

Lizard prey predilections and resource use in restinga habitats on the north coast of Bahia

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Manuscript received: 7 August 2013

Accepted: 3 November 2014 by DENNIS RÖDDER

Abstract. Food acquisition is one of the most important dimensions of a species' ecological niche. A lizard's trophic relations with its environment, and a foraging strategy that results in its acquiring food, are of major relevance to its survival. However, and considering that it might be an obvious conclusion, this group's diet is determined by complex of factors and involves several dimensions such as evolutionary history, body size, specializations, and food availability. Using their positive electivity towards ants in their diet it was possible to assess the trophic niche partitioning among certain lizard species. Arthropods and lizards were sampled in six north coast restinga localities of Bahia. In order to measure food availability we utilized pitfall trap, Winkler extractor, and beating-tray methods in combination with consumption data from lizard stomach contents. The most diverse group was *Scleroglossa*, whereas *Iguania* was the most abundant. *Tropidurus hygomi* and *T. hispidus* diets were mainly composed of ants, representing 80% and 68% of consumption respectively, supporting a positive electivity. The niche overlap verified was 68%, which suggests that these species exhibit some degree of competition for food within the region.

Key words. Restinga, lizards, diet, spatial niching, trophic niching, resource partitioning.

Introduction

An organism's position within a community can be defined by its resource use and interactions with organisms also utilizing these resources (PUTMAN 1994). This idea of an organism's position within a community and its relationships can be expressed by the ecological niche concept (PUTMAN 1994).

The ecological niche concept proposed by HUTCHINSON in 1957 suggests how species interact with the conditions and resources available in their environment to meet their needs. The ecological niche of a species is considered an n-dimension hypervolumetric space (HUTCHINSON 1957). Since the formulation of this concept, scientists have been trying to estimate the breadth and overlap of niches between species (MAY & MACARTHUR 1972, PIANKA 1973).

Studies concerning communities of lizards suggest that these animals subdivide resource access into three forms:

what they eat (trophic) (PIANKA 1974, VITT et al. 2003, VITT 2004, VITT & PIANKA 2005), where and how they forage (spatially and modally) (PIANKA 1974, COLLI & PAIVA 1997, VITT et al. 2003, VITT 2004, VITT & PIANKA 2005), and their activity period (temporal) (PIANKA 1974, COLLI & PAIVA 1997, VITT et al. 2003, VITT 2004).

The regulative mechanisms for trophic relations are the most important in the organization of lizard communities (ROCHA 1994, PIANKA & VITT 2003, VITT & CALDWELL 2009). The diet of this group is determined by a complex that involves historic and evolutionary aspects related to body size, prey availability, and microhabitat specialization (PIANKA & VITT 2003).

VITT et al. (2003) realized that most of a lizard's electivity is determined phylogenetically (PIANKA & VITT 2003, VITT & CALDWELL 2009). Physiology and behavioural differences are related to a positive and negative electivity of ants by *Iguania* and *Scleroglossa*, respectively. Thus,

Scleroglossa, in contrast to Iguania, avoid feeding on prey containing chemically hazardous compounds and consume more nutritious prey instead. This strategy is aided by their vomeronasal specialization, which helps them avoid ingesting ants. Unlike Scleroglossa, Iguanian lizards detect prey through visual cues, largely favouring ants, but also including a wide variety of other prey items (PIANKA & VITT 2003, VITT & PIANKA 2005, VITT et al. 2008).

Lizard foraging modes and the width of their prey spectrum infer electivity patterns existing in the group, as has been demonstrated to be the case in the Atlantic forest of the extreme south of Bahia state (TINÔCO 2004). Likewise, DIAS et al. (1998) found in an area of Caatinga that ants and spiders were the main prey items consumed by four lizard species. In this same biome, *Tropidurus psammonastes* (RODRIGUES et al. 1988) has demonstrated a high degree of predilection for ants (ROCHA & RODRIGUES 2005), as has also been observed in *Tropidurus torquatus* in which ants account for 85.7% of its diet (TEIXEIRA & GIOVANELLI 1999).

These examples illustrate how ants and lizards are linked, suggesting also that ant distribution influences lizard distribution (PIANKA & VITT 2003, TINÔCO 2004). The effects of these interactions on lizard communities require further study. Both groups share similar characteristics, such as physiology, ectothermy, and behavioural expressions, including mode of foraging and activity period (HÖLLDOBLER & WILSON 1990, PIANKA & VITT 2003), which allow these lizards and ants to live in open habitats.

Restinga sand dunes are an example of open habitats in the Atlantic forest and form an important constituent of this biome. It is an expansive coastal habitat with mostly open vegetation and its exposure to high solar irradiation limits the presence of surface water (ROCHA 2000). These environmental characteristics allow only species adapted to open habitats to thrive here (CERQUEIRA 2000, ROCHA 2000).

The vegetation structure and composition of restinga habitats change substantially along the Brazilian coast (ROCHA 2000, DIAS & ROCHA 2005). This results in each region along the coast sporting individual characteristics (DIAS & ROCHA 2005), necessitating local studies to better understand the local habitats.

This paper aims to: 1) evaluate the existence of an occupancy pattern of the vegetal formations by the lizard assemblages; 2) identify the use and feeding electivity of arthropods by lizards; 3) analyse the co-existence of myrmecophagous (ant-feeding) lizards in a restinga habitat according to the niche theory.

