizard species with a geographic distribution restricted to Brazil, inhabiting rock outcrops in Caatinga and in Cerrado as well as transitional zones towards the Atlantic Forest (Carvalho, 2013). Here, we investigate the trophic niche dimensions of *T. hispidus* and *T. semitaeniatus* lizards in syntopy and examine differences in types, sizes, and amounts of food consumed as influenced by body sizes, ontogeny, and body temperatures.

MATERIALS AND METHODS

Study area

Data collection took place in Igatu, in the municipality of Andaraí, state of Bahia, northeastern Brazil (12°53'S, 41°19'W), in the surroundings the Parque Nacional da Chapada Diamantina. The climate is relatively mild (annual averages below 22°C) in comparison to nearby regions (Rocha et al., 2005). The area was composed predominantly of bare rocky outcrops interspersed with herbaceous and shrub vegetation on sandy substrates.

Correspondence: Thiago Maia-Carneiro (tmaiacarneiro@gmail.com)

Table 1. Diet composition of *Tropidurus hispidus* (*n*=27) and *Tropidurus semitaeniatus* (*n*=38) from rock outcrops in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil, showing number (*n*), volume (V, in mm³), and frequency of occurrence (F) of each food item found within stomachs (percentages in parentheses). * Represents hymenopterans non-Formicidae.

Item	<i>Tropidurus hispidus</i>			<i>Tropidurus semitaeniatus</i>		
	<i>n</i> (%)	V (%)	F (%)	<i>n</i> (%)	V (%)	F (%)
Oligochaeta	–	–	–	1 (0.12)	5.9 (0.05)	1 (2.6)
Amblypygi	–	–	–	1 (0.12)	0.2 (0.002)	1 (2.6)
Araneae	7 (0.58)	3119 (3.34)	4 (14.8)	26 (3.2)	104.8 (0.93)	14 (36.8)
Acari	1 (0.08)	1.8 (0.002)	1 (3.7)	2 (0.25)	0.9 (0.01)	2 (5.3)
Pseudoscorpiones	1 (0.08)	1.3 (0.001)	1 (3.7)	1 (0.12)	4.9 (0.04)	1 (2.6)
Isopoda	1 (0.08)	22.6 (0.02)	1 (3.7)	–	–	–
Odonata	1 (0.08)	103.7 (0.11)	1 (3.7)	–	–	–
Collembola	–	–	–	3 (0.37)	0.3 (0.003)	3 (7.9)
Orthoptera	8 (0.66)	682.3 (0.73)	7 (25.9)	5 (0.62)	169.3 (1.51)	5 (13.2)
Isoptera	494 (40.86)	2241 (2.4)	8 (29.6)	104 (12.79)	238.1 (2.12)	11 (28.9)
Mantodea	1 (0.08)	48.4 (0.05)	1 (3.7)	–	–	–
Blattodea	2 (0.17)	61.4 (0.07)	2 (7.4)	1 (0.12)	16.6 (0.15)	1 (2.6)
Hemiptera	13 (1.08)	1117 (1.2)	11 (40.7)	18 (2.21)	538.7 (4.79)	17 (44.7)
Coleoptera	45 (3.72)	1686 (1.8)	17 (63)	78 (9.59)	562.9 (5.01)	27 (71.1)
Coleoptera (larvae)	1 (0.08)	4.2 (0.004)	1 (3.7)	4 (0.49)	13.9 (0.12)	4 (10.5)
Hymenoptera*	35 (2.9)	2322 (2.48)	14 (51.9)	20 (2.46)	101.9 (0.91)	13 (34.2)
Formicidae	545 (45.08)	4378 (4.68)	27 (100)	515 (63.35)	1123 (9.99)	36 (94.7)
Lepidoptera	5 (0.41)	596.6 (0.64)	5 (18.5)	1 (0.12)	71.8 (0.64)	1 (2.6)
Lepidoptera (larvae)	30 (2.48)	803.4 (0.86)	9 (33.3)	22 (2.71)	214 (1.9)	8 (21.1)
Diptera	16 (1.32)	1095 (1.17)	5 (18.5)	10 (1.23)	106.2 (0.95)	5 (13.2)
Diptera (larvae)	2 (0.17)	51.7 (0.06)	1 (3.7)	1 (0.12)	3.7 (0.03)	1 (2.6)
Squamata	1 (0.08)	52.6 (0.06)	1 (3.7)	–	–	–
Leaf	–	132.6 (0.14)	9 (33.3)	–	11 (0.1)	6 (15.8)
Flower	–	49006 (52.43)	14 (51.9)	–	3941 (35.07)	19 (50)
Fruit	–	5603 (5.99)	10 (37)	–	319.9 (2.85)	4 (10.5)
Arthropod remains	–	20345 (21.76)	22 (81.5)	–	3689 (32.83)	32 (84.2)
Total	1209 (100)	93475 (100)	–	813 (100)	11238 (100)	–

Data collection

Data were collected in March 2013 through visual encounter surveys (VES) performed by transects constrained by time (30 minutes) at each hour interval between 0900 and 1700 hours (Brazilian Standard Time). The VES consisted of slow walks across the area carefully searching for lizards on rocky outcrops and on vegetation. Capture attempts with noose technique or by hand were made whenever *T. hispidus* or *T. semitaeniatus* individuals were sighted. Snout-vent length (SVL) and jaw width (JW) of each captured lizard was measured with a caliper (precision of 0.01 mm), and body mass was assessed using spring balances (Pesola, precision of 0.25 g for individuals <30 g and of 1.0 g for those >30 g). Body temperature (T_b) was measured using a Miller and Weber quick-reading cloacal thermometer (precision of 0.2 °C).

