



The diet of six species of lizards in an area of Caatinga, Brazil

Anthony Santana Ferreira¹, Adilson de Oliveira Silva¹, Breno Moura da Conceição¹
& Renato Gomes Faria^{1,2}

¹Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Sergipe, São Cristóvão-Sergipe, Brazil

²Universidade Federal de Sergipe, Departamento de Biologia, Laboratório de Cordados/Herpetologia. São Cristóvão-Sergipe, Brazil

We characterised the diets of a community of lizards in the Caatinga area in the Monumento Natural Grota do Angico (MNGA), Sergipe, Brazil. We evaluated food availability during the wet and dry season, and analysed the stomach contents of 427 individuals from six species, identifying plant material and invertebrates to the taxonomic level of Order. In general, different lizard species had similar diets. Isoptera was the most important prey for *Ameivula ocellifera*, *Gymnodactylus geckoides*, *Lygodactylus klugei* and *Brasiliscincus heathi*, whereas Formicidae was the most important prey for *Tropidurus hispidus* and *Tropidurus semitaeniatus*. Prey consumption by each species in dry and wet seasons was similar with regard to prey categories used, but differed in the most commonly consumed orders (except for *Brasiliscincus heathi*). There was no significant difference between diet and prey availability, with the exception of Collembola and Acari which were rarely consumed. The limited seasonal differences in lizard diets may reflect the abundance and availability of prey.

Key words: electivity, semiarid, squamata, trophic ecology

INTRODUCTION

Lizard diets underlie a strong phylogenetic signature (Carvalho et al., 2007), with a tendency for niche conservatism of species in the same clade (Losos, 1995; Vitt & Zani, 1996; Vitt et al., 2003, 2008). Nevertheless, diets can be influenced by biotic factors such as physiological constraints, resource availability, competition, parasitism and predation (Vitt & Caldwell, 2009), as well as abiotic factors such as temperature and rainfall regimes (Sartorius et al., 1999; Rocha et al., 2009). The use of different habitats is enabled by the differential exploration of food items, and flexibility in diet creates the possibility for the colonisation of new areas (Zamprogno & Teixeira, 1998). Dietary studies provide information on the types of items consumed, the relative importance of each item in the diet, and differences in foraging strategies between species (Sexton et al., 1972; Huey & Pianka, 1981; Parmelle & Guyer, 1995; Duffield & Bull, 1998; Belver & Ávila, 2001; Sousa & Cruz, 2008).

Squamates can be divided into sedentary foragers (or “ambushers”) and active foragers, strategies which represent two extremes of a continuum (Huey & Pianka, 1981; Magnusson et al., 1985; Bergallo & Rocha, 1994; Vitt & Carvalho, 1995; Vitt & Pianka, 2005). These strategies are reflected in different dietary characteristics, activity patterns, habitat use, morphology, reproductive life histories and locomotion, and determine the interactions

among lizards in a community (Huey & Pianka, 1981; Teixeira, 2001; Carvalho & Araújo, 2004). Actively foraging species are more likely to encounter sedentary prey items, whereas ambush predators tend to consume more active prey. Because ambush predators require less energy for locomotion, there are generally less restrictive in the selection of prey types (Huey & Pianka, 1981; Schoener, 1971). The optimal foraging theory initially proposed by Emlen (1966) and MacArthur & Pianka (1966) supports the idea that organisms forage to maximise their energy gain. Predators attempt consume foods of higher energy return relative to the amount of energy spending required, and tend to alter the range of prey consumed when food supply decreases or increases. This theory explains, among others, seasonal variations in the diet of lizards (Schoener & Janzen, 1968).

While traditional ecological studies largely related the niche concept as a property of species or populations (Bolnick et al., 2003), the niche of a population can also be regarded as the sum of individual contributions, showing that populations of generalist species that use different types of resources can actually be composed of individual specialists (Bolnick et al., 2002; Svanbäck & Bolnick, 2007). Variation in diet among individuals of the same species can occur for several reasons, including resource shortages, seasonal variability, ontogeny and sexual divergence (Bolnick et al., 2002; Bolnick et al., 2003). In the present study, we characterised the diets

Correspondence: Anthony Santana Ferreira (anthonyfferreira@hotmail.com)

of lizards in an area of Caatinga in the state of Sergipe, Brazil. Specifically, we address whether (i) the diet of lizards corresponds to the availability of prey, (ii) changes in diet composition are related to seasonal variation, and (iii) diet composition is related to foraging behaviour.

