SINTOPY OF TWO *Tropidurus* LIZARD SPECIES (SQUAMATA: TROPIDURIDAE) IN A ROCKY CERRADO HABITAT IN CENTRAL BRAZIL

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ABSTRACT

We studied the ecology of *Tropidurus itambere* and *T. oreadicus* that occur syntopically in rocky habitats of Cerrado vegetation in central Brazil during the dry season (April to September 2000). The two species are ecologically similar, but somewhat differentiated in vertical microhabitat use. The two species preferred rocky surface microhabitat. Both species demonstrated a unimodal activity pattern, with a peak between 10 and 15 h. Their diets were similar in composition and prey size. The most frequent item used by both species was ants, whereas the most important preys volumetrically were termites and ants. Small morphological differences observed between the two *Tropidurus* species could explain minor microhabitat range. These ecological differences are slight, when compared with those observed between sympatric species of *Tropidurus* in spatially more heterogeneous landscapes. Considering the slight ecomorphological divergence between the two *Tropidurus* species and their high abundance in outcrops, we suggest that interspecific territoriality is the mechanism of coexistence.

Key words: resource partitioning, lizard, saxicolous, Cerrado, Tropidurus itambere, Tropidurus oreadicus.

RESUMO

Sintopia de duas espécies de *Tropidurus* (Squamata: Tropiduridae) em um habitat de cerrado rupestre no Brasil Central

Estudamos a ecologia de *Tropidurus itambere* e *T. oreadicus* que ocorrem sintopicamente em habitats rochosos da vegetação de Cerrado, do Brasil Central, durante a estação seca (de abril até setembro de 2000). As duas espécies são ecologicamente similares, mas diferem no uso vertical do microhabitat, sendo a superfície das rochas o microhabitat mais usado pelas duas espécies. Ambas as espécies tiveram padrão de atividade unimodal, com pico entre as 10 e 15 h. Suas dietas foram similares na composição e tamanho de presa. O alimento mais freqüente das duas espécies de lagartos foi formiga, enquanto as presas volumetricamente mais importantes foram cupins e formigas. Pequenas diferenças morfológicas foram observadas entre as duas espécies de *Tropidurus*, que poderiam estar relacionadas ao uso do microhabitat. *T. itambere* é relativamente menor, mais pesado e robusto, usando poleiros mais baixos. *T. oreadicus* é maior, mais esguio, com extremidades mais longas (cauda, membros anteriores e posteriores), usando uma faixa vertical maior do microhabitat. Estas diferenças ecológicas são pequenas quando comparadas com as diferenças observadas entre espécies simpátricas de *Tropidurus* em paisagens espacialmente mais heterogêneas. Considerando a pequena divergência ecomorfológica entre as duas espécies de *Tropidurus* e sua alta

abundância nos afloramentos, sugerimos que a territorialidade interespecífica é o mecanismo de coexistência.

Palavras-chave: partilha de recursos, lagarto, saxícola, Cerrado, Tropidurus itambere, Tropidurus oreadicus.

INTRODUCTION

Differences among sympatric species in morphology, foraging mode, and spatial use are considered coexistence mechanisms (Pianka, 1973; Vitt et al., 2000). In South America, sympatry is common among co-generic lizard species. However, the degree of niche overlap is often poorly understood. The genus Tropidurus is widely distributed in Brazil, with species in the Amazon Forest, Cerrado, Caatinga (including "Canga" - open vegetation on iron rocks), and Atlantic forest (including "Restinga" vegetation - coastal sand dunes) (Araujo, 1987, 1991; Rodrigues, 1987; Rocha & Bergallo, 1990; Vitt & Caldwell, 1993). Tropidurus are very abundant diurnal lizards, with species occurring anywhere from open formations to forested habitats (Frost, 1992; Harvey & Gutberlet, 2000; Frost et al., 2001).

The Cerrado is the largest savanna and the second largest biome of the Neotropical region, with approximately two million km2. The very heterogeneous landscape ranges from grassland to forest habitats, with open vegetation predominating (Eiten, 1978). Fire and edaphic factors strongly influence cover vegetation variety. In the central Brazilian Cerrado, several species of Tropidurus co-occur in assemblages of two to four species (Rodrigues, 1987; Vitt, 1991; Colli et al., 1992; Colli et al., 2002). The large spatial heterogeneity of the Cerrado, with open and closed (forested) habitats side by side, allows sympatric colonization by arboreal and saxicolous Tropidurus species. However, even in homogeneous open habitats, like the rocky cerrado of mountain outcrops in central Brazil, syntopy of pairs of species is a common phenomenon (Rodrigues, 1987).

Considering the premise that morphological adaptations of species reflect their ecological relationships (Ricklefs *et al.*, 1981), we compared morphology, niche dimensions, and niche relationships of two closely-related, syntopic species of *Tropidurus* (*T. itambere* and *T. oreadicus*), correlating morphological differences with the amount of niche partitioning observed in space, food, and time dimensions.