Individuals were fixed with 10% formalin shortly after capture in the field. We dissected the lizards and

identified food items found in their stomachs under a stereomicroscope to the level of Order (Family in the case of Formicidae), or to the taxonomic level as accurate as possible. Arthropod remains that could not be identified were grouped into one category. Diets of *T. hispidus* and *T. semitaeniatus* were evaluated in terms of number, volume (mm³) and frequency of occurrence. Food items were counted and measured with a caliper (length and width, precision of 0.01 mm) and we estimated their volumes using the ovoid-spheroid formula [$V=\pi(L)(W)^2/6$], where L is the length and W is the width of the item. The frequency of occurrence of each food item category in the diet of each species was expressed as the number of stomachs that contained the category. The proportions of vegetal material (PVM) ingested by lizards of both species was estimated by dividing the total volume of vegetal material within the stomach of each individual by the total food volume consumed by it.

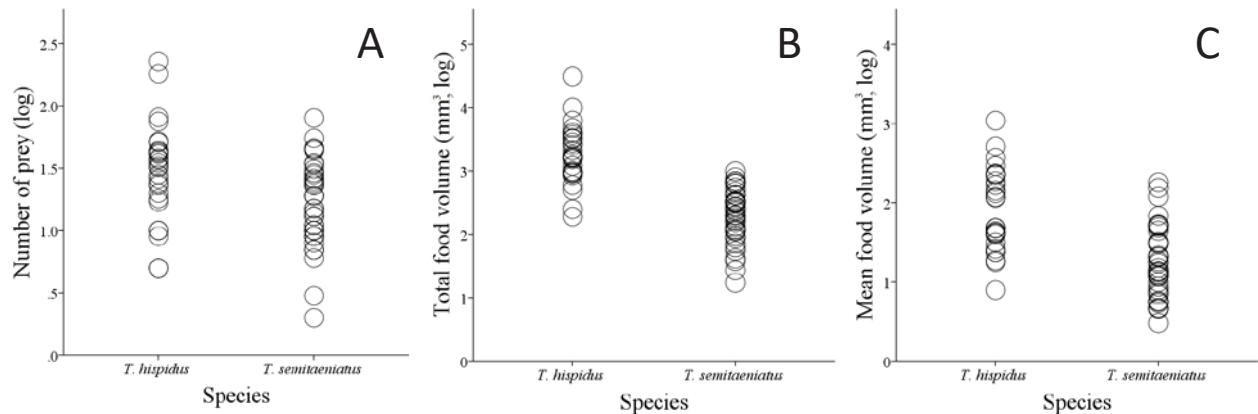


Fig. 1. Differences in (A) number of prey, (B) total food volume (mm^3 , log), and (C) mean volume of the three largest prey items (mm^3 , log) between *Tropidurus hispidus* and *T. semitaeniatus* in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil. All values were greater for the former species in comparison to the latter species.

Analytical procedures

Differences in mean number of prey, total food volume, and mean volume of the three largest prey items consumed between species were tested through analysis of variance (ANOVA). Additionally, we performed analysis of covariance with the same factors using SVL or body mass as covariates. To visualise the distribution of the consumption of the three largest prey items we performed a non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. We

considered that a stress statistic with values closer to zero and higher than 0.3 indicated adjustment and arbitrary ordination, respectively. To evaluate if *T. hispidus* and *T. semitaeniatus* differed in the three largest prey items consumed, we performed a one-way analysis of similarity (ANOSIM) using Bray-Curtis distance measures. R values close to zero suggest similarity, and values close to one indicate dissimilarity. We used linear regressions to test for relationships between number of prey and SVL, mean volume of the three largest prey items and JW, total food volume and SVL, total food volume and body mass, PVM and SVL, PVM and body mass, and total food volume and T_b . For *T. semitaeniatus*, we used Spearman correlations to test for the occurrence of association between PVM and SVL and between PVM and body mass. PVM was transformed to arcsine.

To evaluate the level of trophic niche similarity between *T. hispidus* and *T. semitaeniatus*, numerical and volumetric proportions of food categories were compared between species using Pianka's Niche Overlap Index [$O_{jk} = \sum p_{ij} p_{ik} / \sqrt{\sum (p_{ij}^2)(p_{ik}^2)}$], where p_{ij} and p_{ik} are numerical or volumetric proportions of food categories encountered in the diet of species j and k (Pianka, 1973). To evaluate whether the level of overlap in trophic niche dimensions occurred or not due to interspecific interactions the observed value of the index of Pianka was compared with the expected from 1000 simulations performed through null models with randomisation algorithm 3 and resource states equiprobable (Winemiller & Pianka, 1990). To evaluate the occurrence of differences in number and volume of food consumed between species we used two-sample Kolmogorov-Smirnov tests. To test for differences in PVM consumed between species we performed Mann-