Materials and methods

Study area

The study area lies on the northeast coast of Bahia, stretching 220 km northwards from Salvador to the Real River, Bahia state's boundary. This region covers the coastal municipalities of Salvador, Lauro de Freitas, Camaçari, Mata

de São João, Entre Rios, Esplanada, Conde, and Jandaira (BRASIL 2004). Restinga ecosystem exists within the 200 km² of the Environmental Protection Area (APA) of the Litoral Norte do Estado da Bahia (SOS Mata Atlântica 2010).

Sampling design

Data were sampled at six sites along the northeast coast of Bahia state (Busca Vida 12°51'51.03" S, 38°16'11.87" W; Praia do Forte: 12°35'30.48" S, 38°01'43.21" W; Imbassaí: 12°28'39.79" S, 37°57'34.76" W; Baixio: 12°06'52.27" S, 37°41'49.40" W; Barra do Itariri: 11°56'58.07" S, 37°36'34.51" W, and Costa Azul: 11°41'54.39" S, 37°29'32.05" W) (Fig. 1). Four typical restinga vegetal phyto-physiognomies were present at each site (Figs 2 + 3).

Beach phyto-physiognomy consisting of herbaceous heliophilic species exists from the beach line inland (FRAGA & PEIXOTO 2004, COGLIATTI-CARVALHO et al. 2001). It is highly adapted to saline conditions and sandy soil (COGLIATTI-CARVALHO et al. 2001) and much less diverse compared to the remaining restinga vegetal formations (DIAS & MENEZES 2007).

Floodplains are permanently or periodically flooded by rivers, and their vegetation is adapted to these conditions. The extent of flooding depends on local soil topography, groundwater depth, and the proximity to rivers or lakes (MENEZES 2007).

Scrub consists of herbaceous and scrub vegetation, interspersed with islands of sandy soil or herbaceous vegetation. The lack of trees facilitates a high degree of exposure to sunlight (ROCHA 2000, ROCHA & VAN SLUYS 2007, COGLIATTI-CARVALHO et al. 2001, FRAGA & PEIXOTO 2004, MENEZES 2007).

Restinga dry forest vegetation comprises trees and locally very dense woody vegetation (BRASIL 2004, FRAGA & PEIXOTO 2004, COGLIATTI-CARVALHO et al. 2001) that limits the amount of sunlight penetrating to the understorey and results in thick deposits of leaf litter on the floor (MENEZES 2007).

In each vegetal formation, a 500-metre transect was demarcated for lizard survey, within which sample points (SP) every 100 m were used for verifying arthropod presence, totalling 10 SP (Fig. 2). Surveys were conducted in June, August, and October of 2010, including both the wet and the dry season. Every site was surveyed for one day in all four vegetal formations simultaneously, totalling six days per survey effort.

Sampling methods

For lizard sampling, visual surveys (VS) were employed for two hours along each transect. Sampling to verify lizard diets was conducted according to permit n° 23111-1/SISBIO, which permitted euthanising a maximum of 96 specimens.

Due to the morphological characters required for identifying the species of the genus *Tropidurus*, only collected specimens were identified to species level. All other species listed here were identified on the basis of collected specimens and field observations.

Collected lizards were placed in refrigerated cooler boxes and euthanised with chloroform. They were then fixed with 10% formalin and stored in 70% alcohol. Lizard stomachs were later extracted and their contents separated and sorted by order, with the exception of ants, which were identified to species.

For arthropod sampling, we used two pitfall traps each at each sample point. We used 500-ml plastic bowls shielded by plastic plates mounted on wooden sticks 10 cm above

the bowls. They were filled with a hyper-saline solution that would preserve the collected material for a longer period while the shielding prevented them from overflowing through accumulating rain water or drying up (BESTELMEYER et al. 2000). These pitfall traps were used for 24 hours at each survey location.

At the same sample points, we also used Winkler extractors (BESTELMEYER et al. 2000) for sampling leaf-litter arthropods. We removed 50 × 50 cm of leaf litter, then sieved the material and kept its remnants in Winkler traps for 24 hours.

For arboreal arthropods, entomological umbrellas with 1 m² white sheets were used on one shrub at each sample point, which was shook 10 times. The identification of the