MATERIAL AND METHODS

Tropidurus itambere and T. oreadicus were studied on a mountain top called "Serra dos Pirineus" (Pirenópolis, Goiás; 15°51'S, 48°57'W). The mountain itself is isolated from the others in the area by forested valleys and plantations. Its landscape is a mosaic of scattered quartzite outcrops, surrounded by white sand eroded from the mountains, the elevations of which varies from 900 m to 1200 m. These outcrops are covered by patchy and xeric vegetation, from grass fields to dense shrubs containing a few dispersed trees (rocky cerrado habitat). Both species are very abundant in cerrado rocky outcrops (Van Sluys, 1993; 1995; Vitt, 1993; Avila-Pires, 1995), but are extremely rare in the savannalike vegetation covered with white sands between the outcrops (sandy cerrado habitat).

We accumulated field data in 46 working days during the dry season (April to September 2000). Lizards were collected in the outcrops with an air rifle, elastic bands, or by hand, and we tagged individuals for identification. Time of collection, microhabitat use at first sighting and following the collector's approach (safe site), weather conditions (sunny, cloudy, or rainy), kind of activity (at first sighting and subsequently at the safe site), light exposure (direct sun, filtered sun, or shade) and perch height were recorded for each lizard collected. Within 30 seconds of capture, cloacal temperature was recorded by a Minipa[®] digital thermometer with precision of 0.1°C. Temperatures of substrate, air (both at 1 cm above the substrate and 1.5 m aboveground) were also recorded using the same thermometer.

In the laboratory, lizards were weighted with Pesola[®] dinamometers (scales ranging from 0.1 g to 0.5 g of precision). Ten morphological measurements were taken: snout-vent length; tail length; length of regenerated tail if any (all to 1.0 mm) with a linear ruler; body width and height from the middle of the chest; head width at the widest point of the skull; head length from the anterior edge of the tympanum to snout tip; head height at widest point of the skull and hindleg, and foreleg lengths to 0.01 mm using Mitutoyo[®]

digital calipers. Lizards were fixed in 10% formalin. Later, they were dissected. Sex was confirmed based on internal anatomy, stomachs were removed and placed in 70% alcohol for subsequent examination, and reproductive organs were examined. Females were considered sexually mature if they had oviductal eggs or enlarged vitellogenic follicles. Males were so considered if presenting enlarged testes and convoluted epididymides indicative of breeding activity. The snout-vent length of the smallest female and male presenting these characteristics respectively were used to estimate minimum size at sexual maturity.

All linear morphological variables, as well as dimensions of prey used by the lizards, were \log_{10} -transformed to minimize scale effects. To increase the number of available data, tail length was estimated using a linear regression model for those lizards with broken or regenerated tails.

Body size was defined as a size variable (isometric) following the procedure of Somers (1986). First, scores of a size eigenvector (isometric), defined a priori as p^{-0.5}, were obtained by multiplying matrix n versus p of the \log_{10} -transformed data, where *n* is the number of observations and p is the isometric eigenvector (Jolicoeur, 1963; Somers, 1986). To remove the size effect from the morphological variables, we calculated residuals from the regressions between log₁₀-transformed morphological variables and body size. We performed a principal component analysis (PCA) on the size-adjusted morphological variables to examine similarities or differences in morphology between species. To verify if the differences were significant, we performed a multivariate analysis of variance (MANOVA) with the first five PCA factors. We compared body mass between species and sexes with a two-factor ANOVA on the residuals from the body size versus log₁₀ mass regression. We compared body size between species and sexes with a two-factor ANOVA. Only sexually mature lizards were used in these analyses.

Interspecific differences in microhabitat use at first sighting and after collector's approach (safe site), weather conditions, and lizard's light exposure were tested with Chi-square test. Significance of distribution differences for daily activity patterns and diet composition (by volume and by prey number) were verified using the Kolmogorov-Smirnov test. Divergence between the two species in vertical use of microhabitat (height above ground measured in cm) was tested with a one-way analysis of variance (ANOVA). Species differences in length and width of the largest prey in the stomachs were tested with MANOVA. Lizard's body, substrate, air temperatures at 1 cm above the substrate and air + 1.5 m aboveground were also compared with MANOVA. For each species, the relationship between the lizard's body temperature and the environmental temperatures cited above were tested by a multiple regression (Zar, 1998).

We opened lizard stomachs and contents were carefully removed and spread on a petri dish. Prey items were counted, identified to the lowest taxonomic category possible (usually order), and we measured length and width to 0.01 mm with Mitutoyo[®] digital calipers. The prey volume was estimated using the spheroid volume formula:

Volume = $(\pi$.length.width²)/6

We used Simpson's diversity measure (Simpson, 1949) to estimate niche breadth:

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

where p is the proportional utilization of prey item i and n is the number of resource categories. B varies from 1 (exclusive use of a single resource type) to n (even use of all resource types).