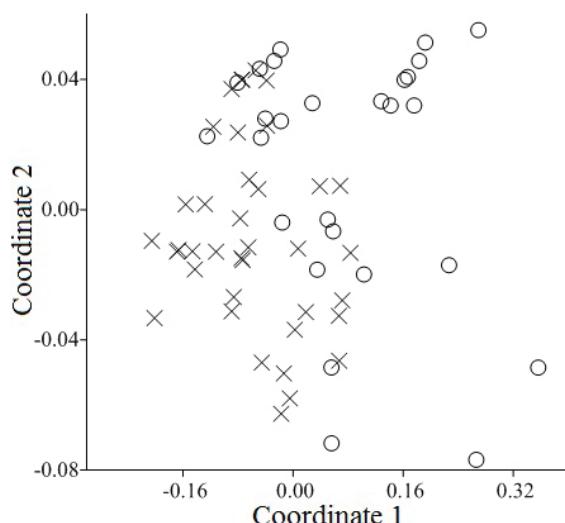


Fig. 2. Non-metric multidimensional scaling in relation to the three largest food items consumed by *Tropidurus hispidus* (○) and *T. semitaeniatus* (×) individuals in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil (stress=0.05414).

Table 2. Means±one standard deviation (SD) and ranges of snout-vent length (mm), jaw width (mm) and body mass (g) of *Tropidurus hispidus* (N=27) and *T. semitaeniatus* (N=39) from rock outcrops in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil.

Data	<i>Tropidurus hispidus</i>		<i>Tropidurus semitaeniatus</i>	
	Mean±SD	Range	Mean±SD	Range
Snout-vent length	90.4±18.7	57.7–133.2	57.2±7.1	41.3–69.6
Jaw width	18.9±4.4	12.8–27.9	11.0±1.5	8.1–14.4
Body mass	29.6±22.2	6–90.5	4.1±1.7	1.3–7.8

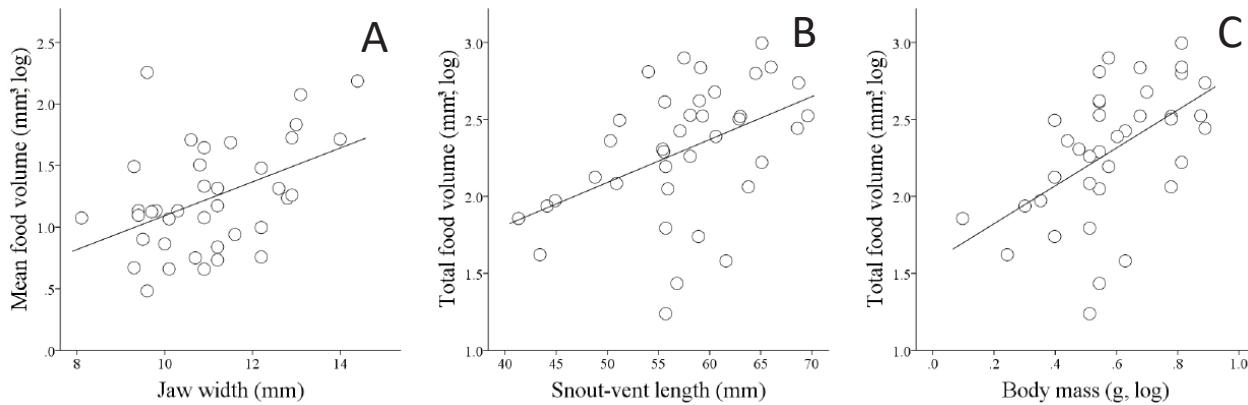


Fig. 3. Relationships (A) between mean volume of the three largest food items (mm^3 , log) and jaw width (mm), (B) between total food volume (mm^3 , log) and snout-vent length (mm), and (C) between total food volume (mm^3 , log) and body mass (g, log) in *Tropidurus semitaeniatus* in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil.

Whitney U tests. Descriptive statistics appear throughout the text as mean \pm one standard deviation, ranges, and number of observations in parentheses or as median with inferior and superior 95% confidence intervals (CI), ranges, and number of observations in parentheses. Data were logarithm-transformed when required to perform parametric statistics.

RESULTS

In total, 66 individuals of both species were collected in Igatu. Of these, 27 (40.9%) were *Tropidurus hispidus* and 39 (59.1%) were *T. semitaeniatus*. All *T. hispidus* had food in their stomachs and only one *T. semitaeniatus* individual (2.6%) had its stomach empty. *Tropidurus hispidus* consumed 22 different food items, and *T. semitaeniatus* individuals ingested 21 different types of food. Numerically, *T. hispidus* consumed predominantly ants (45.08%), followed by termites (40.86%) and beetles (3.72%) (Table 1). In terms of volume, the most representative food items in the diet of this species were flowers (52.43%), fruits (5.99%), and spiders (3.34%, Table 1). All *T. hispidus* individuals ate ants, 63% ingested beetles, and 51.9% of the individuals consumed flowers and hymenopterans non-Formicidae (Table 1). In terms of numbers, *T. semitaeniatus* lizards consumed mainly ants (63.35%), termites (12.79%), and beetles (9.59%, Table 1). In terms of volume, *T. semitaeniatus* lizards

ate predominantly flowers (35.07%), followed by ants (9.99%) and hemipterans (4.79%, Table 1). The food items most commonly ingested by *T. semitaeniatus* lizards were ants (94.7%), beetles (71.1%), and flowers (50%, Table 1).