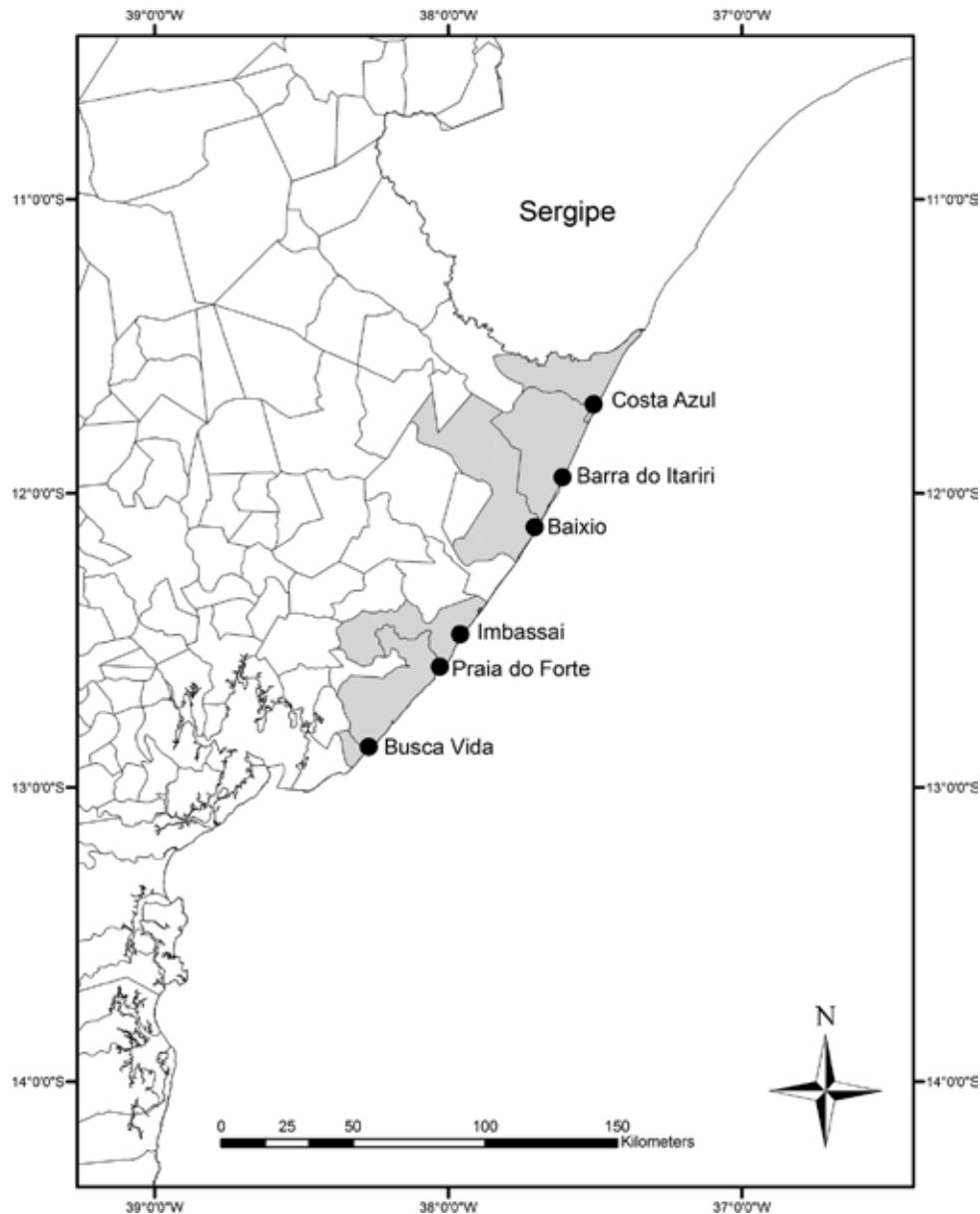


Figure 1. Map showing all study sites.

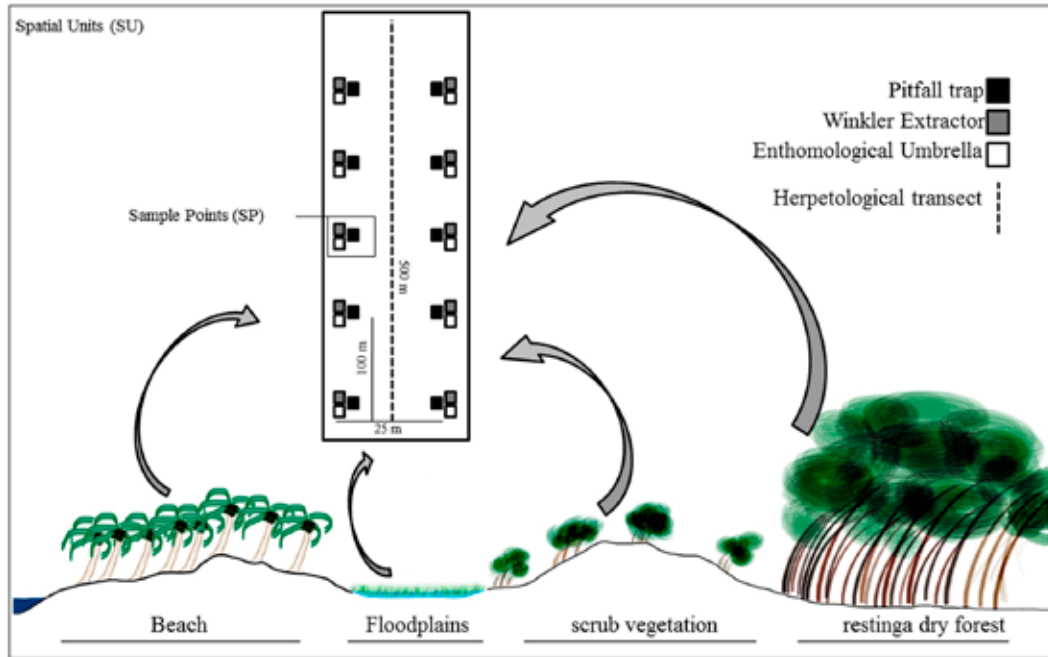


Figure 2. All four main restinga vegetal formations, highlighting the transect and its sample points, including arthropod sampling techniques.



Figure 3. Restinga vegetal formations. A) restinga dry forest; B) scrub vegetation; C) floodplains; and D) beach vegetation.

material followed the same parameters as that obtained from pitfall trap sampling. Voucher material is stored in the Zoological Museum of UFBA (MUZUFBA) and the Myrmecology Laboratory of CEPLAC/UESC, Nos. 5641 through 5646 in CEPLAC/UESC (CPDC Collection).