Niche overlaps were calculated with the symmetrical overlap formula from Pianka (1973):

$$\phi_{jk} = \frac{\sum_{n=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^{2} \sum_{i=1}^{n} p_{ik}^{2}}}$$

where symbols are the same as above but j and k represent lizard species. Values approaching 0 indicate no similarity in resource use whereas values approaching 1 indicate highly similar resources.

To investigate the relationship between prey dimensions and morphological head measurements, we performed a canonical correlation analysis (Tabachnick & Fidell, 1996) between two variable groups (maximum prey length and width versus head length, width, height, and jaw length) for each species. The significance level used in the hypothesis tests was 5%. Means are given + 1 SD. All lizards were deposited in the Herpetological Collection of the University of Brasília (CHUNB).

RESULTS

A summary of the morphological data for *Tropidurus itambere* and *T. oreadicus* is shown in Table 1. We obtained significant differences in body size between the sexually mature *Tropidurus* species $(F_{1,325} = 205.47; p < 0.001)$ and between sexes $(F_{1,325} = 4.89; p < 0.001)$. However, the interaction was not significant $(F_{1,325} = 3.33; p = 0.07)$. The adjusted mass was 0.01 \pm 0.05 g (N = 194) for *T. itambere* and -0.02 \pm 0.03 g (N = 136) for *T. oreadicus*. The mass differed between species $(F_{1,325} = 40.78; p < 0.001)$, but not between sexes $(F_{1,325} = 2.58; p = 0.11)$ or between species and sexes together $(F_{1,325} = 3.43; p = 0.07)$.

Principal components analysis (PCA) on sizeadjusted morphological data suggested morphological differences among species (Table 2 and Fig. 1). A MANOVA applied to the first five PCA factors showed significant differences in body shape between the species (Wilks' Lambda = 0.5832; p < 0.001, N = 328). However, the first two components accumulated less than 60% of the explained variance. Positive values in the first principal component were related with larger body heights, body widths, and head heights, and inversely with smaller extremities (tail, hindleg, and foreleg lengths). Positive values in the second principal component were related with larger dimensions of the head and inversely smaller body height and width. Tropidurus itambere is more robust than T. oreadicus, having smaller tail, hindleg, and foreleg lengths.

Both species used similar microhabitats, mainly rocky surfaces, at first sighting and safe site (after collector's approach) (Fig. 2; $\chi^2 = 6.307$, df = 4; p = 0.1774). The estimated spatial niche breadths were 1.17 for the two *Tropidurus* species, with high microhabitat overlap between them (0.999). However, significant perch height differences were observed between species ($F_{1,460} = 7.14$; p = 0.01), with *T. itambere* on average using lower perches ($\bar{x} = 63.30 \pm$ 46.00 cm) than *T. oreadicus* did ($\bar{} = 75.19 \pm 49.56$ cm; Fig. 2).

The diets of *Tropidurus itambere* and *T. oreadicus* were similar and numerically dominated by Formicidae and Isoptera (Table 3). Considering prey volume, the diet of *T. itambere* mainly consisted of Isoptera, Formicidae, and Orthoptera. *Tropidurus oreadicus* mainly consumed Isoptera, Formicidae,

insect larvae, and Orthoptera. Besides invertebrates, the two *Tropidurus* species ate plant material (mostly flowers) and vertebrates (Table 3). Vertebrates ingested by *T. itambere* were *Cnemidophorus ocellifer* and a foot of an unidentified *Tropidurus*, while vertebrates consumed by *T. oreadicus* were *Micrablepharus maximiliani*, *Amphisbaena* cf. *vermicularis*, and an unidentified lizard tail.

Diet overlap indices calculated using number of preys were 0.999 and 0.921 for volumetric data. The high trophic niche similarity between the two species contrasts with the results of statistical tests: significant differences were obtained for volumetric $(D_{max} = 0.25; p < 0.00001)$ and numeric proportions of prey type ingested ($D_{max} = 0.34$; p < 0.00001). Both species ingested prey of similar size (Wilk's lambda = 0.9951; p = 0.3653; length: *T. itambere*, 8.37 ± 6.85 mm, N = 200; and T. oreadicus, $9.29 \pm$ 7.51 mm, N = 217; width: T. itambere, 2.14 ± 1.53 mm, N = 200; and T. oreadicus, 2.21 ± 1.68 mm, N = 217). Canonical correlation analysis showed significant associations between head measurements and prey dimensions for the two species (Table 4). Considering the first canonical variable, positive relationships were obtained for head length and prey width, and inverse ones for jaw and prey lengths (Table 4).