The mean numbers of prey consumed were 33 (CI: 24.9–64.6; range: 5–228, n=1209) in *T. hispidus* and 17 (CI: 16.1–26.7; range: 2–80, n=813) in *T. semitaeniatus* (ANOVA, $F_{[1, 63]} = 8.199$, $r^2 = 0.115$, $P = 0.006$) (Fig. 1A). The total food volumes ingested by *T. hispidus* and *T. semitaeniatus* individuals were 1678.4 mm^3 (CI: 1125.5–5798.5; range: 189.4–31019.7) and 237.5 mm^3 (CI: 214.6–372.4; range: 17.3–991.3, Fig. 1B), respectively (ANOVA, $F_{[1, 63]} = 73.329$, $r^2 = 0.538$, $P < 0.0001$). Similarly, the mean volume of the three largest prey differed significantly between species (ANOVA, $F_{[1, 63]} = 30.734$, $r^2 = 0.328$, $P < 0.0001$, Fig. 1C), being 47.9 mm^3 (CI: 69.8–246.6; range: 7.9–1088.9) in *T. hispidus* and 13.6 mm^3 (CI: 17.2–43.6; range: 3–180.8) in *T. semitaeniatus*. However, when accounting for the effects of SVL and body mass (Tables 2 and 3), these differences were in general statistically non-significant, excepting for total food volume and body mass (Tables 2 and 3). The ANOSIM suggested a subtle divergence ($R = 0.2909$, $P = 0.0001$) and the NMDS revealed some level of separation between *T. hispidus* and *T. semitaeniatus* regarding the consumption of the three largest food items (Fig. 2). The NMDS yielded a stress coefficient of 0.0541, indicating reliability of the ordination.

Table 3. Results of analyses of covariance for differences in number of prey, total food volume, and volume of the three largest prey items consumed by *Tropidurus hispidus* and *T. semitaeniatus* individuals in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil, disregarding the effects of snout-vent length (SVL) and of body mass. For all analyses, there were 65 observations and 62 degrees of freedom.

Variable tested	Variable factored out	F	P
Number of prey	SVL	0.005	0.945
Number of prey	Body mass	0.001	0.978
Total food volume	SVL	3.721	0.058
Total food volume	Body mass	6.352	0.014
Volume of the three largest prey items	SVL	0.533	0.468
Volume of the three largest prey items	Body mass	1.197	0.278

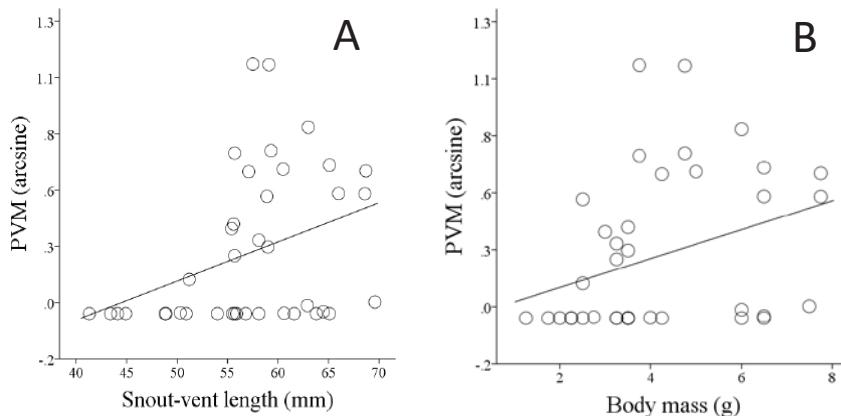


Fig. 4. Correlations (A) between proportion of vegetal material (PVM, arcsine transformed) (mm^3) and snout-vent length (mm) and (B) between PVM and body mass (g) in *Tropidurus semitaeniatus* in Igatu, municipality of Andaraí, state of Bahia, northeastern Brazil.

The trophic niche overlap (O_{jk}) between species in terms of numerical proportions of food categories consumed was 0.857, and considering volumetric proportions of food was 0.834. The means of simulated indexes in numerical and volumetric terms were 0.115 (variance=0.039) and 0.122 (variance=0.033), respectively. The levels of overlap observed in trophic niche dimensions were higher than expected by chance (numerical: $P<0.0001$; volumetric: $P=0.005$). Diet composition did not differ between species numerically (Kolmogorov-Smirnov, $D_{\max}=0.091$, $P=1.0$) but it did volumetrically (Kolmogorov-Smirnov, $D_{\max}=0.4$, $P=0.03$).

