Austral
ECOLOGY A Journal of ecology in the Southern Hemisphere

Ecological Society of Australia

Austral Ecology (2017) **42**, 677–689

Extreme specialization to rocky habitats in *Tropidurus* lizards from Brazil: Trade-offs between a fitted ecomorph and autoecology in a harsh environment

NICOLÁS PELEGRIN,[1]* DANIEL OLIVEIRA MESQUITA,[2] PÂMELA ALBINATI,[2] FRANCIS LUIZ SANTOS CALDAS,[2] LUCAS BARBOSA DE QUEIROGA CAVALCANTI,[2] TAIS BORGES COSTA,[2] DIEGO ALEJANDRO FALICO,[3] JÉSSICA YARA A. GALDINO,[2] DEREK B. TUCKER[4] AND ADRIAN ANTONIO GARDA[5]

[1]*Laboratorio de Ecología y Conservación de la Herpetofauna, Instituto de Diversidad y Ecología Animal (IDEA), CONICET-UNC and Centro de Zoología Aplicada, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Rondeau 798, X5000AVP Córdoba, Argentina, (Email: nicolas.pelegrin@conicet.gov.ar)* [2]*Laboratório de Herpetologia, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba Campus I, João Pessoa, Paraiba, Brazil,* [3]*Centre for Proteome Analysis & Mass Spectrometry (CeProMa), University of Antwerp, Antwerpen, Belgium,* [4]*Department of Biology, University of West Florida, Pensacola, Florida, USA and* [5]*Laboratório de Anfíbios e Répteis-LAR, Departamento de Botânica, Ecologia e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil*

Abstract Ecomorphological theory indicates that different ecological requirements lead to different organismal designs. Given that species with equal requirements could not coexist, traits leading to more efficient use of resources may be selected to avoid competition among closely related syntopic species, generating specialized ecomorphs. We compared habitat use, diet, thermal biology and morphology among the syntopic *Tropidurus semitaeniatus*, *T. helenae* and *T. hispidus* in the Caatinga of Northeastern Brazil. *Tropidurus semitaeniatus* and *T. helenae* are flattened lizards specialized to rocks and rock crevices, whereas *T. hispidus* has a robust body and generalist habits. We aimed to test the hypothesis that morphological modifications observed in the flattened ecomorphs are related to modifications in diet and habitat use. Also, we hypothesized that specialization to habitat induces morphological modifications, which in turn may constrain lizard performance. Flattened species differed in habitat use, morphology and prey size when compared with the generalist ecomorph. Morphological modifications were related to specializations to rocky habitats and constrained the variety of prey items consumed. This phenotype also reduced their reproductive output when compared with a robust, generalist ecomorph.

Key words: Caatinga, ecomorphology, flattened lizards, rocky habitats.

INTRODUCTION

Two concepts are central in niche theory: niche breadth, the variety of resources used by a species, and niche overlap, the amount of resources shared among species (Pianka 1974, 1981). These two concepts have had a huge influence on competition theory, leading to a series of hypotheses aimed at explaining composition and diversity of assemblages. Among these, character displacement (Brown & Wilson 1956) and the principle of competitive exclusion (Hardin 1960) explore mechanisms of species coexistence. They demonstrate that species cannot coexist if they have equal requirements. Competition will result in one species overcoming the other, or will induce differentiation among them (Brown & Wilson 1956; Hardin 1960).

Thus, resource partitioning may avoid competition, allowing the coexistence of species with similar ecological requirements and, ultimately, help explain species diversity at a given locality (Hutchinson 1959; Schoener 1974; Roughgarden 1976). Numerous examples of resource partitioning were reviewed by Schoener (1974), including both partition in a single niche dimension (like lowland Jamaican *Anolis* lizards, Schoener & Schoener 1971) or in complementary dimensions (like in grassland bird communities, Cody 1968). Although species can segregate in any niche dimension, it is time, space and food that arose as the three main niche dimensions by which animals segregate (Pianka 1973; Schoener 1974).

---

*Corresponding author.

Accepted for publication January 2017.

doi:10.1111/aec.12486

Habitat is usually more important than food, and food more important than time (Pianka 1973; Schoener 1974).

Traits leading to a more efficient use of resources may be selected to avoid competition among closely related sympatric species, and may generate specialized ecomorphs (Brown & Wilson 1956; Hutchinson 1959). Accordingly, ecomorphological theory indicates that different ecological requirements lead to different organismal designs (Hutchinson 1959). However, adaptations to increase performance by exploiting specific resources may imply a reduction in the performance to exploit others. For example, a lizard cannot perform equally well as a ground-dwelling and a climbing species because of constraints or trade-offs between conflicting functions (Aerts *et al.* 2000; Vanhooydonck & Van Damme 2001; but see Clemente *et al.* 2013; Gomes *et al.* 2016).

The ecomorphological theory is straight forward for distantly related taxa, but at lower taxonomic levels the correlation between design and ecology is less clear (Zaaf & Van Damme 2001). In studies on reptiles we have found contradictory results. Examples include Caribbean *Anolis*, which radiated from a generalized ancestor to species specialized for particular structural and climatic habitats, leading to a highly diverse fauna with up to 40 or more species (Losos *et al.* 1994). Likewise, more arboreal populations of *Sceloporus occidentalis* have shorter limbs and better performance on arboreal surfaces than terrestrial populations, apparently with a genetic basis (Sinervo & Losos 1991). In contrast, other studies do not support the ecomorphological theory. Some Chilean *Liolaemus* species showed a diversification in resource utilization without being accompanied with morphological divergence (Jaksić *et al.* 1980). Moreover, comparing morphology between arboreal and terrestrial gekkonid lizards showed no relationship between habitat use and limb proportions (Zaaf & Van Damme 2001). A similar result was recently found in wall lizards (*Podarcis* sp.) when testing the association between morphology and locomotor performance. The saxicolous *Podarcis bocagei lusitanicus* performed as well as the ground-dwelling *P. bocagei* in climbing and running tests (Gomes *et al.* 2016). Also, no differences in speed were found in *Varanus* lizards comparing climbing and non-climbing species; modifications in kinematics may account for the equal performance of these ecomorphs (Clemente *et al.* 2013).

Lizards of the genus *Tropidurus* can be used as models to test the ecomorphological theory. *Tropidurus* species are diurnal lizards, usually abundant and widely distributed in South America, occupying a variety of habitats like sand dunes, hardwood forests, restingas and rock outcrops (Rodrigues 1987; Rocha & Bergallo 1990; Vitt 1995). Several aspects of *Tropidurus* lizard ecology have been largely studied in different parts of their distributional range, including reproduction, diet, habitat use, thermoregulation and activity (Rocha & Bergallo 1990; Vitt 1995; Cruz 1998; Pinto *et al.* 2005; Meira *et al.* 2007; Ribeiro & Freire 2011; Santana *et al.* 2014; Caldas *et al.* 2015; among others). Given that *Tropidurus* species are usually found in syntopy, studies about resource partitioning are not scarce in the literature (Colli *et al.* 1992; Faria & Araujo 2004; Van Sluys *et al.* 2004; Kolodiuk *et al.* 2010; Eloi & Leite-Filho 2013; Gomes *et al.* 2015). Morphological differences among and within species of the genus may reflect habitat and microhabitat use (Colli *et al.* 1992; Kohlsdorf *et al.* 2001; Faria & Araujo 2004), sexual selection (Pinto *et al.* 2005), and intraspecific competition (Kohlsdorf *et al.* 2006).