During fieldwork aggressive encounters among Tropidurus lizards were commonly observed but not quantified. Tropidurus itambere and T. oreadicus were active throughout the day, showing the same activity pattern ($D_{max} = 0.02$, p = 1.00). Both species have extensive and unimodal activity, usually from 8 h to 18 h (Fig. 3). The estimated temporal niche breadths were 7.27 for T. itambere and 7.48 for T. oreadicus. Temporal niche overlap for the two species was also high (0.988). There were no significant differences in activity at the first sighting (= 0.65, df = 2, p = 0.72), at which both species were usually motionless but ran after observer's approach (Fig. 4), hiding mainly in rock crevices (= 4.12, df = 4, p = 0.39; Fig. 2). The two species were usually active when the sun was out (= 3.98, df = 2, p = 0.14; Fig. 5) and were mainly exposed to direct sunlight (= 1.179, df = 2, p = 0.5547; Fig. 5), demonstrating the behavior common to heliothermic "sit-and-wait" lizards.

Body and environmental temperatures were similar for both species (Wilk's lambda = 0.9863; p = 0.1892; Table 5). However, the two species

temperature (R² = 0.316; $F_{1,212}$ = 14.59; p < 0.001). Body temperatures of *T. oreadicus* were significantly associated with air temperature 1 cm above the substrate (R² = 0.071; $F_{1,223}$ = 17.15; p < 0.001).

 TABLE 1

 Morphological characteristics summary of sexually mature males and females for *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil.

Character		Tropidur	us itambere		Tropidurus oreadicus					
	Female	(N = 84)	Male	(N = 110)	Female	(N = 53)	Male (N = 83)			
	Mean <u>+</u> SD	MinMax.	Mean <u>+</u> SD	MinMax.	Mean <u>+</u> SD	MinMax.	Mean <u>+</u> SD	MinMax.		
Body size (mm)	3.91 <u>+</u> 0.10	3.97-4.52	3.99 <u>+</u> 0.15	3.54-4.33	4.13 <u>+</u> 0.13	3.87-4.42	4.28 <u>+</u> 0.21	3.85-4.62		
Mass (g)	7.64 <u>+</u> 2.06	4.50-14.00	9.25 <u>+</u> 3.00	3.40-17.00	10.70 <u>+</u> 3.26	4.90-20.00	15.82 <u>+</u> 6.53	6.10-30.50		
SVL (mm)	58.31 <u>+</u> 4.78	52.00-70.00	61.94 <u>+</u> 6.87	47.00-80.00	67.81 <u>+</u> 6.58	59.00-82.00	76.07 <u>+</u> 10.76	59.00-95.00		
Body width (mm)	16.26 <u>+</u> 2.47	10.00-23.70	15.80 <u>+</u> 2.43	8,96-22,27	18.00 <u>+</u> 3.33	12.38-26.61	18.56 <u>+</u> 3.38	11.69-24.71		
Body height (mm)	9.02 <u>+</u> 1.70	5.32-14.07	9.11 <u>+</u> 1.59	3.95-12.97	9.56 <u>+</u> 1.54	6.77-14.05	10.60 <u>+</u> 2.62	5.14-16.94		
Head width (mm)	11.31 <u>+</u> 1.01	9.91-14.99	12.64 <u>+</u> 1.72	9.39-16.99	13.02 <u>+</u> 1.53	10.37-17.22	15.03 <u>+</u> 2.42	10.62-20.71		
Head length (mm)	13.89 <u>+</u> 1.05	10.16-16.14	15.41 <u>+</u> 1.70	11.58-19.59	15.83 <u>+</u> 1.48	12.47-18.61	18.24 <u>+</u> 2.42	13.71-23.06		
Head height (mm)	6.71 <u>+</u> 0.75	4.92-8.92	7.77 <u>+</u> 1.23	4.82-11.72	7.70 <u>+</u> 1.09	5.56-10.66	9.24 <u>+</u> 1.73	5.45-12.42		
Tail length (mm)	74.84 <u>+</u> 6.79	59.00-92.79	81.59 <u>+</u> 9.44	59.00-107.00	106.16 <u>+</u> 9.55	80.00-128.69	119.00 <u>+</u> 18.33	77.00-152.00		
Foreleg length	23.41 <u>+</u> 1.87	18.62-28.22	24.76 <u>+</u> 2.73	16.38-32.29	29.67 <u>+</u> 3.21	23.24-39.82	33.05 <u>+</u> 5.25	21.58-42.75		
Hind-leg length (mm)	34.62 <u>+</u> 2.88	29.53-45.07	38.14 + 3.89	29.36-47.34	45.97 + 4.36	34.62-59.99	53.19 + 8.44	37.36-66.28		

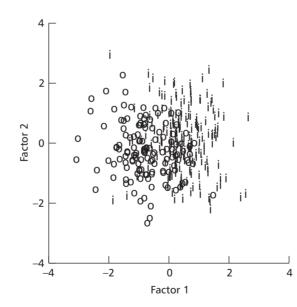


Fig. 1— Plot of unrotated factor scores for PCI and PCII on size-adjusted morphological variables for *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil. Factor I was related to larger body heights, body width, and head height, and inversely with smaller extremities (tail, hindleg, and foreleg lengths). Factor II was related with larger dimensions of the head and inversely smaller body height and width.