The number of prey items ingested was not related to SVL in both *T. hispidus* ($F_{[1, 25]}=0.007$, $P=0.933$, $n=27$) and *T. semitaeniatus* ($F_{[1, 36]}=0.186$, $P=0.669$, $n=38$; Table 2). The mean volume of the three largest food items consumed by individuals was significantly related to JW in *T. semitaeniatus* ($F_{[1, 36]}=9.279$, $r^2=0.205$, $P=0.004$, $n=38$; Figure 3A; Table 2), but not in *T. hispidus* ($F_{[1, 25]}=0.082$, $P=0.777$, $n=27$). There was no relationship between SVL and total food volume in *T. hispidus* ($F_{[1, 25]}=0.685$, $P=0.416$, $n=27$), although this relationship was significant in *T. semitaeniatus* ($F_{[1, 36]}=9.380$, $r^2=0.389$, $P=0.004$, $n=38$; Figure 3B; Table 2). Similar results occurred considering total food volume and body mass (*T. semitaeniatus*: $F_{[1, 36]}=14.208$, $r^2=0.283$, $P=0.001$, $n=38$; *T. hispidus*: $F_{[1, 25]}=0.494$, $P=0.489$, $n=27$; Figure 3C; Table 2).

The PVM ingested was 0.452 mm^3 (CI: $0.231 - 0.530$; range: $0-0.98$, $n=27$) in *T. hispidus* and 0.037 mm^3 (CI: $0.150 - 0.344$; range: $0-0.90$, $n=39$) in *T. semitaeniatus*. *Tropidurus hispidus* and *T. semitaeniatus* did not differ with respect to PVM ingested (Mann-Whitney, $U=0.668$, $P=0.061$). There were no relationships between PVM and SVL ($F_{[1, 25]}=0.632$, $P=0.434$, $n=27$) and between PVM and body mass ($F_{[1, 25]}=0.792$, $P=0.382$, $n=27$) in *T. hispidus*. The consumption of plant matter was correlated to body size in *T. semitaeniatus* (PMV \times SVL: $r=0.461$, $P=0.003$, $n=39$; PMV \times body mass: $r=0.472$, $P=0.002$, $n=39$; Figures 4A and 4B). The body temperature was $35.5 \pm 2.3^\circ\text{C}$ (range=30.2–39.2, $N=27$) in *T. hispidus* and $36.0 \pm 1.8^\circ\text{C}$ (range=32.0–39.8, $N=39$) in *T. semitaeniatus*. Total food volume and T_b were unrelated in *T. hispidus* (Simple linear regression analysis, $F_{[1, 25]}=0.171$, $P=0.683$); however, they were in *T. semitaeniatus* ($F_{[1, 36]}=8.717$, $r^2=0.195$, $P=0.006$).

DISCUSSION

By acquiring food items of different sizes, *T. hispidus* and *T. semitaeniatus* in Igatu segregated with respect to the consumption of trophic resources. The non-metric multidimensional scaling in relation to the three largest food items revealed a subtle interspecific divergence, with *T. semitaeniatus* predominantly located in negative coordinate values, linked to the narrower body size range of *T. semitaeniatus* and the consequently lower variation of food sizes. Small *T. hispidus* and *T. semitaeniatus* have similar body sizes and are capable of acquiring food items with similar sizes, whereas large *T. hispidus* individuals may consume large food items that are not accessible to *T. semitaeniatus*. This may be responsible for the widespread distribution of *T. hispidus* in the NMDS. The acquisition of food items containing higher energetic and nutritional profitability is favourable for maintenance, growth and reproduction. Capture and manipulation of small food items might be more difficult for large individuals and might decrease the amount of energy acquired (Costa et al., 2008). This might also explain the relationships between volume of the largest food items and jaw width, total food volume and SVL, and total food volume and body mass in *T. semitaeniatus*. Small lizards have morphological limitations that restrict the food sizes they might ingest (e.g., Van Sluys et al., 2004; Ribeiro & Freire, 2011). Increased body size may be advantageous, as it enables the acquisition of more and larger food items. These inter and intra-specific differences in size of food items might be important in separating individuals in relation to trophic resources consumed.

The absence of relationship between volume of the largest food items ingested and jaw width in *T. hispidus* indicated the consumption of a wide range of sizes of food independently of body size. Apparently, individuals of this species with different sizes did not consume food items based on their sizes. The non-significant association between total food volume and SVL and between total food volume and body mass indicated that *T. hispidus* lizards with different body sizes ingested similar volumes of food. We suggest different non-exclusive possible explanations for these phenomena. Small lizards may have ingested great amounts of food, comparable to those of larger individuals to maximize their growth rates (Stamps & Tanaka, 1981; Rocha, 1995). Furthermore, larger individuals might have spent time that could

have been used for food acquisition performing other activities (e.g., territorial defence). We obtained the data for this study during a period when *T. hispidus* individuals might be potentially reproductive (Ribeiro et al., 2012) and regularly observed agonistic interactions between individuals.

Body size is a relatively variable trait in lizards and is relevant for different aspects of their lives (Pianka, 1973; Peters, 1983; Calder, 1996; Brown et al., 2004; Costa et al., 2008; Maia-Carneiro & Rocha, 2013). The absence of interspecific differences in prey number and sizes between *T. hispidus* and *T. semitaeniatus* after accounting for the effects of body sizes highlights the importance of morphology to explore different trophic resources. Differential utilisation of food resources allowed by differences in body size might contribute to reduce overlaps in niche dimensions (Pianka, 1973; Colli et al., 1992; Costa et al., 2008; Ribeiro & Freire, 2011; this study). The higher total food volume ingested by *T. hispidus* in comparison to *T. semitaeniatus* in Igatu even after factored out the effect of body size suggest that *T. hispidus* acquired on average a proportionally (relative to body sizes) greater amount of food than *T. semitaeniatus*, which might have occurred due to differential energetic/nutritional requirements of each species.