We should highlight that 'abundance' here refers to the total number of arthropods and Formicidae sampled for assessing 'food resource availability'.

Statistical analysis

To compare lizard communities of various restinga vegetation habitats, we used the Shannon-Wiener index (H') of diversity (MAGURRAN 1988), dominance of Simpson (c), assuming values between 0 and 1 (diversity is higher when closer to 1), and the Pielou equitability index (J), which estimates how similar species proportions are, assuming values from 0 (only one dominant species) to 1 (all species are equally dominant) (KREBS 1999). All these indices were computed with PAST® software.

To test for differences in habitat utilization, we used the non-parametric Multiple Response Permutation Procedure (MRPP). This test necessitates that all sample units are ecologically independent, although it does not require normality presupposition and sample homoscedasticity (MCCUNE & GRACE 2002). MRPP produces statistical significance (p) and a T -test, describing the separation between groups. The more negative the T -value, the stronger the separation of groups. MRPP also provides the effect size of group A , describing intra-group homogeneity. When all items of a group have the same value, then A will have a value of 1. In ecological communities, value A is usually less than 0.1, whereas $A > 0.3$ is considered high. Groups with less similarity are $A < 0$. If significant differences were found, the model was tested pair-to-pair with PC Ord® 2002 (MCCUNE & GRACE 2002) to visualize how habitats differ in lizard composition. To assess the importance of prey categories for lizard species, those that had the highest contribution to the total preyed-upon items by most lizards were considered important. Preys were only considered important in lizard diets if their mass represented 30% of total items in at least 30% of the sampled specimens (TINOCO 2004, ROCHA & RODRIGUES 2005).

However, a high frequency of some prey categories does not necessarily infer a high electivity for some prey items. To estimate prey consumption and electivity, we followed TINOCO (2005) and ROCHA & RODRIGUES (2005). Information on prey selection in restinga habitats was obtained through pitfall, Winkler, and entomological umbrella collecting methods. Consumption for each species was estimated by summing all items consumed by the sampled specimens of that species.

If the difference between consumption percentage and the predilection for a feeding category was > 20 , we considered the lizard species to have a highly positive electivity to that category. If it was < -20 , it had a negative electivity to the category.

To verify niche overlap (ϕ) (PIANKA 1973), we considered the proportionality of resource utilization for each pair of species, using the formula:

$$\Phi_{jk} = \frac{\sum_{i=1}^n P_{ij} \cdot P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \cdot \sum_{i=1}^n P_{ik}^2}}$$

where 'i' represents the resource category, 'p' the proportion of used resources of the 'i' category, 'n' the total number of categories, and 'j' and 'k' represent the species involved. The result may range from 0 to 1. The overlap will be higher the closer it is to 1.

This index was used to verify trophic niche overlaps only between lizard species that presented a high electivity for ants. This enabled us to understand the processes of lizard and prey coexistence in restinga vegetation habitats. We used ECOSIM® for this analyses.

Results

We recorded 1,835 lizards of eight families, nine genera and 14 species. Scleroglossa represented 70% of the sampled species, with ten species. However, with regard to the frequency of species, four Iguania accounted for 60% of the sampled lizards, of which 52.4% (962 specimens) were *Tropidurus* spp., followed by the Scleroglossid *Ameivula ocellifera* at 29.8% (548 specimens) (Tab. 1).

The Shannon Wiener index indicated the greatest diversity to exist in the forest vegetation type ($H' = 1.39$). Both the Simpson and Pielou indices revealed some dominance and low equitability of the species in all formations (Tab. 2).

The MRPP analyses of lizard composition per vegetal formation resulted in significant differences ($p < 0.05$), clearly separating lizard assemblages ($T = -3.04$) and homogeneity within each group ($A = 0.09$). However, pair-wise MRPP between vegetal formations resulted in some pairs not presenting any statistical difference (Tab. 3).

The most common prey category was Formicidae (8,572), followed by Acari (4,119), Araneae (2,067), Isopoda (1,593), Coleoptera (1,260), and Isoptera (1,231). The remaining orders were not representative (Tab. 4).

Analysing the prey consumption of *T. hygomi* and *A. ocellifera*, both species can be considered generalists, as they had ingested a wide variety of arthropods. However, they differ in how important these arthropods are in their diets (Tab. 5). The most important prey items to lizard species are (in descending order): Isoptera (important to four species), Orthoptera (important to three species), Coleoptera, Formicidae, and larvae (all important to two species), and Isopoda and Acari (important to only one species). As for arthropod electivity, four species presented a positive electivity for Isoptera, three species for Coleoptera

Table 1. Lizards species occurrences as per vegetation type along the north coast of Bahia (forest: n = 24 samples, scrub: n = 24, beach vegetation type: n = 24, and floodplains: n = 24) as indicated by samples from Busca Vida, Praia do Forte, Imbassaí, Baixio, Barra do Itariri and Costa Azul in June, August, and October of 2010.