Variable	Factor								
Variable	Ι	II	III	IV	V				
Snout-vent length (SVL)	-0.25	0.29	-0.73	-0.28	-0.42				
Body width	0.41	-0.45	-0.53	0.54	0.20				
Body height	0.67	-0.43	0.28	-0.48	-0.05				
Head length	0.04	0.74	0.03	0.24	0.15				
Head width	0.14	0.65	-0.15	-0.31	0.54				
Head height	0.39	0.49	0.40	0.29	-0.48				
Tail length	-0.84	-0.07	-0.12	-0.08	-0.19				
Foreleg length	-0.71	-0.25	0.16	0.02	0.21				
Hind-leg length	-0.81	0.01	0.34	0.12	0.06				
Eigenvalues	2.72	1.77	1.23	0.86	0.84				
% of variance	30.24	19.66	13.66	9.54	9.38				

 TABLE 2

 Unrotated factor scores from principal components of size-adjusted morphological variables for *Tropidurus itambere* and *T. oreadicus*.

DISCUSSION

Morphological differences in lizard limbs and body shape are usually associated with general use of space, whereas morphological differences in head characteristics in particular suggest diet divergence. Relatively longer limbs increase the possibility of escaping predators by running, or by climbing to higher perches, while more voluminous heads permit the ingestion of larger prey (Pianka, 1969; Pianka & Parker, 1972; Moermond, 1979; Pounds, 1988; Losos, 1990; Vitt & Caldwell, 1993; Milles, 1994; Vitt et al., 2000). Like other "sit-and-wait" lizards, body shape and ecology are well related among Tropidurus species (Kohlsdorf et al., 2001). However, when populations of the same species were compared, morphology is variable between habitats (Vitt et al., 1997).

Tropidurus itambere and *T. oreadicus* belong to a taxonomic group that uses essentially open habitats and the ecomorphological similarity observed in the outcrops was expected (Harvey & Gutberlet, 2000). Size differences between the two *Tropidurus* species studied at Pirenopolis are relatively smaller than the differences found between sympatric *Tropidurus* species in more heterogeneous habitats (Araujo, 1987; Colli *et al.*, 1992; Vitt, 1991, 1993; Vitt & Goldberg, 1983; Vitt & Carvalho, 1995). However, the relatively larger, flatter and more elongated body of *T. oreadicus* may provide additional advantages when disputing space in the outcrops. Finally, *Tropidurus itambere* is a smaller, more robust, and proportionally heavier species than *T. oreadicus*.

High predation pressure can prevent competition among lizard populations by reducing lizard numbers. Vitt et al. (1996) suggested that predation risk in open areas, such as rocky outcrops, can be minimized by reducing the amount of time necessary for basking in the sun, due to the high temperatures on rocky surfaces exposed to direct sunlight. Predation risk for the two Tropidurus at Pirenópolis is high, since the most frequently chosen microhabitat (rocky surface) is largely exposed to predator attack. In Pirenópolis both species are cryptic in the outcrops and their camouflageis similar. Several birds and snakes species that eat lizards were recorded in the study area. Compared with the "good colonist" T. *itambere*, the elongated and flattened body of T. oreadicus may increase the area exposed to direct sunlight, allowing rapid thermoregulation under high insulation. This characteristic also increases crevice use for refuge in the rocks (safe sites), reducing predation risks and overheating. Crevice use as refuge has already been recorded for T. oreadicus (Vitt, 1993), T. semitaeniatus (Vitt & Goldberg, 1983), and T. hispidus (Vitt & Carvalho, 1995). Sites with great amounts of resources, like thermoregulation perches and crevices for hiding, may be battled over by territorial Tropidurus lizards.