Three *Tropidurus* species are sympatric at Serra da Capivara National Park (Piauí State, northeastern Brazil): *T. semitaeniatus*, *T. helenae*, and *T. hispidus*. *Tropidurus semitaeniatus* and *T. helenae* are specialized to rocky habitats (Passos *et al.* 2011). They have flattened bodies and heads, which allow them to use rock crevices as refuges (Vitt 1981; Ribeiro *et al.* 2012). *Tropidurus hispidus* is a robust, generalist species, widely distributed in South America across different habitats (de Carvalho *et al.* 2013). Studies on comparative ecology between *T. semitaeniatus* and *T. hispidus* are available in the literature (Kolodiuk *et al.* 2010; Ribeiro & Freire 2011; Ribeiro *et al.* 2012; Eloi & Leite-Filho 2013; Gomes *et al.* 2015), but none of these tested the ecomorphological theory. Reduction in clutch size associated with the specialized morphology of *T. semitaeniatus* was described by Vitt (1981), who related the morphology of this lizard to its specialized habit, and compared it with the African cordylid *Platysaurus*, which is also a rock specialist with a flattened body and reduced clutch size.

In this work, we analyse the trade-offs and constraints between species having a specialized morphology and the ability to efficiently use food and habitat resources in the context of the harsh Caatinga. We specifically test the following hypotheses: (i) morphological modifications observed in flattened lizards (*T. helenae* and *T. semitaeniatus*) are related to modifications in diet and habitat use. Our prediction is that morphological differences between ecomorphs (flattened *vs.* robust) can be recognized as adaptations to the microhabitat used; (ii) specialization to habitat induces morphological modifications, which in turn may constrain lizard performance. We predict that flattened lizards will have a constrained reproductive output, and a reduced ability to consume prey items, when compared with the robust ecomorph.

doi:10.1111/aec.12486

METHODS

Study site

Sampling was conducted within Serra da Capivara National Park, PNSC, (8°46′S; 42°29′W) (Fig. 1), a federally protected area of about 100 000 ha located in Piauí State, northeastern Brazil. The PNSC is located within the Caatinga morphoclimatic domain (Ab'Saber 2005) with dense arboreal caatinga as the dominant vegetation type and small areas of shrub vegetation over compact sandy soils. These areas are also punctuated by rocky outcrops covered with shrubs, bromeliads and cacti (Lemos 2004). The edge of the mountainous areas (Chapadas) have steep hillsides forming canyons that are locally known as 'Boqueirões' and are characterized by semideciduous and mesic forest with high canopies (Cavalcanti *et al.* 2014). The high temperatures and unpredictable rains of the Caatinga have heavily influenced the native fauna and flora, as can be seen in several examples (Prado 2000, 2003).

Data sampling

The sampling period was from 7 May to 6 June 2012. Lizards were collected through active searching and trap arrays at several areas of the park. Active searches were made from 08.00 to 18.00 hours, and lizards were captured using telescopic fishing rods with nooses, rubber bands or by hand, in two 'Boqueirões ('Baixão da Esperança' and 'Toca do Inferno'), and in the surrounding areas of 'Albergue PARNA Serra da Capivara' (Fig. 1). At the time of capture, we measured the body, substrate and air temperatures (at 5 cm from substrate and at chest height) to the nearest 0.2°C with Minipa cloacal thermometers. We also recorded microhabitat, activity of individuals at first sight, activity after the researcher approached, hour, date of capture and exposure to sunlight (i.e. sun, filtered sun or shade). Microhabitat was classified as: fallen log, rock surface, rock crevice, leaf litter or man-made structures.

We also installed 37 trap arrays distributed in two transects (each containing 18 and 19 trap arrays, respectively). Each trap array was composed of four 30 L buckets connected with three 6 m drift fences constructed in a Y shape, with one central bucket and three at the end of each fence (Corn 1994). At each drift fence, we placed two funnel traps (one on each side of the fence), totalling six funnel traps per array. Four glue traps were placed in different microhabitats nearby each trap array. Traps were checked for lizards daily in the morning and before sunset to avoid overheating, digestion of stomach contents, and to reduce predation at night.

A sample of the captured individuals was euthanized with an injection of Lidocaine® 2% for further analysis of diet and morphometry. For each individual, we measured snout-vent length (SVL); body width (BW, at its broadest point) and body height (BH, at its highest point); head width (HW, at widest point on skull), head height (HH, at widest point on skull), and head length (HL, from anterior edge of tympanum to tip of snout); and tail length (TL, from the cloaca to the tip of the tail). All measurements were taken using electronic calipers to the nearest 0.01 mm. After data collection, euthanized individuals were preserved with 10% formalin and stored in 70% ethanol. The corresponding capture permits were granted to AAG (SISBIO # 33402-1) and TBC (SISBIO # 29550-2). Specimens are deposited at Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB), in João Pessoa, Brazil.

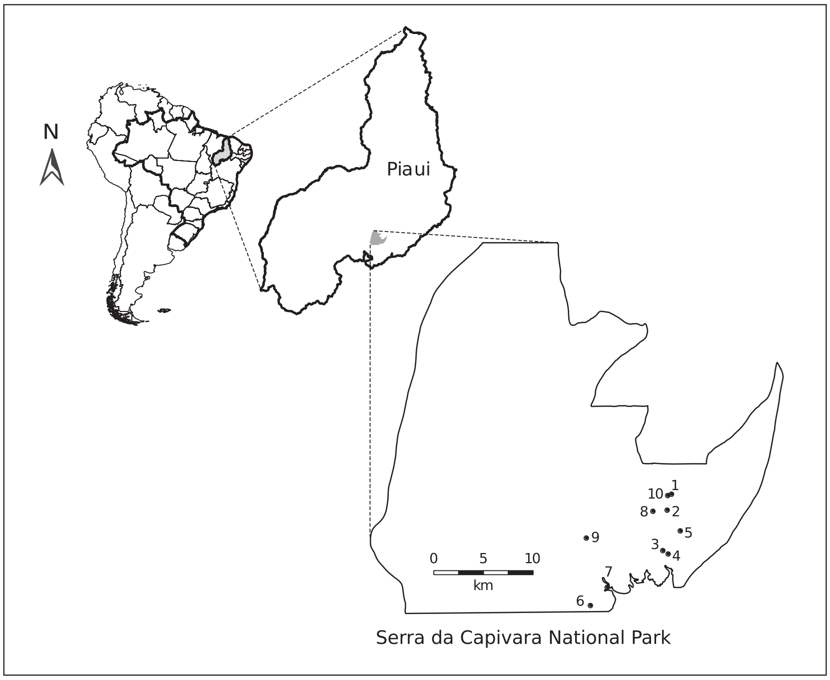

Fig. 1. Schematic map showing study site location and habitats sampled. Points 1 and 2 were sampled with traps. Points 3 to 10 were sampled with active searching techniques.

doi:10.1111/aec.12486

Morphological analyses

Before comparisons of morphological variables among species, we transformed measurements to remove the effect of size and shape. We defined body size as a variable resulting from the product of an isometric vector, with values of $p^{-0.5}$ (where p is the number of variables) by the $n \times p$ matrix of log10 transformed morphometric data, where n is the number of observations (Jolicoeur 1963; Somers 1986; Rohlf & Bookstein 1987). To remove the effect of size on the log10 transformed variables (related to body shape), we followed the method proposed by Burnaby (1966), multiplying the $n \times p$ matrix of log transformed data by a symmetric matrix (L) defined as $L = I_p - V(V^TV)^{-1}V^T$, where I_p is a $p \times p$ identity matrix, V is the isometric size eigenvector, and V^T is the transpose of V (Rohlf & Bookstein 1987). Body size was compared among species through the Analysis of Variance (ANOVA). Once the effect of size was removed from body shape variables, a Principal Component Analysis (PCA) was performed to examine the distribution of the three species in multidimensional morphological space. The main principal components were selected using the Kaiser criterion (Kaiser 1991). Individual loadings for each selected component were then compared through a Multivariate Analysis of Variance (MANOVA) to test for significant differences in morphology among species (Faria & Araujo 2004). Both PCA and MANOVA were performed in R 2.2.4 (R Core Team 2016).