Taxon	Formation				Total
	Forest	Scrub	Floodplains	Beach	
IGUANIA					
Dactyloidae					
<i>Norops ortonii</i> (COPE, 1868)	1	-	-	-	1
Tropiduridae					
<i>Tropidurus hispidus</i> (SPIX, 1825)	-	7	-	2	9
<i>Tropidurus hygomi</i> REINHARDT & LÜTKEN, 1861	12	53	6	70	141
<i>Tropidurus</i> sp.	150	399	78	335	962
SCLEROGLOSSA					
Diploglossidae					
<i>Ophiodes striatus</i> (SPIX, 1825)	-	-	3	-	3
Gekkonidae					
<i>Hemidactylus brasilianus</i> (AMARAL, 1935)	-	1	-	-	1
<i>Hemidactylus mabouia</i> (MOREAU DE JONNÈS, 1818)	-	2	1	18	21
Gymnophthalmidae					
<i>Micrablepharus maximiliani</i> (REINHARDT & LÜTKEN, 1862)	-	-	-	1	1
Mabuyidae					
<i>Brasiliscincus heathi</i> (SCHMIDT & INGER, 1951)	1	4	2	5	12
<i>Psychosaura macrorhyncha</i> (HOGE, 1947)	3	3	2	6	14
Sphaerodactylidae					
<i>Coleodactylus meridionalis</i> (BOULENGER, 1888)	54	22	2	-	78
Teiidae					
<i>Ameiva ameiva</i> (LINNAEUS, 1758)	3	-	1	-	4
<i>Ameivula abaetensis</i> (DIAS, ROCHA & VRCIBRADIC, 2002)	17	20	2	1	40
<i>Ameivula ocellifera</i> (SPIX, 1825)	51	228	145	124	548

Table 2. Description of lizard diversity per vegetal formation in restinga: richness, abundance, Simpson dominance index (c), Shannon-Wiener diversity index (H'), and Pielou equitability (J). All indices for each vegetal formation.

	richness	abundance	c	H'	J
Forest	9	292	0.330	1.39	0.63
Scrub	10	739	0.390	1.20	0.52
Beach	10	562	0.420	1.14	0.52
Floodplains	9	242	0.460	1.02	0.53

and Orthoptera, two species for larvae and Formicidae, and one species for Acari (Tab. 6).

Two species presented positive electivity for formicids: *T. hygomi* and *T. hispidus*. All ants consumed by these two species were identified as precisely as possible (Tab. 7). The most consumed ant subfamily was Myrmicinae with 16 species (50% of all ant species), followed by Formicinae with seven species (21.8%), Dolichoderinae with three

Table 3. MRPP values, comparing pair-to-pair the composition of lizards in all restinga vegetation habitats.

	Forest	Scrub	Beach	Floodplain
Forest	-	-	-	-
Scrub	p < 0,05 T = -2.71 A = 0.13	-	-	-
Beach	p < 0,05 T = -1.97 A = 0.08	p > 0,05 T = 0.68 A = -0.002	-	-
Floodplain	p > 0,05 T = -1.58 A = 0.05	p < 0,05 T = -2.99 A = 0.12	p > 0,05 T = -0.7 A = 0.02	-

species (9.3%), and Ectatomminae, Pseudomyrmecinae, and Ponerinae with two species (6.25%) each. The niche overlap index (PIANKA 1973) for these two lizards was $\phi = 0.68$.

Table 4. Arthropod selection in each vegetal formation of restinga.

Arthropods	Prey disponibility per formation				Total
	Forest	Scrub	Beach	Floodplains	
INSECTA					
Blattaria	82	73	107	83	345
Collembola	254	34	25	152	465
Coleoptera	257	282	342	379	1260
Dermaptera	0	0	1	2	3
Diptera	89	62	86	54	291
Embioptero	9	21	12	4	46
Hemiptera	65	89	82	131	367
Hymenoptera (excl. Formicidae)	34	72	10	41	157
Formicidae	1941	2403	2225	2003	8572
Isoptera	383	428	294	126	1231
Lepidoptera	1	4	0	2	7
Mantodea	2	2	0	1	5
Neuroptera	8	9	0	2	19
Odonata	1	0	0	3	4
Orthoptera	135	86	49	118	388
Protura	0	3	2	5	10
Psocoptero	9	9	5	3	26
Thysanoptero	3	3	31	7	44
Thysanura	14	15	14	16	59
Larvae	163	212	179	151	705
ARACHNIDA					
Acari	560	1771	1059	808	4198
Araneae	633	597	353	484	2067
Opiliones	16	3	8	21	48
Pseudoscorpiones	98	89	88	73	348
Scorpiones	5	2	1	6	14
CRUSTACEA					
Isopoda	141	149	1243	60	1593
MYRIAPODA					
Chilopoda	10	12	21	10	53
Diplopoda	20	10	13	9	52

Discussion

The taxonomic dominance of *Scleroglossa* can be attributed to the fact that this infraorder presents an altogether larger generic and specific diversity among the lizards in the world (VITT & CALDWELL 2009). This dominance suggests that they are more competitive than Iguanians, because they are more skilled at exploiting the available resources (i.e., food, microhabitat) besides of their including a group of species with nocturnal habits (*Gekkota*) (VITT & CALDWELL 2009).

The differences found between lizard assemblages in restinga formations can be attributed to a combination of factors. This result may be a reflection of the variation in the structural complexity of restinga formations, which creates a variety of microhabitats. These resources are

some of the most ecologically relevant features to lizards, especially to heliophilic species that occupy open areas, as the availability of different microhabitats can influence their thermoregulatory behaviour and consequently the performance of basic physiological functions (CLOUDSLEY-THOMPSON 1965, HUEY 1982). Besides that, the range of possible microhabitats that can be occupied contributes to an increased food resource availability (i.e., arthropods) for lizards (LASSAU & HOCHULI 2004, VARGAS et al. 2007, TRAVASSOS et al. unpubl. data).