Prey type	Tropidurus itambere ($N = 244$)						Tropidurus oreadicus (N = 255)					
	N	%N	V (mm ³)	%V	F	F%	Ν	%N	V (mm ³)	%V	F	F%
Acarina	2	0.02	3.58	0.01	2	0.82						
Araneae	46	0.41	810.35	2.67	41	16.80	79	0.97	345.16	1.14	47	18.43
Blattaria	3	0.03	1448.36	4.78	3	1.23	2	0.02	57.23	0.19	2	0.78
Coleoptera	354	3.19	1605.06	5.29	135	55.33	155	1.90	896.82	2.96	97	38.04
Diptera	5	0.05	12.57	0.04	4	1.64	11	0.13	118.48	0.39	5	1.96
Ephemeroptera							1	0.01	4.30	0.01	1	0.39
Gastropoda	2	0.02	142.02	0.47	1	0.41	3	0.04	122.57	0.40	3	1.18
Hemiptera	129	1.16	612.96	2.02	74	30.33	129	1.58	1754.85	5.78	84	32.94
Homoptera	16	0.14	15.57	0.05	15	6.15	33	0.40	1304.97	4.30	28	10.98
Hymenoptera												
Formicidae	6118	55.16	5868.28	19.35	221	90.57	4441	54.32	6929.41	22.83	231	90.59
Other	22	0.20	504.29	1.66	18	7.38	42	0.51	261.04	0.86	17	6.67
Isoptera	4186	37.74	11781.31	38.84	117	47.95	2994	36.62	7785.17	25.65	94	36.86
Insect larvae	86	0.78	1881.11	6.20	62	25.41	117	1.43	4213.62	13.89	68	26.67
Lepidoptera	2	0.02			2	0.82	2	0.02	301.59	0.99	2	0.78
Mantodea	1	0.01			1	0.41	4	0.05	514.27	1.69	4	1.57
Unidentified	5	0.05	181.00	0.60	5	2.05	1	0.01			1	0.39
Neuroptera	7	0.06	181.26	0.60	7	2.87	7	0.09	311.08	1.03	6	2.35
Odonata							1	0.01	11.59	0.04	1	0.39
Orthoptera	51	0.46	3809.26	12.56	49	20.08	66	0.81	3670.17	12.09	62	24.31
Phasmida	2	0.02	270.93	0.89	2	0.82						
Pseudoscorpionida	4	0.04	3.18	0.01	4	1.64	4	0.05	3.05	0.01	4	1.57
Psocoptera	1	0.01	0.44	0.002	1	0.41						
Scolopendromorpha							1	0.01	578.69	1.91	1	0.39
Scorpiones							2	0.02	18.68	0.06	2	0.78
Vertebrates	4	0.04	1141.25	3.76	4	1.64	5	0.06	175.01	0.58	5	1.96
Plant material	45	0.41	57.97	0.19	45	18.44	75	0.92	968.61	3.19	75	29.41
Sums	11091	100.00	30330.55	100.00			8175	100.00	30346.36	100.00		
Niche breadths		2.23		4.63				2.32		6.25		

 TABLE 3

 Diet summary for Tropidurus itambere and T. oreadicus. Frequency (F) is the number of lizards containing a particular prey type, (V) is the volume, and (N) is the number of prey type.

Huey & Pianka (1981) showed that the kind of prey consumed by lizards is related with their foraging mode: "sit-and-wait" lizards eat active and mobile preys and "widely foraging" lizards eat more sedentary ones. In the present work, both active (Formicidae, Orthoptera) and sedentary preys (termites and insect larvae) were important items in the diet of both *Tropidurus* species. *Tropidurus itambere* and *T. oreadicus* are probably less selective and consume a larger range of prey during the dry season. In addition, at this time their daily activity pattern was unimodal. This was not surprising since seasonal differences in diet and daily activity pattern are expected for these species (Van Sluys, 1992, 1995; Rocha & Bergallo, 1990).

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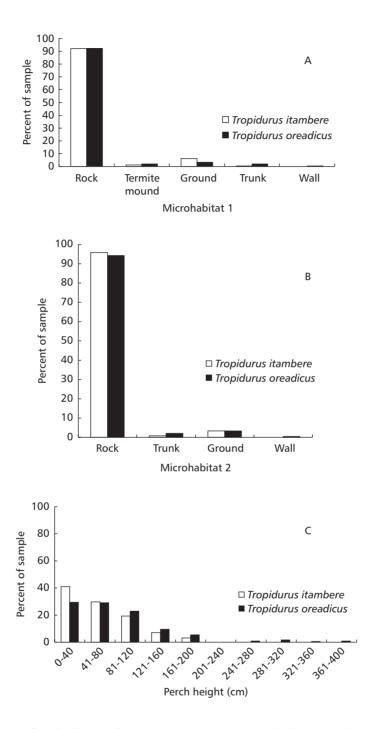


Fig. 2— Microhabitat (A – first sighting; B – after the observer's approach; N = 243 Ti and N = 250 To) and C – perch height (N = 240 Ti and N = 244 To) occurrence of *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil.

	Tropiduru	s itambere	•	Tropidurus oreadicus			
	Canonical	S	Canonical coefficients				
Head measurements	First canonical variable	Second c varia		First canonical variable	Second canonica variable		
Head width	0.22	0.8	30	-0.08	1.04		
Head height	-0.11	-0.58		-0.75	1.68		
Head length	1.92	1.26		0.71	0.86		
Jaw length	-1.24	-2.10		-0.89	-3.61		
Prey measurements							
Maximum prey length	-0.40	1.73		0.54	-1.64		
Maximum prey width	1.31 -1.2		20	0.51	1.65		
Canonical variable	Canonical correlation	χ^2 p		Canonical correlation	χ^{2}	р	
Ι	0.26	15.98 0.04		0.37	33.30	< 0.05	
II	0.11	2.38 0.50		0.11	2.40	0.49	

 TABLE 4

 Canonical correlation analysis of prey dimensions versus head dimensions of *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil.