Diet

To analyse the food content, we removed stomachs from preserved specimens (115 *T. hispidus*, 50 *T. helenae* and 43 *T. semitaeniatus*) and identified items under a stereoscopic microscope to the lowest taxonomic level possible, usually at the order level. We measured length and width of intact prey with digital calipers and estimated prey volume using the formula for the ellipsoid (Magnusson *et al.* 2003). To evaluate the importance of each prey item, we calculated the Index of Relative Importance (IRI) (Pinkas *et al.* 1971). Mean volume of consumed prey was compared among lizard species through a Kruskal-Wallis test. A Tukey-Kramer test was used to perform *post-hoc* multiple comparisons using the R package PMCMR (Pohlert 2014).

Niche breadth was calculated for diet (based on numeric and volumetric percentages) and microhabitat using the normalized Levins' index (Colwell & Futuyma 1971). We also calculated Pianka's standardized Niche Overlap Index (Winemiller & Pianka 1990) for food and microhabitat. Both indices were calculated using the R package spaa (Zhang *et al.* 2013).

RESULTS

Resource use among species

Microhabitat

Microhabitat niche breadth was lower for *T. helenae* (1.29, five microhabitat categories used) and *T. semitaeniatus* (1.56, five microhabitat categories used), than for *T. hispidus* (5.37, seven microhabitat categories used). Rocks were the main microhabitat used by *T. helenae* (88% of captures) and *T. semitaeniatus* (78% of captures), whereas *T. hispidus* used a higher diversity of microhabitats, with a tendency to use leaf litter (27%) and logs (23%) in higher proportions. Thus, the microhabitats used by *T. helenae* and *T. semitaeniatus* overlapped highly (Pianka index = 0.987), whereas overlap was low between *T. hispidus* and either of the flattened species (*T. hispidus vs. T. helenae* = 0.346, *T. hispidus vs. T. semitaeniatus* = 0.362).

Microhabitat fidelity was higher in *T. helenae* and *T. semitaeniatus* than in *T. hispidus*. When escaping from observers, the rock-dwelling species *T. helenae* and *T. semitaeniatus* tended to not move from rocks, while the habitat generalist *T. hispidus* tended to escape to a variety of microhabitat categories (Fig. 2). Mean perch height of *T. hispidus* (26.03 ± 31.83 cm) was lower than that of *T. helenae* (245.66 ± 159.97 cm) and *T. semitaeniatus* (221.46 ± 169.83 cm). No differences were found in perch height between the latter two (Kruskal-Wallis, KW = 50.14, $P < 0.001$, Tukey-Kramer *post-hoc* test, $P > 0.05$).

Thermal environment

The use of sun was not different among species ($\chi^2_{[NA]} = 8.73$, $P = 0.072$). Body temperature (T_B) of *T. hispidus* was correlated with substrate temperature (Pearson's $R = 0.52$, $P = 0.001$), while the T_B of *T. helenae* was correlated with substrate temperature (T_s), air temperature (T_a) and air temperature at 5 cm (T_{5cm}) ($R_{T_s} = 0.49$, $P = 0.002$, $R_{T_a} = 0.39$, $P = 0.014$, $R_{T_{5cm}} = 0.41$, $P = 0.009$). No significant correlations were found between T_B and T_s, T_a, or T_{5cm} for *T. semitaeniatus* (Pearson's correlation, $P > 0.05$) (Table 1). Mean body temperature of *T. helenae* (34.67 ± 1.97°C) did not differ from that of *T. hispidus* (36.67 ± 2.36°C) or *T. semitaeniatus* (34.93 ± 1.87°C), however, *T. hispidus* had a significantly higher T_B than *T. semitaeniatus* (34.93 ± 1.87°C) (Kruskal-Wallis test, KW = 0.9, $P < 0.001$, Tukey-Kramer *post-hoc* test, $P < 0.05$) (Table 1).

Morphology

Though body size did not differ between species (ANOVA $F_{2,233} = 0.022$, $P = 0.978$) (Table 2), flattened lizards (*T. helenae* and *T. semitaeniatus*) were strongly separated from the robust model (*T. hispidus*) in the multidimensional morphological space (Fig. 3). The first two Principal Components (selected using the Kaiser criterion, eigenvalue >1) showed significant differences in body shape among

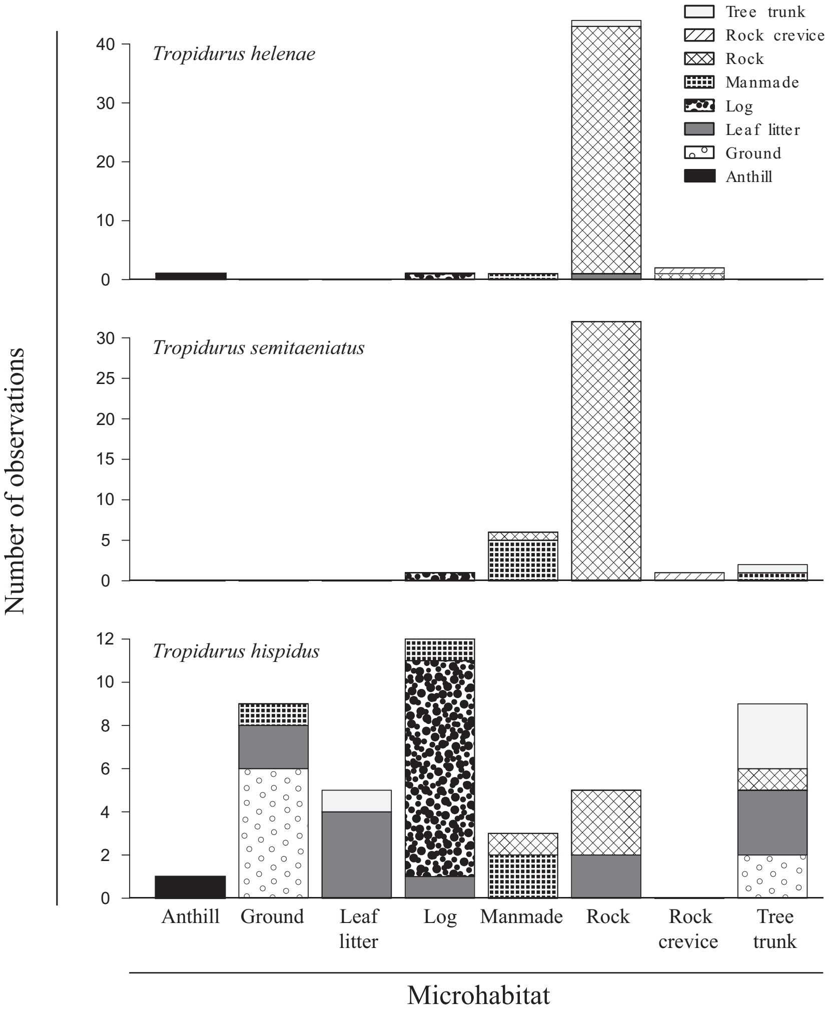

Fig. 2. Fidelity to microhabitats used by *Tropidurus helenae* (top), *Tropidurus semitaeniatus* (middle) and *Tropidurus hispidus* (bottom) at Serra da Capivara National Park. Microhabitat categories in the abscissa indicate the microhabitat used at first sight. Colours in bars indicate the microhabitat chosen at escape.