The forest formation is distinct from the other three, and consequently harbours a more specific assembly. However, the forest did not differ significantly from the humid zone. The humid zone, bush and beach, are open spaces, and due to this characteristic, they seem not to be too different among themselves. The similarity between the forest and

Table 5. Percentage of arthropod consumption by lizards. Ame_ame – *A. ameiva*; Nor_ort – *N. ortonii*; Ame_aba – *A. abaetensis*; Ame_oce – *A. ocellifer*; Col_mer – *C. meridionalis*; Hem_bra – *H. brasiliensis*; Hem_mab – *H. maboia*; Bra_heath – *B. heathi*; Psy_mac – *P. macrorhyncha*; Mic_max – *M. maximiliani*; Oph_str – *O. striatus*; Tro_his – *T. hispidus*; Tro_hyg – *T. hygomi*.

Arthropod taxon	Arthropod consumption by lizards												
	Ame_ame	Nor_ort	Ame_aba	Ame_oce	Col_mer	Hem_bra	Hem_mab	Bra_heath	Psy_mac	Mic_max	Oph_str	Tro_his	Tro_hyg
INSECTA													
Blattaria	-	-	-	-	-	-	0.05	-	-	-	-	-	-
Coleoptera	-	1	-	0.243	-	-	0.3	0.5	-	-	-	0.224	0.046
Dermaptera	-	-	-	-	-	-	-	-	-	-	-	-	0.001
Diptera	-	-	-	0.005	-	-	-	-	-	-	-	-	-
Embioptero	-	-	-	-	-	-	-	-	-	-	-	-	0.001
Formicidae	-	-	-	0.073	0.04	0.167	0.2	0.13	-	-	-	0.684	0.803
Hemiptera	-	-	-	0.046	0.04	-	-	-	-	-	-	0.013	0.004
Isoptera	0.979	-	0.989	0.234	0.214	0.833	0.35	-	-	-	-	-	0.025
Neuroptera	-	-	-	0.005	0.036	-	-	-	-	-	-	-	-
Odonata	-	-	-	-	-	-	-	-	-	-	-	-	0.001
Orthoptera	-	-	-	0.018	0.04	-	-	0.13	0.333	0.5	0.5	-	0.007
Protura	-	-	-	-	-	-	-	-	-	-	-	-	-
Larvae	-	-	-	0.17	0.107	-	-	0.25	0.333	0.5	-	0.02	0.034
ARACHNIDA													
Acari	-	-	-	0.005	-	-	-	-	-	-	0.5	-	0.022
Araneae	0.01	-	-	0.174	0.286	-	0.1	-	-	-	-	-	0.019
Pseudoscorpiones	-	-	-	0.018	-	-	-	-	-	-	-	-	0.01
Scorpiones	-	-	-	-	-	-	-	-	-	-	-	-	-
CRUSTACEA													
Isopoda	-	-	0.011	-	0.25	-	-	-	0.333	-	-	-	0.001
MYRIAPODA													
Chilopoda	-	-	-	-	-	-	-	-	-	-	-	0.007	0.001

the humid zone may be due to the existence of microhabitats and comparable degrees of humidity and soil moisture. There was no difference between beach and bush, as they presented the same composition of lizard species.

There is a moderate dominance in the lizard assemblages in all formations, which applies in particular to *Tropidurus* spp. and *A. ocellifera* in open and sunny environments (ROCHA 2000, MESQUITA & COLLI 2003a, b) and in almost all local restinga formations.

We decided to maintain even those species with only one analysed specimen as they exhibited similar dietary habits compared to the literature: *N. ortonii* (Araneae, Hemiptera, and Coleoptera) (LARANJEIRAS 2012); *A. ameiva* (Isoptera and Coleoptera larvae) (SILVA et al. 2003); *A. abaetensis* (Isoptera, Lepidoptera larvae, and Coleoptera) (DIAS & ROCHA 2007); *M. maximiliani* (Araneae, Hemiptera, and Orthoptera) (WERNECK et al. 2009); and *O. striatus* (Blattaria, Araneae, and Orthoptera) (BARROS & TEIXEIRA 2007).

In spite of the wide range of food resources available, their consumption by the lizards was heavily biased towards a limited number of relatively abundant resources. The majority of lizard species fed preferably on termites and orthopterans whilst avoiding ants. Only two species presented a positive electivity of ants. However, VITT et al. (2003) recommended that ants should be treated different-

ly from other hymenopterans when evaluating the diet of squamates, because of their particular morphotype, diversity, abundance, and also because some lizards specialize in preying upon this category, which could be the case here for *T. hygomi* and *T. hispidus*.

This study corroborates the hypothesis that the diet of lizards is determined by historical factors (PIANKA & VITT 2003, VITT & CALDWELL 2009), where a group like the Iguania would prefer feeding on ants, while the Scleroglossa would avoid them and feed mainly on termites. The high consumption of termites by the majority of lizard species is a reflection of the richness of the Scleroglossa sampled. This is probably related to the fact that Scleroglossa are more efficient than Iguania with regard to capturing prey of high-energy value (VITT et al. 2003, PIANKA & VITT 2003, VITT & CALDWELL 2009). Hence, these authors (VITT et al. 2003, PIANKA & VITT 2003) suggest that lizards may have developed this predilection directly from ancestors in two forms, be it due to a tongue structure that facilitates the detection and catching of prey (Iguania), or due to the possession of a vomeronasal apparatus (Scleroglossa) that refines the discrimination of prey.