 TABLE 5

 Summary of temperature characteristics for *Tropidurus itambere* and *T. oreadicus*.

Temperature	Trop	oidurus itam	bere	Tropidurus oreadicus				
	Mean <u>+</u> SD	Ν	MinMax.	Mean <u>+</u> SD	Ν	MinMax.		
Body	33.07 <u>+</u> 2.84	218	22.00-38.00	33.48 <u>+</u> 2.08	232	22.00-38.00		
Substrate	27.42 <u>+</u> 4.21	218	17.50-38.80	28.03 <u>+</u> 3.54	232	19.30-39.40		
Air 1 cm	25.72 <u>+</u> 3.34	218	14.70-34.80	26.37 <u>+</u> 2.81	232	17.60-34.30		
Air	24.69 <u>+</u> 3.00	216	15.00-31.00	25.21 <u>+</u> 2.54	232	15.70-32.00		

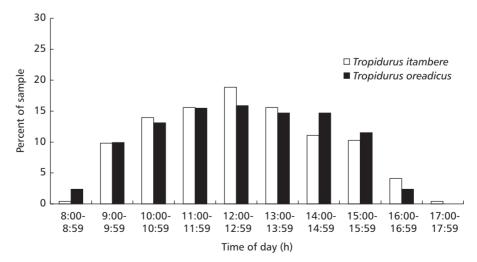


Fig. 3 — Activity times of Tropidurus itambere and T. oreadicus (N = 240 Ti and N = 244 To) from Goiás, Brazil.

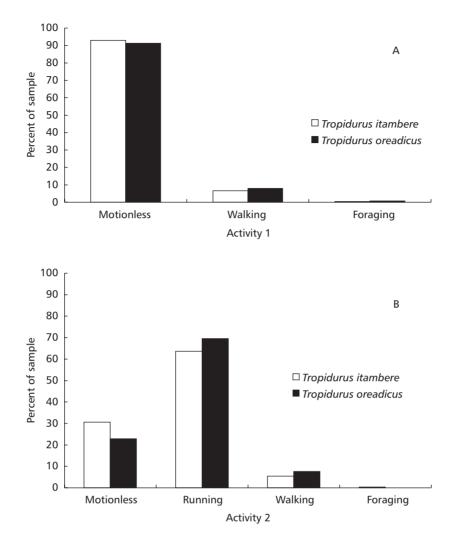


Fig. 4 — Behaviour (A – first sighting; B – after the observer's approach; N = 240 Ti and N = 244 To) of *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil.

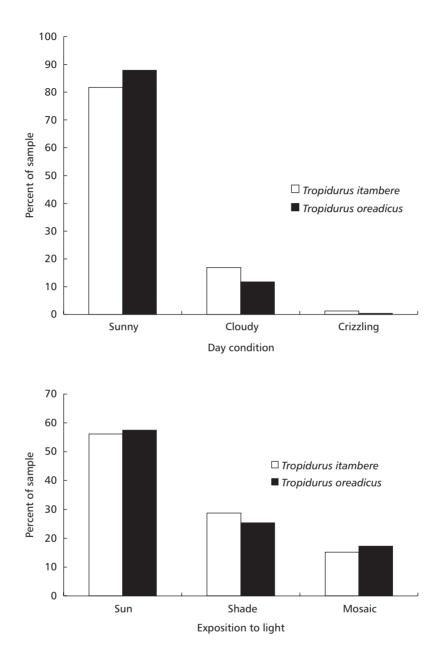


Fig. 5 — Weather conditions (A; N = 236 Ti and N = 247 To) and light exposure (B; N = 237 Ti and N = 249 To) for *Tropidurus itambere* and *T. oreadicus* from Goiás, Brazil.

REFERENCES

- ARAUJO, A. F. B., 1987, Comportamento alimentar dos lagartos: o caso dos *Tropidurus* do grupo *Torquatus* da Serra de Carajás, Pará (Sauria: Iguanidae). *Encont. An. Etol. V*, 203-234.
- ARAUJO, A. F. B., 1991, Structure of a white sand dune lizard community of coastal Brazil. *Rev. Bras. Biol.*, 51: 857-865.
- AVILA-PIRES, T. C. S., 1995, Lizards of Brazilian Amazonia (Reptilia: Squamata). Zoo. Verhand., 299: 3-706.
- 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. *Journ. Herpet.*, 26: 66-69.