Table 1. Temperature of the microhabitats used by *Tropidurus helenae*, *T. semitaeniatus* and *T. hispidus* at Serra da Capivara National Park

Microhabtat	*N*	*T. helenae*	*N*	*T. semitaeniatus*	*N*	*T. hispidus*	KW	*P*
All	39	34.67 ± 1.97ab	41	34.93 ± 1.87b	34	33.67 ± 2.36a	8.02	0.018
Anthill	1	34.80	–	–	1	31.90		
Rock crevice	–	–	1	32.60	–	–		
Ground	–	–		–	6	33.35 ± 1.60		
Leaf litter	1	34.40		–	9	33.09 ± 3.88		
Log	1	33.60	1	28.80	8	33.59 ± 1.43		
Man-made	1	34.70	6	35.43 ± 1.89	2	34.85 ± 0.92		
Rock	34	34.63 ± 2.05	32	35.12 ± 1.57	4	33.80 ± 1.28	2.77	0.2497
Tree trunk	1	37.20	1	34.50	4	35.33 ± 1.85		

Different letters indicate significant difference in temperatures among species (Kruskal-Wallis test, $P < 0.05$, Tukey-Kramer *post-hoc* test, $P < 0.05$).

species (MANOVA, Pillai = 0.106, $F = 6.51$, $P < 0.0001$), and accounted for 71.3% of the variance. Principal Component 1 was positively associated with BH and HH, and negatively associated with SVL (isometric size), FlL and HlL. Principal Component 2 was negatively associated with

Table 2. Detail of the morphological variables measured

Variable	*Tropidurus semitaeniatus* $N = 52$	*Tropidurus helenae* $N = 61$	*Tropidurus hispidus* $N = 137$
Body size (isometric)	3.53 ± 0.25	3.54 ± 0.20	3.53 ± 0.37
Snout-vent length			
Raw values	66.67 ± 13.21	67.55 ± 11.31	61.61 ± 19.50
Size-free values	0.57 ± 0.02	0.57 ± 0.02	0.52 ± 0.02
Body width			
Raw values	16.86 ± 4.18	16.29 ± 2.76	14.52 ± 5.10
Size-free values	−0.03 ± 0.04	−0.05 ± 0.04	−0.11 ± 0.04
Body height			
Raw values	6.55 ± 1.38	6.32 ± 1.32	9.51 ± 3.75
Size-free values	−0.44 ± 0.05	−0.46 ± 0.05	−0.30 ± 0.05
Head width			
Raw values	11.29 ± 2.33	11.21 ± 1.87	11.89 ± 3.81
Size-free values	−0.20 ± 0.02	−0.21 ± 0.03	−0.19 ± 0.02
Head height			
Raw values	5.20 ± 1.12	5.53 ± 0.92	7.56 ± 2.50
Size-free values *a*	−0.54 ± 0.03	−0.52 ± 0.03	−0.39 ± 0.03
Head length			
Raw values	14.76 ± 2.65	15.02 ± 2.44	14.51 ± 4.23
Size-free values	−0.09 ± 0.02	−0.08 ± 0.04	−0.11 ± 0.02
Hind limbs length			
Raw values	34.96 ± 6.62	34.96 ± 5.71	29.38 ± 8.97
Size-free values	0.29 ± 0.02	0.29 ± 0.04	0.20 ± 0.03
Fore limbs length			
Raw values	51.00 ± 8.98	51.97 ± 8.51	45.55 ± 13.70
Size-free values	0.45 ± 0.02	0.46 ± 0.03	0.39 ± 0.03

Values are expressed as mean ± SD. For all variables but Body size (isometric), in the first line are raw values, while in the second line are size-free values.

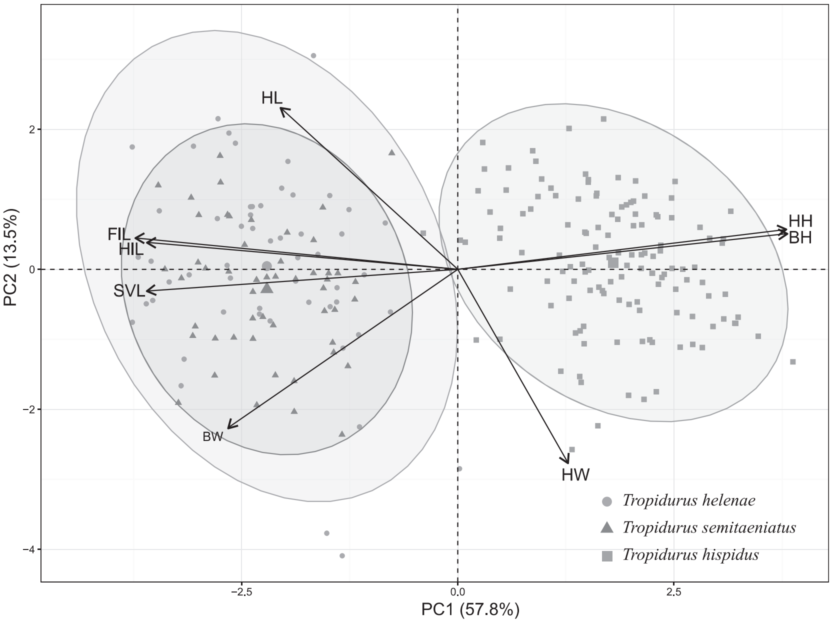

Fig. 3. Principal Component Analysis for morphological shape-free variables of *Tropidurus helenae* (●), *Tropidurus semitaeniatus* (▲) and *Tropidurus hispidus* (■). More details on Table 3.

HW and BW (Table 3). *Tropidurus semitaeniatus* and *T. helenae* differed from *T. hispidus* because of their flattened bodies and heads, and longer limbs (Appendix S1 and Fig. 3) (Table 2).

Food

Food niche breadth was smaller for *T. helenae* (1.89) than for *T. semitaeniatus* (2.63) and *T. hispidus*

doi:10.1111/aec.12486

Table 3. Principal Component Analysis results showing correlation among morphological variables of the first five PC's

Variable	PC1	PC1	PC3	PC4	PC5
SVL	−0.854	−0.073	0.026	−0.058	−0.493
BW	−0.632	−0.538	−0.322	−0.407	0.194
BH	0.909	0.122	−0.232	−0.050	−0.124
HW	0.303	−0.657	0.677	0.100	−0.012
HH	0.909	0.137	0.093	0.091	0.051
HL	−0.486	0.137	0.528	−0.419	0.088
FlL	−0.887	0.137	−0.024	0.283	0.051
HlL	−0.854	0.137	0.028	0.383	0.165
Eigenvalue	4.627	1.079	0.905	0.592	0.336
Proportion of variance explained	0.578	0.713	0.826	0.900	0.942

Eingenvalues and cumulative proportion of explained variance are shown for each PC.

(2.46). Overlap in diet was high for the three species, but even higher for the flattened species (*T. hispidus vs. T. helenae* = 0.863, *T. hispidus vs. T. semitaeniatus* = 0.948, *T. helenae vs. T. semitaeniatus* = 0.975). The most important food items for the three species were Formicidae and Isoptera (Table 4, Fig. 4). Mean volume of *T. hispidus* prey items (90.3 mm^3) was higher than that for *T. helenae* (10.8 mm^3) and *T. semitaeniatus* (16.4 mm^3), whereas no significant differences were found between mean volume of prey consumed by *T. helenae* and *T. semitaeniatus* (Kruskal-Wallis test, KW = 18.55, d.f. = 2, $P < 0.001$ Tukey-Kramer *post-hoc* test, $P < 0.05$).

DISCUSSION

Closely related species are expected to show similar ecologies (Richardson 2001; Losos 2008). Similarities in diet, microhabitat use, and morphology followed this phylogenetic trend: *T. helenae* and *T. semitaeniatus* (both from the *semitaeniatus* group; Frost 2001) were more similar to each other than to *T. hispidus* (of the *torquatus* group; Frost 2001). Nevertheless, all three species have much in common including similar diets, although differing in microhabitat use and morphology.