Our evaluation of the niche overlap revealed that the species of myrmecophagous lizards overlap in the trophic niche (ants) by 68%. Amongst the species of ants that are commonly represented in the diet of *Tropidurus hygomi*

Lizard prey predilections and resource use in restinga habitats in Bahia

Table 6. Consumption percentage by selection percentage (electivity) of arthropods by lizard species. TS – total of analysed stomach contents; TE – total of electivity for item (FO – forest; SC – scrub; FL – floodplains; BE – beach) and total arthropod electivity by lizards per vegetation habitat. Ame_ame – *A. ameiva*; Nor_ort – *N. ortorii*; Ame_aba – *A. abbaetensis*; Ame_oce – *A. ocellifera*; Col_mer – *C. meridionalis*; Hem_bra – *H. brasiliensis*; Hem_mab – *H. maboi*; Bra_heal – *B. heathii*; Psy_mac – *P. macrorhyncha*; Mic_max – *M. maximiliani*; Oph_str – *O. striatus*; Tro_his – *T. hispidus*; Tro_hyg – *T. hygomi*.

	Arthropod electivity by lizards																										
	Acari			Aranea			Coleoptera			Formicidae			Isoptera			Larva			Orthoptera								
	TS	TE	FO	SC	FL	BE	TE	FO	SC	FL	BE	TE	FO	SC	FL	BE	TE	FO	SC	FL	BE	TE	FO	SC	FL	BE	
Ame_ame	1	-	-	-	-	-	-	-	-	-	-	0.92	0.91	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nor_ort	1	-	-	-	-	-	0.94	0.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ame_aba	1	-	-	-	-	-	-	-	-	-	-	0.93	0.92	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ame_oce	25	-	-	-	-	-	0.18	-	-	-	-	0.18	0.42	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-
Col_mer	21	-	-	-	-	0.16	-	-	-	-	-	0.16	0.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hem_bra	2	-	-	-	-	-	-	-	-	-	-	0.78	-	0.81	-	-	-	-	-	-	-	-	-	-	-	-	-
Hem_mab	7	-	-	-	-	-	0.27	-	-	-	0.22	0.3	-	0.26	-	-	-	-	-	-	-	0.31	-	-	-	-	0.47
Bra_heal	2	-	-	-	-	-	0.44	-	-	-	0.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psy_mac	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	0.47	0.3	1	-	-	-
Mic_max	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	0.47	0.5	-	-	-	-	0.49
Oph_str	1	0.31	-	-	-	-	0.48	-	-	0.5	-	0.48	-	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-
Tro_his	5	-	-	-	-	-	-	-	-	-	-	0.3	0.31	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Tro_hyg	52	-	-	-	-	-	-	-	-	-	-	0.42	0.47	0.44	0.2	0.46	-	-	-	-	-	-	-	-	-	-	-

Table 7. Ants and their relative consumption by lizards. TI – Total ingested.

Taxon Formicidae	Ant consumption			
	<i>Tropidurus hygomi</i>		<i>Tropidurus hispidus</i>	
	TI	%	TI	%
DOLICHODERINAE				
Dolichoderini				
<i>Dorymyrmex</i> sp. 1	5	0.01	-	-
<i>Dorymyrmex</i> spp.	34	0.06	3	0.18
<i>Forelius</i> sp. 1	16	0.03	-	-
ECTATOMMINAE				
Ectatommini				
<i>Ectatomma muticum</i> MAYR, 1870	3	0.01	-	-
<i>Gnamptogenys striatula</i> MAYR, 1884	4	0.01	1	0.06
FORMICINAE				
Brachymyrmecini				
<i>Brachymyrmex patagonicus</i> MAYR, 1868	129	0.23	-	-
<i>Brachymyrmex</i> sp. 2	3	0.01	-	-
<i>Brachymyrmex</i> spp.	7	0.01	-	-
Camponotini				
<i>Camponotus arboreus</i> (SMITH, 1858)	14	0.03	-	-
<i>Camponotus crassus</i> MAYR, 1862	1	0	-	-
<i>Camponotus novogranadensis</i> MAYR, 1870	3	0.01	-	-
Lasiini				
<i>Nylanderia fulva</i> MAYR, 1862	1	0	-	-
MYRMICINAE				
Attini				
<i>Acromyrmex rugosus</i> (SMITH, 1858)	1	0	-	-
<i>Atta laevigata</i> (SMITH, 1858)	8	0.01	1	0.06
<i>Cyphomyrmex transversus</i> EMERY, 1894	64	0.11	-	-
<i>Mycetophylax simplex</i> (EMERY, 1888)	21	0.04	-	-
<i>Trachymyrmex</i> sp. 3	7	0.01	-	-
Cephalotini				
<i>Cephalotes minutus</i> (FABRICIUS, 1804)	40	0.07	-	-
<i>Cephalotes pallens</i> (KLUG, 1824)	2	0	-	-
<i>Cephalotes clypeatus</i> (FABRICIUS, 1804)	1	0	-	-
Crematogastrini				
<i>Crematogaster erecta</i> MAYR, 1866	1	0	-	-
<i>Crematogaster</i> spp.	9	0.02	-	-
Leptothoracini				
<i>Nesomyrmex tristani</i> (EMERY, 1896)	1	0	-	-
Pheidolini				
<i>Pheidole radoszkowskii</i> MAYR, 1884	142	0.25	11	0.65
<i>Pheidole</i> sp.1	1	0	-	-
<i>Pheidole</i> (group <i>diligens</i>) sp. 2	12	0.02	-	-
<i>Pheidole</i> spp.	7	0.01	1	0.06
Solenopsidini				
<i>Solenopsis</i> spp.	10	0.02	-	-
PONERINAE				
Ponerini				
<i>Odontomachus bauri</i> EMERY, 1892	6	0.01	-	-
<i>Pachycondyla inversa</i> SMITH, F. 1858	1	0	-	-
PSEUDOMYRMECINAE				
Pseudomyrmecini				
<i>Pseudomyrmex simplex</i> (Smith, 1877)	1	0	-	-
<i>Pseudomyrmex</i> spp.	4	0.01	-	-