MATERIAL AND METHODS

Study site

The study was conducted in a Caatinga area in the state of Sergipe, the Monumento Natural Grota do Angico - MNGA (9°41'S and 38°31'W). The Caatinga comprises a large part of northeastern Brazil (Andrade et al., 2005), and is defined by semi-arid and deciduous xerophytic vegetation on shallow, rocky and sometimes saline soils and high levels of solar radiation, low cloud cover, low humidity and low precipitation (Nimer, 1972; Ab'Sáber, 1977). The average annual rainfall in MNGA is around 500 mm, marked by a rainy season from April to August and a dry season coinciding with spring and summer (Nimer, 1972; Santos & Andrade, 1992). The MNGA has an area of 2,182 ha, with an average altitude of 100 m. The climate is arid, with semiarid bounded areas (BShw - Köppen) with higher annual average temperatures (26 to 28°C). Predominant plants are representatives of the families Fabaceae, Asteraceae and Euforbiaceae (Silva et al., 2013).

Sampling

We collected the specimens in monthly field trips between January 2012 and June 2013, each of which lasting for five consecutive days and totaling 90 days in the field. Animals were sampled using active searches close to pitfall trap locations (see below). Whenever possible we collected at least five individuals of each species per month to minimise interference with ongoing long-term monitoring of lizards at MNGA. Animals were sacrificed immediately with 2% lidocaine, fixed in 10% formalin, and later preserved in 70% alcohol and deposited in the Herpetological Collection of the Universidade Federal of Sergipe (CHUFS).

We sampled invertebrate prey availability monthly between July 2012 and June 2013. We used 48 pitfall traps (250 ml), containing a solution of alcohol, formaldehyde, mild detergent and water. Traps were arranged to cover different environmental conditions and remained open for three consecutive days, during daytime, coinciding with the activity time of the studied lizards. Invertebrates from traps and stomach contents were examined under a stereomicroscope and identified to the level of order consulting Buzzi (2002) and Triplehorn & Johnson (2011); the order Hymenoptera was divided into Formicidae and other representatives following Mesquita et al. (2006). We defined months corresponding to wet and dry periods using the historical average rainfall for the region (Poço Redondo, 2003-2013, source: SEMARH/SE). A threshold of 45 mm per month on average was adopted to define the months considered as belonging to the rainy season (April to August), with the remainder allocated to the dry season.

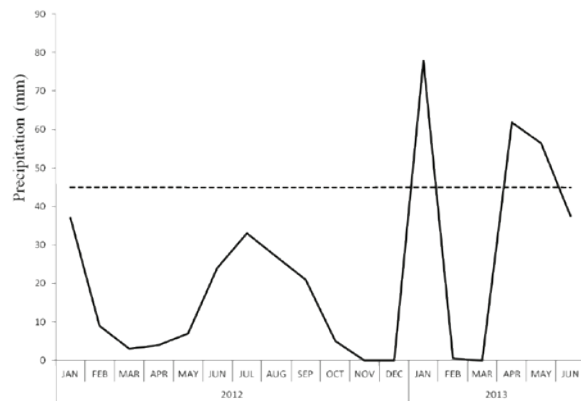


Fig. 1. Monthly rainfall data (—) and historical average (---) during the study period at the nearest weather station (Poço Redondo). Source: Secretaria de Meio Ambiente e Recursos Hídricos (SEMARH/SE).

Data analysis

All prey items consumed by lizards were counted and measured (length, l and width, w) with the aid of a digital caliper (accuracy 0.01 mm). Volumes (v) of whole prey were estimated using the formula of an ellipsoid as $(\pi * l * w^2) / 6$ (following Magnusson et al., 2003). To assess the relative contribution of each category of prey to the diet of different species, the importance value index (IVI) was used following Bjørndal et al. (1997): $IVI = (F\% + N\% + V\%) / 3$, where F is the frequency, N the number and V the volume of each category of prey (in %). The diversity of prey available in the environment and food niche amplitudes (B , number and volume) was calculated using the inverse of the diversity index of Simpson (1949). The values of B range from 1 (predominance of one category) to n (homogeneous distribution of all categories). Subsequently, we calculated the average of the two amplitudes to obtain a single value that was used as a reference to niche breadth (see Werneck et al., 2009).