The flattened heads of saxicolous lizards may reduce bite force and restrict their diet to soft prey, as reported for lacertid and xenosaurid lizards (Herrel *et al.* 2001a,b; McBrayer 2004; Vanhooydonck *et al.* 2007). Although having flattened heads, *T. semitaeniatus* and *T. helenae* had a diet very similar to that of the robust *T. hispidus*, based on both soft (Isoptera and Araneae), and hard (Coleoptera, Hymenoptera, Hemiptera) prey items. Similarly, *T. semitaeniatus* and *T. hispidus* from a northernmost location in the Caatinga overlapped in diet, both with a generalist feeding habit (Kolodiuk *et al.* 2010; Ribeiro & Freire 2011; Gomes *et al.* 2015). *Tropidurus* lizards have a generalist diet consuming mainly ants, termites, wasps, bees and beetles according to availability, and usually include plant material in their diet (Cruz 1998; Van Sluys *et al.* 2004; Kolodiuk *et al.* 2010; Ribeiro & Freire 2011). Still, even though there were no apparent differences in the 'hardness' of consumed items, *T. semitaeniatus* and *T. helenae* preyed on smaller items than *T. hispidus*, which is likely a trade-off because of specialized morphology. A previous study comparing the diet of *T. hispidus* and *T. semitaeniatus* concluded that *T. semitaeniatus* may consume smaller preys than *T. hispidus* because of its smaller body size (Ribeiro & Freire 2011). In our study, however, *T. semitaeniatus* and *T. helenae* had significantly larger body sizes than *T. hispidus*. These results from our comparisons were based on the body size variable we created (which accounts for all measurements in the body) and not only SVL as proxy of body size (as in other studies). This method has been shown to be more effective at discriminating size and shape differences than other methods, like using covariates (Somers 1986). Hence, although flattened with smaller SVLs, *T. semitaeniatus* and *T. helenae* are larger when overall morphology is considered. However, the flattened morphology of the head could impose a prey size restriction to these lizards. Reduced bite force because of head flattening could account for the smaller size of prey consumed by these species (Vanhooydonck *et al.* 2007). Gomes *et al.* (2015) related prey size with head size of *T. semitaeniatus* and *T. hispidus* in another area within Caatinga. Those authors found a relationship between wider prey and *T. semitaeniatus*, and longer prey with *T. hispidus*. However, a quick analysis of the table containing diet of the species (Gomes *et al.* 2015; Table 3) shows that mean volume of the preys consumed by *T. hispidus* is about 3.5 times higher than that of the prey consumed by *T. semitaeniatus*, which supports our findings.

Tropidurus helenae and *T. semitaeniatus* used rocks in a much higher proportion than other microhabitat categories, whereas *T. hispidus* used a higher variety of microhabitats. The *semitaeniatus* group is composed of four lizard species, all inhabiting rock outcrops in the Caatinga of northeastern Brazil, while *T. hispidus* belongs to a group of generalist lizards, distributed across Caatinga, Cerrado, Chaco, Atlantic Forest and Amazon Forest domains (Passos *et al.* 2011; de Carvalho *et al.* 2013). The generalist habits of *T. hispidus* were also noted when we analysed microhabitat fidelity associated with the approach of a potential predator (Fig. 2). Both *T. semitaeniatus* and *T. helenae* of PARNASC generally used rocks

Table 4. Comparison of the diet of *Tropidurus hispidus*, *T. helenae* and *T. semitaeniatus* at Serra da Capivara National Park

	T. hispidus							*T.* heleane							*T.* semitaeniatus						
Category	VOL	VOL%	*N*	*N*%	*F*	*F*%	IRI	VOL	VOL%	*N*	*N*%	*F*	*F*%	IRI	VOL	VOL%	*N*	*N*%	*F*	*F*%	IRI
Acari	8.56	0.03	2.00	0.07	2.00	1.77	0.63	0.00	0.00	1.00	0.05	1.00	1.85	0.63	–	–	–	–	–	–	–
Araneae	1463.41	5.85	33.00	1.20	24.00	21.24	9.43	18.90	0.53	12.00	0.60	12.00	22.22	7.79	50.23	0.96	13	8.18	13	29.55	12.89
Blattaria	352.40	1.41	18.00	0.65	15.00	13.27	5.11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chilopoda	1574.77	6.30	15.00	0.54	15.00	13.27	6.71	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coleoptera	1316.61	5.26	118.00	4.29	61.00	53.98	21.18	242.69	6.87	51.00	2.56	26.00	48.15	19.19	3.82	0.07	20	12.58	18	40.91	17.85
Diplopoda	18.27	0.07	2.00	0.07	2.00	1.77	0.64	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diptera	0.00	0.00	1.00	0.04	1.00	0.88	0.31	79.58	2.25	11.00	0.55	9.00	16.67	6.49	25.62	0.49	5	3.14	3	6.82	3.48
Formicidae	10593.98	42.36	1129.00	41.01	102.00	90.27	57.88	1074.31	30.41	1370.00	68.88	49.00	90.74	63.34	563.59	10.75	50	31.45	33	75.00	39.06
Hemiptera	38.33	0.15	4.00	0.15	4.00	3.54	1.28	8.20	0.23	7.00	0.35	7.00	12.96	4.52	35.29	0.67	12	7.55	11	25.00	11.07
Hymenoptera	2382.14	9.52	55.00	2.00	27.00	23.89	11.81	5.67	0.16	8.00	0.40	6.00	11.11	3.89	907.3	17.30	23	14.47	23	52.27	28.01
Isopoda	4.52	0.02	1.00	0.04	1.00	0.88	0.31	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isoptera	6081.05	24.31	1334.00	48.46	49.00	43.36	38.71	1958.71	55.44	485.00	24.38	28.00	51.85	43.89	3549.06	67.67	19	11.95	19	43.18	40.93
Ixodida	–	–	–	–	–	–	–	0.07	0.00	1.00	0.05	1.00	1.85	0.63	–	–	–	–	–	–	–
Insect larvae	60.48	0.24	8.00	0.29	5.00	4.42	1.65	29.50	0.84	31.00	1.56	10.00	18.52	6.97	–	–	–	–	–	–	–
Lepidoptera	–	–	–	–	–	–	–	82.70	2.34	2.00	0.10	3.00	5.56	2.67	–	–	–	–	–	–	–
NI	0.00	0.00	1.00	0.04	1.00	0.88	0.31	–	–	–	–	–	–	–	27.97	0.53	8	5.03	8	18.18	7.92
Orthoptera	145.60	0.58	5.00	0.18	5.00	4.42	1.73	–	–	–	–	–	–	–	4.28	0.08	2	1.26	1	2.27	1.20
Plant material	255.92	1.02	14.00	0.51	14.00	12.39	4.64	–	–	–	–	–	–	–	34.01	0.65	1	0.63	1	2.27	1.18
Pseudoescorpiones	7.53	0.03	8.00	0.29	7.00	6.19	2.17	3.81	0.11	5.00	0.25	3.00	5.56	1.97	0.4	0.01	1	0.63	1	2.27	0.97
Scorpiones	627.07	2.51	3.00	0.11	2.00	1.77	1.46	28.07	0.79	2.00	0.10	2.00	3.70	1.53	–	–	–	–	–	–	–
Solifuga	80.51	0.32	2.00	0.07	1.00	0.88	0.43	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thysanoptera	–	–	–	–	–	–	–	0.95	0.03	4.00	0.20	2.00	3.70	1.31	–	–	–	–	–	–	–
Thysanura	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.1	0.27	1	0.63	1	2.27	1.06