- COLLI, G. R., BASTOS, R. P. & ARAUJO, A. F. B., 2002, The character and dynamics of the cerrado herpetofauna, pp. 223-241. In: P. S. Oliveira & R. J. Marquis (eds.), The cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press, New York.
- EITEN, G., 1978, Delimitation of the Cerrado concept. Veget., 36: 169-178.
- FROST, D. R., 1992, Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). Am. Mus. Novit., 3033: 1-68.
- FROST, D. R., RODRIGUES, M. T., GRANT, T. & TITUS, T. A., 2001, Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descritive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Mol. Phylog. Evol.*, 21: 352-371.
- HARVEY, M. B. & GUTBERLET, R. L., 2000, A phylogenetic analysis of the tropidurine lizards (Squamata: Tropiduridae), including new characteres of squamation and epidermal microstructure. Zoo. Journ. Lin. Soc., 128: 189-233.
- HUEY, R. B. & PIANKA, E. R., 1981, Ecological consequences of foraging mode. *Ecol.*, 62: 991-999.
- JOLICOEUR, P., 1963, The multivariate generalization of the allometry equation. *Biom.*, 19: 497-499.
- KOHLSDORF, T., GARLAND-JÚNIOR, T. & NAVAS, C. A., 2001, Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journ. Morph.*, 248: 151-164.
- LOSOS, J. B., 1990, Ecomorphology, performace capability, and scaling of west indian Anolis lizards: an evolutionary analysis. *Ecol. Monogr.*, 60: 369-388.
- MILLES, D. B., 1994, Covariation between morphology and locomotory performance in sceloporine lizards, pp. 207-235. *In*: L. J.Vitt & E. R. Pianka, *Lizard Ecology*. Historical and experimental perspectives. Princeton University Press, New Jersey.
- MOERMOND, T. C., 1979, Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecol.*, 60: 152-164.
- PIANKA, E. R., 1969, Habitat specificity, speciation, and species density in Australian desert lizards. *Ecol.*, 50: 498-502.
- PIANKA, E. R., 1973, The structure of lizard communities. *An. Rev. Ecol. Syst.*, *4*: 53-74.
- PIANKA, E. R. & PARKER, W. S., 1972, Ecology of the iguanid Callisaurus draconoides. Copeia, 1972: 493-508.
- POUNDS, J. A., 1988, Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecol. Monogr.*, 58: 299-320.
- RICKLEFS, R. E., COCHRAN, D. & PIANKA, E. R., 1981, A morphological analysis of the structure of communities of lizards in desert habitats. *Ecol.*, 62: 1474-1483.

- ROCHA, C. F. D. & BERGALLO, H. G., 1990, Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. & Evol.*, 2: 263-268.
- RODRIGUES, M. T., 1987, Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauridae, Iguanidae). Arq. Zoo., 31: 105-230.
- SIMPSON, E. H., 1949, Measurement of diversity. *Nature*, *163*: 688.
- SOMERS, K. M., 1986, Multivariate allometry and removal of size with principal components analysis. *Syst. Zoo.*, *35*: 359-368.
- TABACHNICK, B. G. & FIDELL, L. S., 1996, Using multivariate statistics. HarperCollins Publishers Inc., New York.
- VAN SLUYS, M., 1992, Aspectos da ecologia do lagarto *Tropidurus itambere* (Tropiduridae), em uma área do sudeste do Brasil. *Rev. Bras. Bio.*, 52: 181-185.
- VAN SLUYS, M., 1993, Food habits of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. *Journ. Herp.*, 27: 347-351.
- VAN SLUYS, M., 1995, Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. *Ciênc. Cult.*, 47: 61-65.
- VITT, L. J., 1991, An introduction to the ecology of cerrado lizards. *Journ. Herp.*, 25: 79-90.
- VITT, L. J., 1993, Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. *Can. Journ. Zoo.*, 71: 2370-2390.
- VITT, L. J. & CALDWELL, J. P., 1993, Ecological observations on Cerrado lizards in Rondônia, Brazil. *Journ. Herp.*, 27: 46-52.
- 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. S. & GOLDBERG, S. R., 1983, Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia*, 1983: 131-141.
- VITT, L. J., CALDWELL, J. P., ZANI, P. A. & TITUS, T. A., 1997, The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. *Proceedings National Academic Science USA*, 94: 3828-3832.
- VITT, L. J., SOUZA, R. A., SARTORIUS, S. S., AVILA-PIRES, T. C. S. & ESPÓSITO, M. C., 2000, Comparative ecology of sympatric *Gonatodes* (Squamata: Gekkonidae) in the western Amazon of Brazil. *Copeia*, 2000: 83-95.
- VITT, L. J., ZANI, P. A. & CALDWELL, J. P., 1996, Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *Journ. Trop. Ecol.*, 12: 81-101.
- ZAR, J. H., 1998, *Biostatistical analysis* (4th ed.), Prentice-Hall, Inc., Englewood Cliffs, New Jersey.