and *T. hispidus*, only *Gnamptogenys striatula* has a low abundance in the studied restinga (TRAVASSOS et al. unpubl. data). However, other species of ants, like *Dorymyrmex thoracicus*, *Wasmannia auropunctata*, *Crematogaster erecta*, *Ectatomma muticum* and *Gnamptogenys moelleri*, which are extremely abundant and widespread in the studied areas (TRAVASSOS et al. unpubl. data), were poorly or not at all represented in the stomach contents of the lizards, which might suggest their possible predilection for different species of ants.

Tropidurus hygomi is endemic to the studied restinga, with its distribution being limited to the region between Salvador (Bahia) in the south and Santo Amaro das Brotas (Sergipe) in the north (VANZOLINI & GOMES 1979). Until recently, it was believed that *T. hispidus* existed only in the Atlantic Forest of the Recôncavo Baiano, and having not being described from the North Littoral Zone (DIAS & ROCHA 2005). This species seems to be well adapted to urban environments, and it is more commonly found in anthropogenic areas than its congener, *T. hygomi*, which appears to be largely restricted to undisturbed areas. Hence, it is suggested that *T. hispidus* uses the anthropisation of sandbanks in its favour to colonize these areas, and in this way it can compete with *T. hygomi*.

The results of this study corroborate those proposed in the literature, illustrating a wide dietary separation between *Scleroglossa* and *Iguania*. The first avoid feeding on ants even if they are the prominent potential food resource. In contrast, ants constitute the main prey of *Iguania*, occurring with a strong niche overlap. In this case, coexistence potentially occurs due to *T. hispidus* expanding its distribution to anthropogenically influenced habitats. This suggests that competitive exclusion must be happening between the latter and *T. hygomi*, as the former species is larger, territorial, and favours degraded areas.

As a conclusion, there is still a necessity for serious study on the sharing of food resources (ants) between *Tropidurus* species. In particular as *T. hygomi* is endemic to the region and does not at present occur within fully urbanized areas, which could contribute to conservation measures for the preservation of the species and its ecosystem.

Acknowledgements

We thank the “Habitat change and the herpetofauna status in the Atlantic Forest” research group. In addition, we thank ROB WARD for his contributions to the manuscript and English review. Logistic support was provided by the Herpetofauna Foundation, Reptile Technologies, and Lacerta Ambiental. Fieldwork was conducted under SISBIO permit No. 23111-1. They also acknowledge their grants from CAPES and CNPq.

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Appendix 1

Specimens examined (from litoral norte da Bahia, Brazil)

Ameiva ameiva (n = 1), (CHECOA 2472); *Ameivula abaetensis* (n = 1), (CHECOA 2491); *Ameivula ocellifera* (n = 25), (CHECOA 2383, 2384, 2402, 2411, 2419, 2439, 2442, 2446, 2447, 2448, 2470, 2471, 2473, 2475, 2476, 2477, 2483, 2484, 2486, 2488, 2515, 2521, 2523, 2551, and 2560); *Brasiliscincus heathi* (n = 2), (CHECOA 2413 and 2464); *Coleodactylus meridionalis* (n = 21), (CHECOA 2495, 2496, 2443, 2492, 2493, 2395, 2554, 2390, 2391, 2392, 2405, 2409, 2410, 2386, 2508, 2414, 2418, 2499, 2393, 2394, and 2451); *Hemidactylus brasiliensis* (n = 2), (CHECOA 2558 and 2567); *Hemidactylus mabouia* (n = 7), (CHECOA 2387, 2403, 2441, 2482, 2378, 2519, and 2436); *Micrablepharus maximiliani* (n = 1), (CHECOA 2463); *Norops ortonii* (n = 1), (CHECOA 2400); *Ophiodes striatus* (n = 1), (CHECOA 2501); *Psychosaura macrorhyncha* (n = 3), (CHECOA 2497, 2559 and 2550); *Tropidurus hygomi* (n = 52), 2382, 2389, 2408, 2494, 2404, 2407, 2423, 2430, 2437, 2444, 2445, 2485, 2487, 2489, 2490, 2406, 2478, 2479, 2480, 2481, 2498, 2500, 2506, 2516, 2429, 2517, 2522, 2525, 2556, 2555, 2557, 2377, 2422, 2432, 2433, 2434, 2435, 2450, 2524, 2547, 2549, 2376, 2426, 2449, 2457, 2552, 2562, 2564, 2565, 2566, 2469, and 2379); (CHECOA *Tropidurus hispidus* (n = 5), (CHECOA 2452, 2420, 2401, 2563 and 2417).