Considering the consumption of broadly diversified food categories *T. hispidus* and *T. semitaeniatus* might be classified as generalists as are other *Tropidurus* species (Bergallo & Rocha, 1994; Vitt & Carvalho, 1995; Teixeira & Giovanelli, 1999; Carvalho et al., 2007; Meira et al., 2007; Rocha & Siqueira, 2008; Kolodiuk et al., 2010; Ribeiro & Freire, 2011). However, the consumption of similar predominant food items and high overlaps of trophic niche dimensions between species of *Tropidurus* would indicate selective behaviour (e.g., Faria & Araujo, 2004; Rocha & Siqueira, 2008; Kolodiuk et al., 2010; Ribeiro & Freire, 2011; Siqueira et al., 2011, 2014). Alternatively, these types of food may be widely available in different localities and the diet of these lizards may reflect food availability. Nevertheless, evaluation of diets with more specific taxonomic levels of prey (e.g., family, genus or species) should reveal additional differences in consumption of trophic resources between species.

Overall, ants, termites, beetles, and flowers were important food resources acquired by *T. hispidus* and *T. semitaeniatus* individuals in Igatu and in other localities (Vitt, 1995; Vitt & Carvalho, 1995; Vitt, 1996; Van Sluys et al., 2004; Pontes et al., 2008; Kolodiuk et al., 2010; Ribeiro & Freire, 2011), as well as by other species of *Tropidurus* (e.g., Rocha et al., 2002; Carvalho et al., 2007; Meira et al., 2007; Rocha & Siqueira, 2008; Freitas et al., 2012) and, in fact, in the group Iguania as a whole (Vitt & Pianka, 2005). Although local environmental conditions might importantly influence ecological niches (Melville et al., 2006; Lopez-Darias et al., 2012; Maia-Carneiro et al., 2012; Sinervo et al., 2010), phylogenetic effects appears to determine general patterns of niche dimensions (Vitt et al., 1999; Gainsbury & Colli, 2003; Vitt & Pianka, 2005; Mesquita et al., 2006). Present-day divergences in ecological traits related to feeding habits among lizard species apparently arose early in the evolutionary history

of major clades (Vitt & Pianka, 2005), which implies that niche dimensions are at least partly determined by pre-existing phylogenetic differences.

The plant materials most ingested by *T. hispidus* and *T. semitaeniatus* individuals in Igatu were flowers and fruits, food items that have also been found in the diet of other *Tropidurus* species (Côrtes-Figueira et al., 1994; Fialho et al., 2000; Dutra et al., 2011; Siqueira et al., 2011, 2014). Lizards commonly consume flowers and fruits probably because petals and fruit pulps contain more digestible components, water and nutrients than green structures such as leaves and stems (Van Marken Lichtenbelt, 1992; Rocha, 2000; Cooper & Vitt, 2002; Olesen & Valido, 2003; Dutra et al., 2011). Furthermore, the consumption of more digestible vegetal parts does not require specialisations for digestion (Cooper & Vitt, 2002).

The proportion of plant material consumed by *T. semitaeniatus* lizards in Igatu increased as individuals grew. Such ontogenetic shift also occurred in other lizard species, including in the genus *Tropidurus* (Rocha, 1998; Cooper & Vitt, 2002; Fialho et al., 2000; Siqueira et al., 2011), and might be due to plant materials requiring comparatively low energy expenditure for acquisition (Pough, 1973). The consumption of large-sized animal prey might be inefficient at low abundance in the environment, also exposing individuals to predators (Siqueira et al., 2011) and/or high temperatures (Maia-Carneiro & Rocha 2013), whereas the acquisition of small animal prey may be linked to low amounts of energetic and nutritional values (Costa et al., 2008; Siqueira et al., 2011). A higher consumption of animal prey by young lizards also may occur due to differential nutritional demands to favour body growth (Pough, 1973; Rocha 1998).

The relationship between total food volume and T_b in *T. semitaeniatus* might have been caused by high body temperatures increasing foraging efficiency (Avery, 1982; Van Damme et al., 1991; Verwaijen & Van Damme, 2007), resulting in more food acquired. High body temperatures also improve digestion of specific food compounds (Harlow et al., 1976; Harwood, 1978; Pafilis et al., 2007; Janzen, 1973; Zimmerman & Tracy, 1989; Tracy et al., 2005). Therefore, *T. semitaeniatus* lizards would maintain high body temperatures to accomplish thermal requirements related to food acquisition and digestion.

Body size differences within and between species of lizard may relate to differential exploitation of food resources. Larger individuals are capable of consuming greater amounts of food and larger-sized food items that have greater nutritional and energetic contents, which might result in reduction of ecological niche overlaps. Despite variations in sizes of acquired food items, phylogenetically closely related lizards may tend to access similar types of food even in distinct environments. Omnivorous feeding habits occur in different lizard species, with individuals eating mainly flowers and fruits, plant parts that are easier to digest in comparison to green structures besides having commonly relevant water, nutritional, and energetic contents. The consumption of plant matter may increase

with age when the acquisition of animal prey does not match specific requirements. The maintenance of high body temperatures may be advantageous for lizards due to improvement of food acquisition and digestion.