Volume (VOL), number (*N*) and frequency (*F*) of each prey category are also expressed as percentages. The Index of Relative Importance (IRI) is shown for each species.

doi:10.1111/aec.12486

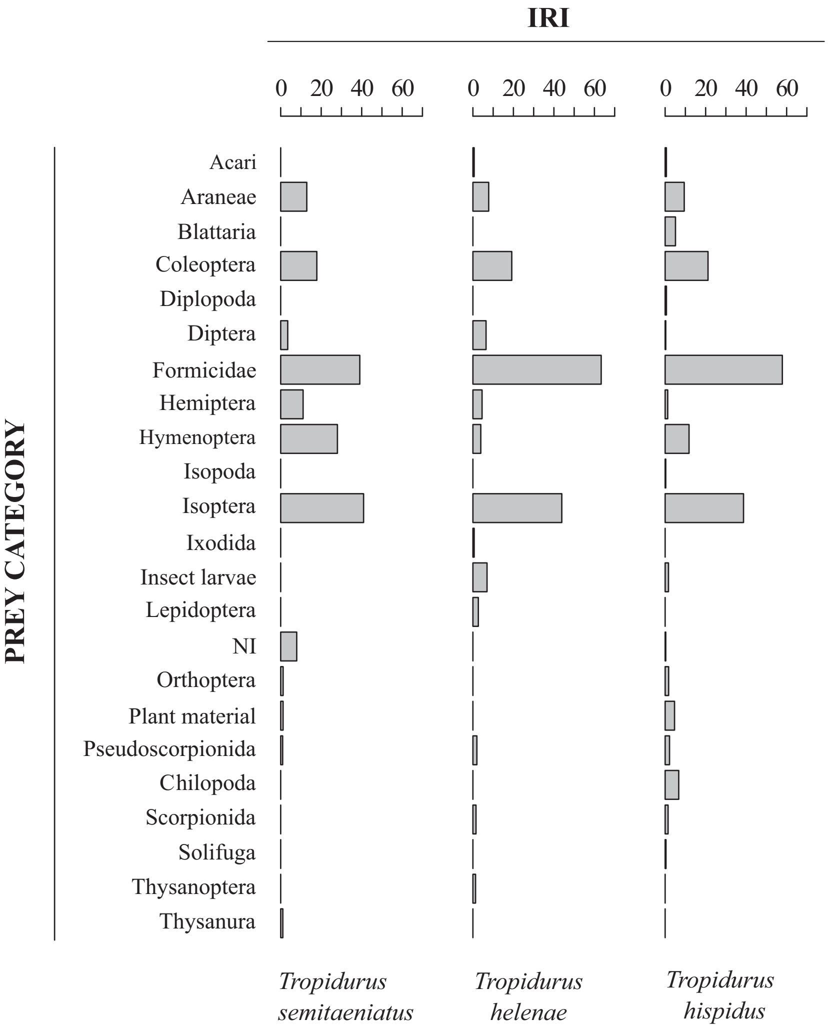

Fig. 4. Diet of *Tropidurus semitaeniatus*, *Tropidurus helenae*, and *Tropidurus hispidus* at Serra da Capivara National Park. Bars represent Index of Relative Importance (Pinkas *et al.* 1971). Note the high similitude in both the items consumed and their importance to the diet of studied species.

independently of the microhabitat where they were found, whereas *T. hispidus* generally changed its microhabitat category for a variety of other microhabitats. Rocks were the microhabitat most used by *T. semitaeniatus* and *T. hispidus* in other sites (Santana *et al.* 2014; Caldas *et al.* 2015; Gomes *et al.* 2015) as well. Gomes *et al.* (2015) found a higher fidelity of *T. hispidus* to rocks than that found in this study, probably because of the differences in the typology of the rock habitats: while in PARNASC rocky habitats were mostly represented by high rock walls, in the study site of Gomes *et al.* (2015) rocky habitats were mostly rock outcrops within flat areas.

Even though *T. helenae* and *T. semitaeniatus* overlapped in all aspects of their biology studied here, they did not share rock walls in our study site. The observed segregation in space between *T. helenae* and *T. semitaeniatus* could be the result of past competition in an environment where preferred microhabitat is not a limiting resource (e.g. Connell 1980). These two species overlapped in microhabitat use, in the proportion of sunny or shady spots used, in their body temperature, in the food they eat, and in most aspects of their morphometry. Given that *Tropidurus* species are generally territorial (Faria & Araujo 2004; Van Sluys *et al.* 2004; Meira *et al.* 2007), it is likely that aggressive behaviours related to reproductive barriers between these two closely related species are responsible for the spatially segregated distribution observed in the field.

Rock outcrops are very common in the Caatinga landscape (Ab'Saber 2005). Within these rocky habitats the *semitaeniatus* group has diversified into four species (*T. semitaeniatus*, *T. helenae*, *T. jaguaribanus* and *T. pinima*), all of them endemic and specialized in using rock crevices. The high availability of rocks apparently exerts an evolutionary pressure on the morphology of Caatinga lizards, to the point that populations of *T. hispidus* living in rocky habitats are more flattened than those living in open savannas (Vitt *et al.* 1997).

Still, studies on habitat segregation among sympatric *Tropidurus* species in rocky areas showed different results: a low overlap in activity and microhabitat use between *T. hispidus* and *T. semitaeniatus* was reported by Eloi and Leite-Filho (2013). According to those authors, thermoregulatory strategies and thermal constraints accounted for the segregated pattern observed. Gomes *et al.* (2015) found a high overlap in space, food and time niche between these two species. However, little differences in the use of basking sites, size and shape of prey items consumed, and a differential use of prey among seasons could reduce competition between species (Gomes *et al.* 2015). Contrarily, in studies comparing the ecology of species belonging to the *torquatus* group (*T. oreadicus vs. T. itambere*, Faria & Araujo 2004; *T. hispidus vs. T. montanus*, Van Sluys *et al.* 2004), lizards overlapped significantly in microhabitat, diet and activity. *Tropidurus oreadicus* and *T. itambere* were slightly different in morphology and segregated in height of the perch used, probably because of the aggressive behaviour between these species (Faria & Araujo 2004). In the case of *T. hispidus* and *T. montanus*, the authors did not provide explanations for the high overlap observed between the species (Van Sluys *et al.* 2004).

Different ecomorphs have been proposed for species adapted to different habits (Vanhooydonck & Van Damme 1999). Ground-dwelling species tend to have laterally compressed bodies and long limbs, which would provide greater lateral flexion, enhance manoeuvrability and reach higher speeds (Snyder 1954; Van Damme *et al.* 1997). On the other hand, species that climb are dorsoventrally compressed, which lowers the body's centre-of-gravity, and reduces the chances of toppling back while climbing (Jaksić *et al.* 1980; Pounds 1988; Sinervo & Losos 1991). In saxicolous species, a flat body could also allow them to hide in cracks and crevices (Miles 1994). According to this, a species cannot be adapted to every habitat, because of constraints or trade-offs between conflicting functions (Aerts *et al.* 2000; Vanhooydonck & Van Damme 2001). Although this might be true for many species, some exceptions are known (Goodman 2007; Clemente *et al.* 2013; Gomes *et al.* 2016; Tulli *et al.* 2016). Tropidurids tend to have a generalized morphology that allows them to perform well in a variety of substrates (Tulli *et al.* 2016). However, a relationship between both internal and external morphology and habit used has been found in *Tropidurus* (Tulli *et al.* 2016). The flattened models studied here (*T. semitaeniatus* and *T. helenae*) had longer limbs and flatter bodies than *T. hispidus*, which fits with their rock-climbing behaviour. Accordingly, these species had wider flexor digitorum longus aponeurosis, typical of strict saxicolous lizards (Tulli *et al.* 2016).