ACKNOWLEDGEMENTS

We thank Tim Moulton for the valuable suggestions for improvement of the manuscript. Field sampling took place with licence IBAMA/ICMBio nº 17474-1. We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) which provided grants to CFDR (processes nº 304791/2010-5, nº 472287/2012-5 and 302974/2015-6), the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) which supports CFDR through Programa Cientistas do Nosso Estado (processes nº 304791/2010-5, nº 472287/2012-5 and 302974/2015-6), and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and FAPERJ, which granted PhD scholarships to TMC. We also give thanks to CAPES and FAPERJ, which granted a M.Sc. scholarship to TMT.

REFERENCES

- Avery, R.A., Bedford, J.D. & Newcombe, C.P. (1982). The role of thermoregulation in lizard biology: Predatory efficiency in a temperate diurnal basker. *Behavioral Ecology and Sociobiology* 11, 261–267.
- Avila-Pires, T.C.S. (1995). Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen* 299, 1–706.
- Bergallo, H.G. & Rocha, C.D.F. (1994). Spatial and trophic niche differentiation in two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics. *Australian Journal of Ecology* 19, 72–75.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Calder, W.A. (1996). *Size, function, and life history*. Dover Publications, Mineola, NY.
- Carvalho, A.L.G. (2013). On the distribution and conservation of the South American lizard genus *Tropidurus* Wied-Neuwied, 1825 (Squamata: Tropiduridae). *Zootaxa* 3640, 42–56.
- 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. *Zoologia* 24, 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, 66–69.
- Cooper, W.E. Jr. & Vitt, L.J. (2002). Distribution, extent, and evolution of plant consumption by lizards. *Journal of Zoology* 257, 487–517.
- Côrtes-Figueira, J.E., Vasconcellos-Neto, J., Garcia, M.A. & Souza, A.L.T. (1994). Saurocory in *Melocactus violaceus* (Cactaceae). *Biotropica* 22, 423–424.
- Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O. & Colli, G.R. (2008). Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards.
- Dutra, G.F., Siqueira, C.C., Vrcibradic, D., Kiefer, M.C. & Rocha, C.F.D. (2011). Plant consumption of insular and mainland populations of a tropical lizard. *Herpetologica* 67, 32–45.
- Faria, R.G. & Araujo, 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, 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, 325–330.
- Freitas, A.M., Teixeira, R.L. & Ferreira, R.B. (2012). Food partitioning between the sympatric lizards *Tropidurus torquatus* and *Ameiva ameiva* in the Atlantic rainforest, northeastern Brazil. *Salamandra* 48, 63–70.
- Gainsbury, A.M. & Colli, G.R. (2003). Lizard assemblages from natural Cerrado enclaves in southwestern Amazonia: The role of stochastic extinctions and isolation. *Biotropica* 35, 503–519.
- Harlow, H.J., Hillman, S.S. & Hoffman, M. (1976). The effect of temperature on digestive efficiency in the herbivorous lizard, *Dipsosaurus dorsalis*. *Journal of Comparative Physiology* 11, 1–6.
- Harwood, R.H. (1978). The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus Occidentalis*. *Comparative Biochemistry and Physiology* 63A, 417–433.
- Janzen, D.H. (1973). Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54, 687–708.
- Koloduk, M.F., Ribeiro, L.B. & Freire, E.M.X. (2010). Diet and foraging behavior of two species of *Tropidurus* (Squamata, Tropiduridae) in the Caatinga of northeastern Brazil. *South American Journal of Herpetology* 5, 35–44.
- Lopez-Darias, M., Schoener, T.W., Spiller, D.A. & Losos, J.B. (2012). Predators determine how weather affects the spatial niche of lizard prey: exploring niche dynamics at a fine scale. *Ecology* 93, 2512–2518.
- Maia-Carneiro, T., Dorigo & T.A., Rocha, C.F.D. (2012). Influences of seasonality, thermal environment and wind intensity on the thermal ecology of Brazilian sand lizards in a restinga remnant. *South American Journal of Herpetology* 7, 241–251.
- Maia-Carneiro, T. & Rocha, C.F.D. (2013). Influences of sex, ontogeny and body size on the thermal ecology of *Liolaemus lutzae* (Squamata, Liolaemidae) in a restinga remnant in southeastern Brazil. *Journal of Thermal Biology* 38, 41–46.
- Meira, K.T.R., Faria, R.G., Silva, M.D.M., Miranda, V.T. de & Zahn-Silva, W. (2007). História Natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. *Biota Neotropica* 7, 155–163.
- Melville, J., Harmon, L.J. & Losos, J.B. (2006). Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society of London B* 273, 557–563.
- Mesquita, D.O., Colli, G.R., França, F.G.R. & Vitt, L.J. (2006). Ecology of a Cerrado lizard assemblage in the Jalapão region of Brazil. *Copeia* 2006, 460–471.
- Olesen, J. M. & Valido, A. (2003). Lizards as pollinators and seed dispersers: An island phenomenon. *Trends in Ecology and*

- Evolution* 18, 177–181.
- Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P. & Valakos, E. (2007). Digestive performance in five Mediterranean lizard species: effects of temperature and insularity. *Journal of Comparative Physiology B* 177, 49–60.
- Peters, R.H. (1983). *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology, Evolution, and Systematics* 1973, 53–74.
- Pontes, M.C., Garri, R.G. & Chiamenti, A. (2008). Atividade de predação de *Tropidurus hispidus* (Sauria, Tropiduridae) de Nisia floresta-RN, Brasil. *Revista Brasileira de Zoociências* 10, 201–207.
- Pough, F.H. (1973). Lizard energetics and diet. *Ecology* 54, 837–844.
- Ribeiro, L.B. & Freire, E.M.X. (2011). Trophic ecology and foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a Caatinga area of northeastern Brazil. *Iheringia* 101, 225–232.
- Ribeiro, L.B., Silva, N.B. & Freire, E.M.X. (2012). Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a Caatinga area of northeastern Brazil. *Revista Chilena de Historia Natural* 85, 307–320.
- Rocha, C.F.D. (1995). Growth of the tropical sand lizard *Liolaemus lutzae* in southeastern Brazil. *Amphibia-Reptilia* 16, 257–264.
- Rocha, C.F.D. (1998). Ontogenetic shift in the rate of plant consumption in a tropical lizard (*Liolaemus lutzae*). *Journal of Herpetology* 32, 274–279.
- Rocha, C.F.D. (2000). Selectivity in plant food consumption in the lizard *Liolaemus lutzae* from southeastern Brazil. *Studies on Neotropical Fauna and Environment* 35, 14–18.
- Rocha, C.F.D., Dutra, G.F., Vrcibradic, D. & Menezes, V.A. (2002). The terrestrial reptile fauna of the Abrolhos archipelago: Species list and ecological aspects. *Brazilian Journal of Biology* 62, 285–291.
- 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, 109–113.
- Rocha, W.J.S.F., Chaves, J.M., Rocha, C.C., Funch, L. & Juncá, F.A. (2005). Avaliação ecológica rápida da Chapada Diamantina. Pp. 29–45. In Juncá FA, Funch L and Rocha, WJSF (Eds.). *Biodiversidade e Conservação da Chapada Diamantina*. Brasília: Ministério do Meio Ambiente. 411 p.
- Rodrigues, M.T. (1987). Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). *Arquivos de Zoologia* 31, 105–230.
- Rodrigues, M.T. (1988). Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). Pp. 305–315. In Heyer, W. R. and Vanzolini, P. E. (Eds). Proceeding of a workshop on neotropical distribution patterns. Academia Brasileira de Ciência, Rio de Janeiro.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899.
- Siqueira, C.C., Kiefer, M.C., Van Sluys, M. & Rocha, C.F.D. (2011). Plant consumption in coastal populations of the lizard *Tropidurus torquatus* (Reptilia: Squamata: Tropiduridae): how do herbivory rates vary along their geographic range? *Journal of Natural History* 45, 171–182.
- Siqueira, C.C., Kiefer, M.C., Van Sluys, M. & Rocha, C.F.D. (2014). Variation in the diet of the lizard *Tropidurus torquatus* along its coastal range in Brazil. *Biota Neotropica* 13, 93–101.
- Stamps, J. & Tanaka, S. (1981). The influence of food and water on growth rates in a tropical lizard (*Anolis Aeneus*). *Ecology* 62, 33–40.
- Teixeira, R.L. & Giovanelli, M., 1999. Ecologia de *Tropidurus torquatus* (Sauria: Tropiduridae) da restinga de Guriri, São Mateus, ES. *Brazilian Journal of Biology* 59, 11–18.
- Tracy, C.R., Flack, K.M., Zimmerman, L.C., Espinoza, R.E. & Tracy, C.R. (2005). Herbivory imposes constraints on voluntary hypothermia in lizards. *Copeia* 2005, 12–19.
- Van Damme, R., Bauwens, D. & Verheyen, R.F. (1991). The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Functional Ecology* 5, 507–517.
- Van Marken Lichtenbelt, W.D. (1992). Digestion in an ectothermic herbivore, the green iguana (*Iguana iguana*): Effect of food composition and body temperature. *Physiological Zoology* 65, 649–673.
- 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, 606–611.
- Verwijen, D. & Van Damme, R. (2007). Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. *Journal of Thermal Biology* 32, 388–395.
- Vitt, L.J. (1991). An Introduction to the Ecology of Cerrado Lizards. *Journal of Herpetology* 25, 79–90.
- Vitt, L.J. (1993). Ecology of open formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. *Canadian Journal of Zoology* 71, 2370–2390.
- Vitt, L.J. (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. (1996). Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *Journal of Tropical Ecolology* 12, 81–101.
- Vitt, L.J. & Carvalho, C.M. (1995). Niche Partitioning in a Tropical Wet Season: Lizards in the Lavrado Area of Northern Brazil. *Copeia* 1995, 305–329.
- Vitt, L.J. & Pianka, E.R. (2005). Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences* 102, 7877–7881.
- Vitt, L.J., Zani, P.A. & Espósito, M.C. (1999). Historical ecology of Amazonian lizards: implications for community ecology. *Oikos* 87, 286–294.
- Winemiller, K.O. & Pianka, E.R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60, 27–55.
- Zimmerman, L.C. & Tracy, C.R. (1989). Interactions between the environment and ectothermy and herbivory in reptiles. *Physiological Zoology* 62, 374–409.

Accepted: 20th June 2016