The studied species offer a clear example of trade-offs between a specialized morphology and ecology. *Tropidurus helenae* and *T. semitaeniatus* are specialized for living in rocky environments. Their flattened bodies may allow them to use rock crevices as refuges, and take advantage of the thermal properties of the rocks to rapidly increase their body temperature (Vitt 1981; Eloi & Leite-Filho 2013). Caldas *et al.* (2015) frequently observed *T. semitaeniatus* fleeing to rock crevices even at low temperatures when a potential predator approached. Moreover, their longer limbs allow them to lower their centre-of-gravity and easily move on rock surfaces, even on steep slopes (Zaaf & Van Damme 2001). The well-developed tendinous-muscular system of these species provide them with a higher resistance to the effort of climbing (Tulli *et al.* 2016). These specializations may be helpful when avoiding predators by reducing being exposed for long periods.

However, having a specialized ecomorph has associated costs. *Tropidurus semitaeniatus* and *T. helenae* have their diet apparently restricted to smaller prey than sympatric *Tropidurus* species like *T. hispidus* (Ribeiro & Freire 2011). Reproductive output is also affected. In the flattened ecomorphs clutch size is limited to two eggs per clutch (Vitt 1981; Ribeiro *et al.* 2012), low when compared with other *Tropidurus* species, with a clutch size of about six eggs (Vitt & Goldberg 1983; Ribeiro *et al.* 2012). Moreover, reproductive timing in *T. semitaeniatus* is similar to that of other sympatric *Tropidurus* species in different areas within its distribution (Vitt 1981; Vitt & Goldberg 1983; Ribeiro *et al.* 2012). It may indicate that flattened *Tropidurus* species do not compensate for their low clutch size by increasing the number of clutches per reproductive season. However, we were not able to corroborate reproductive constraints because none of the captured individuals of *T. helenae* and *T. semitaeniatus* were reproductively active during field work, preventing us from acquiring clutch size and egg volume data.

Habitat shift as a mechanism to avoid competition in the past might have been a trigger for the specialized morphology of the *semitaeniatus* group. Some evidences in this direction have been previously reported for the sympatric *T. hispidus* (Vitt *et al.* 1997) and in Lygosominae (Scincidae) lizards from Australia (Goodman & Isaac 2008). Dorsoventrally flattened heads and bodies are a consistently evolved trait of rock-dwelling lizards (Goodman & Isaac 2008), an indication of how environment may affect the evolution of lizard morphology (Vitt *et al.* 1997).

doi:10.1111/aec.12486

ACKNOWLEDGEMENTS

Daniel Mesquita thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for a Research Fellowship (303610/2014-0). Adrian Garda thanks CNPq for financial support (552031/2011-9 and 309531/2015-2). NP thanks CNPq and Guarino R. Colli for a Postdoctoral Fellowship in the period 10/2011–10/2012 (563320/2010-9, 47/2010-SISBIOTA), and Consejo Nacional de Investigaciones Científicas y Técnicas – CONICET for the Postdoctoral Fellowship.

REFERENCES

Ab'Saber A. N. (2005) Caatingas: O domínio dos sertões secos. In: *Os Domínios de Natureza no Brasil, Potencialidades Paisagísticas* (ed. A. N. Ab'Saber) pp. 83–100. Ateliê, São Paulo.

Aerts P., Van Damme R., Vanhooydonck B., Zaaf A. & Herrel A. (2000) Lizard locomotion: how morphology meets ecology. *Neth. J. Zool.* **50,** 261–77.

Brown W. L. & Wilson E. O. (1956) Character displacement. *Syst. Zool.* **5,** 49–64.

Burnaby T. (1966) Growth-invariant discriminant functions and generalized distances. *Biometrics* **22,** 96–110.

Caldas F. L. S., Santana D. O., dos Santos R. A., Gomes F. F. A., da Silva B. D. & Faria R. G. (2015) Atividade e uso do espaço de *Tropidurus semitaeniatus* (Iguania) em área de Mata Atlântica, Nordeste do Brasil. *Neotrop. Biol. Conserv.* **10,** 85–92.

Clemente C. J., Withers P. C., Thompson G. G. & Lloyd D. (2013) Lizard tricks: overcoming conflicting requirements of speed versus climbing ability by altering biomechanics of the lizard stride. *J. Exp. Biol.* **216,** 3854–62.

Cody M. L. (1968) On the methods of resource division in grassland bird communities. *Am. Nat.* **102,** 107–47.

Colli G. R., de Araújo A. F. B., da Silveira R. & Roma F. (1992) Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. *J. Herpetol.* **26,** 66–9.

Colwell R. K. & Futuyma D. J. (1971) On the measurement of niche breath and overlap. *Ecology* **52,** 567–76.

Connell J. H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35,** 131–8.

Corn P. S. (1994) Straight-line drift fences and pitfall traps. In: *Measuring and monitoring biological diversity: standard methods for amphibians* (eds. W. R. Heyer, M. A. Donnely, R. W. McDiarmid, L.-A. C. Hayek & M. S. Foster) pp. 109–17. Smithsonian Institution Press, Washington.

Cruz F. B. (1998) Natural history of *Tropidurus spinulosus* (Squamata: Tropiduridae) from the Dry Chaco of Salta, Argentina. *Herpetol. J.* **8,** 107–10.

de Carvalho A. L. G., de Britto M. R. & Fernandes D. S. (2013) Biogeography of the lizard genus *Tropidurus* Wied-Neuwied, 1825 (Squamata: Tropiduridae): distribution, endemism, and area relationships in South America. *PLoS One* **8,** e59736.

Cavalcanti L. B. Q., Costa T. B., Colli G. R. *et al.* (2014) Herpetofauna of protected areas in the Caatinga II: Serra da Capivara National Park, Piauí, Brazil. *Check List* **10,** 18–27.

Eloi F. J. & Leite-Filho E. (2013) Competing for a place in the sun: a short study with *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata: Tropiduridae). *Rev. Nordest. Biol.* **21,** 59–69.

Faria R. G. & Araujo A. F. B. (2004) Sintopy of two *Tropidurus* lizard species (Squamata: Tropiduridae) in a rocky Cerrado habitat in central Brazil. *Braz. J. Biol.* **64,** 775–86.

Frost D. (2001) Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Mol. Phylogenet. Evol.* **21,** 352–71.

Gomes F. F. A., Caldas F. L. S., dos Santos R. A. *et al.* (2015) Patterns of space, time and trophic resource use by *Tropidurus hispidus* and *T. semitaeniatus* in an area of Caatinga, northeastern Brazil. *Herpetol. J.* **25,** 27–39.

Gomes V., Carretero M. A. & Kaliontzopoulou A. (2016) The relevance of morphology for habitat use and locomotion in two species of wall lizards. *Acta Oecol.* **70,** 87–95.

Goodman B. A. (2007) Divergent morphologies, performance, and escape behaviour in two tropical rock-using lizards (Reptilia: Scincidae). *Biol. J. Linn. Soc.* **91,** 85–98.

Goodman B. A. & Isaac J. L. (2008) Convergent body flattening in a clade of tropical rock-using lizards (Scincidae: Lygosominae). *Biol. J. Linn. Soc.* **94,** 399–411.

Hardin G. (1960) The competitive exclusion principle. *Science* **131,** 1292–7.

Herrel A., Damme R. V., Vanhooydonck B. & Vree F. D. (2001a) The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* **79,** 662–70.

Herrel A., De Grauw E. D. & Lemos-Espinal J. A. (2001b) Head shape and bite performance in xenosaurid lizards. *J. Exp. Zool.* **290,** 101–7.

Hutchinson G. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93,** 145–59.

Jaksić F. M., Núnez H. & Ojeda F. P. (1980) Body proportions, microhabitat selection, and adaptive radiation of *Liolaemus* lizards in central Chile. *Oecologia* **45,** 178–81.

Jolicoeur P. (1963) 193. Note: the multivariate generalization of the allometry equation. *Biometrics* **19,** 497–9.

Kaiser H. F. (1991) Coefficient alpha for a principal component and the Kaiser-Guttman rule. *Psychol. Rep.* **68,** 855–8.

Kohlsdorf T., Garland T. Jr & Navas C. A. (2001) Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *J. Morphol.* **248,** 151–64.

Kohlsdorf T., Ribeiro J. M. & Navas C. A. (2006) Territory quality and male dominance in *Tropidurus torquatus* (Squamata, Tropiduridae). *Phyllomedusa* **5,** 109–18.

Kolodiuk 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 Am. J. Herpetol.* **5,** 35–44.

Lemos J. R. (2004) Composição florística do parque nacional Serra da Capivara, Piauí, Brasil. *Rodriguésia* **55,** 55–66.

Losos J. B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11,** 995–1003.

Losos J. B., Irschick D. J. & Schoener T. W. (1994) Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution* **48,** 1786–98.

doi:10.1111/aec.12486

Magnusson W. E., Lima A. P., Alves da Silva W., Carmozina de Araújo M. & Montgomery W. (2003) Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia* **2003,** 13–9.

McBrayer L. D. (2004) The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. *Zool. J. Linn. Soc.* **140,** 403–16.

Meira K. T. R., Faria R. G., Silva M. D. D. M., Miranda V. T. D. & Zahn-Silva W. (2007) História natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. *Biota Neotrop.* **7,** 155–64.

Miles D. (1994) Covariation between morphology and locomotory performance in sceloporine lizards. In: *Lizard Ecology: Historical and Experimental Perspectives* (eds L. Vitt & E. Pianka) pp. 207–35. Princeton University Press, Princeton.

Passos D. C., Lima D. C. & Borges-Nojosa D. M. (2011) A new species of *Tropidurus* (Squamata, Tropiduridae) of the *semitaeniatus* group from a semiarid area in Northeastern Brazil. *Zootaxa* **2930,** 60–8.

Pianka E. R. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4,** 53–74.

Pianka E. R. (1974) Niche overlap and diffuse competition. *Proc. Nat. Acad. Sci. USA* **71,** 2141–5.

Pianka E. R. (1981) Competition and niche theory. In: *Theoretical Ecology Principles and Applications* (ed. R. M. May) pp. 167–96. Sunderland.

Pinkas L., Oliphant M. S. & Iverson I. L. K. (1971) Food habits of Albacore, Bluefin Tuna, and Bonito in California waters. *Fish. Bull.* **152,** 47–63.

Pinto A. C. S., Wiederhecker H. C. & Colli G. R. (2005) Sexual dimorphism in the Neotropical lizard, *Tropidurus torquatus* (Squamata, Tropiduridae). *Amphibia-Reptilia*, **26,** 127–37.

Pohlert T. (2014) The pairwise multiple comparison of mean ranks package (PMCMR). *R package*.

Pounds J. A. (1988) Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland Anolis community. *Ecol. Monogr.* **58,** 299–320.

Prado D. (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. *Edinb. J. Bot.* **57,** 437–61.

Prado D. E. (2003) As Caatingas da América do Sul. In: *Ecologia e Conservação da Caatinga* (eds I. R. Leal, M. Tabarelli & J. M. Cardoso da Silva) pp. 3–74. Universidade Federal de Pernambuco, Recife.

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ribeiro L. B. & Freire E. M. (2011) Trophic ecology and foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. *Iheringia Sér. Zool.* **101,** 225–32.

Ribeiro L. B., Silva N. B. & Freire E. M. (2012) Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. *Rev. Chil. Hist. Nat.* **85,** 307–20.

Richardson J. M. (2001) The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. *Am. Nat.* **157,** 282–99.

Rocha C. & Bergallo H. (1990) Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. Evol.* **2,** 263–8.

Rodrigues M. T. (1987) Systematics, ecology and zoogeography of the *Tropidurus* of the *torquatus* group south of the Amazonian River [South America] (Sauria, Iguanidae). *Arq. Zool.* **31,** 105–230.

Rohlf F. J. & Bookstein F. L. (1987) A comment on shearing as a method for "size correction". *Syst. Biol.* **36,** 356–67.

Roughgarden J. (1976) Resource partitioning among competing species – a coevolutionary approach. *Theor. Popul. Biol.* **9,** 388–424.

Santana D. O., Caldas F. L. S., Gomes F. F. A. *et al.* (2014) Aspectos da História Natural de *Tropidurus hispidus* (Squamata: Iguania: Tropiduridae) em área de Mata Atlântica, nordeste do Brasil. *Neotrop. Biol. Conserv.* **9,** 55–61.

Schoener T. W. (1974) Resource partitioning in ecological communities. *Science* **185,** 27–39.

Schoener T. W. & Schoener A. (1971) Structural habits of rest Indian Anoles lizards I. Lowland Jamaica. *Breviora* **368,** 53.

Sinervo B. & Losos J. B. (1991) Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* **72,** 1225–33.

Snyder R. C. (1954) The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *Am. J. Anat.* **95,** 1–45.

Somers K. M. (1986) Multivariate allometry and removal of size with principal components analysis. *Syst. Biol.* **35,** 359–68.

Tulli M. J., Cruz F. B., Kohlsdorf T. & Abdala V. (2016) When a general morphology allows many habitat uses. *Integr. Zool.* **11,** 483–99.

Van Damme R., Peter A. & Vanhooydonck B. (1997) No trade-off between sprinting and climbing in two populations of the Lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.* **60,** 493–503.

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. *J. Herpetol.* **38,** 606–11.

Vanhooydonck B. & Van Damme R. (1999) Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol. Ecol. Res.* **1,** 785–805.

Vanhooydonck B. & Van Damme R. (2001) Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers? *J. Evol. Biol.* **14,** 46–54.

Vanhooydonck B., Herrel A. & Van Damme R. (2007) Interactions between habitat use, behavior, and the trophic niche of lacertid lizards. In: *Lizard ecology: The evolutionary consequences of foraging mode* (eds. S. M. Reilly, L. D. McBrayer & D. B. Miles) pp. 427–49. Cambridge University Press, Cambridge.

Vitt L. J. (1981) Lizard reproduction: habitat specificity and constraints on relative clutch mass. *Am. Nat.* **117,** 506–14.

Vitt L. J. (1995) The ecology of tropical lizards in the caatinga of northeast Brazil. *Occ. Pap. Oklahoma Mus. Nat. Hist.* **1,** 1–29.

Vitt L. J. & Goldberg S. R. (1983) Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia* **1983,** 131–41.

Vitt L. J., Caldwell J. P., Zani P. A. & Titus T. A. (1997) The role of habitat shift in the evolution of lizard morphology:

doi:10.1111/aec.12486

evidence from tropical *Tropidurus*. *Proc. Natl Acad. Sci. USA* **94,** 3828–32.

Winemiller K. O. & Pianka E. R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.* **60,** 27–55.

Zaaf A. & Van Damme R. (2001) Limb proportions in climbing and ground-dwelling geckos (Lepidosauria, Gekkonidae): a phylogenetically informed analysis. *Zoomorphology* **121,** 45–53.

Zhang J., Ding Q. & Huang J. (2013) spaa: Species association analysis. R package version 0.2.1.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Picture of studied species. A) *T. hispidus*, B) *T. helenae*, and C) *T. semitaeniatus*. Note the flattened body and head, and the longer limbs of the latter two when compared to *T. hispidus*.

doi:10.1111/aec.12486