The Pianka niche overlap metric in the package EcosimR (Gotelli et al., 2015), software R version 3.2.1 (R Core Team, 2015) was used to determine the presence of non-random patterns in food niche overlap, using the randomisation algorithm RA3. This algorithm retains the niche breadth and zero states for each species, but randomises the assignment of each utilisation value to a different niche category. It performs effectively in simulation studies and is recommended for analysis of niche overlap patterns (Winemiller and Pianka, 1990). We also use the randomisation algorithm Sim2. This algorithm assumes preys are equiprobable, but preserves differences among species (Gotelli, 2000). The importance value indices (IVI) of each consumed prey were used. For the period when data diet and prey availability were taken simultaneously we evaluated the electivity of food items by using the I_{vle} index (Krebs, 1989) as $E = (U_i - A_i) / (U_i + A_i)$, where U_i is the proportion of use of a given resource and A_i is the proportion of their availability. The index ranges from -1 (total rejection of the resource category) to 1 (complete selection). The relative abundances of prey categories consumed by each species, and the availability of prey in the environment,

Table 1. Prey availability and general composition of the diets of lizards in Monumento Natural Grota do Angico, Sergipe, Brazil, between 2012 and 2013. Values correspond to the importance value indices (IVI) and electivity (E) of prey categories used. Species: *Ao* = *Ameivula ocellifera*, *Gg* = *Gymnodactylus geckoides*, *Lk* = *Lygodactylus klugei*, *Bh* = *Brasiliscincus heathi*, *Ts* = *Tropidurus semitaeniatus*, *Th* = *Tropidurus hispidus*.

Categories / Species	Ao (n=85)		Gg (n=76)		Lk (n=57)		Bh (n=16)		Ts (n=76)		Th (n=90)		
	Avail.	IVI	E	IVI	E	IVI	E	IVI	E	IVI	E	IVI	E
Acari	7427	-	-1	1.29	-0.6	-	-1	-	-1	-	-1	0.38	-1
Araneae	1223	13.77	0.2	5.17	0.3	9.62	0.7	5.36	0.1	13.31	0.2	12.89	-0.03
Blattaria	192	4.29	0.4	3.53	-1	-	-1	-	-1	2.58	-0.5	2.42	-0.3
Chilopoda	30	1.02	0.2	-	-1	0.78	0.9	-	-1	2.02	0.6	2.11	0.7
Collembola	70584	-	-1	0.54	-1	2.40	-0.9	2.20	-1	1.09	-0.9	0.79	-0.9
Coleoptera	4530	30.85	-0.2	7.53	-0.2	22.76	0.7	12.49	-0.3	20.58	0.0	39.97	0.3
Dermaptera	1	-	-1	-	-1	-	-1	6.93	-1	0.46	-1	-	-1
Diplopoda	5	-	-1	-	-1	-	-1	-	-1	0.57	1	-	-1
Diplura	6	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Diptera	5838	-	-1	-	-1	5.85	0.3	-	-1	5.08	-0.7	0.38	-1
Ephemeroptera	1	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Formicidae	8705	3.95	-1	17.82	0.0	2.82	-0.5	2.21	-0.5	68.52	0.8	56.33	0.8
Gastropoda	0	2.45	1	-	-	6.24	1	-	-	0.46	1	0.77	1
Hemiptera	29	2.25	0.5	1.08	0.9	4.57	1	-	-1	3.53	0.9	2.75	0.9
Homoptera	0	0.70	1	-	-	-	-	-	-	-	-	0.40	-
Hymenoptera (no ants)	90	-	-1	-	-1	3.14	0.9	-	-1	7.81	0.8	9.93	0.8
Isoptera	75	44.95	1	44.75	1	23.15	1	64.08	1	10.38	1	10.83	1
Isopoda	12	-	-1	-	-1	-	-1	-	-1	0.86	-1	0.42	0.6
Insect Larvae	536	16.49	0.6	3.82	-1	19.14	0.9	15.53	0.7	25.53	0.8	19.52	0.8
Lepidoptera	159	4.21	0.6	0.78	-1	1.13	0.8	2.51	0.7	3.15	0.6	9.63	0.8
Mantoidea	12	1.38	0.8	-	-1	-	-1	-	-1	-	-1	-	-1
Plant Material	0	1.57	1	-	-	-	-	2.08	1	8.33	1	18.15	1
Mecoptera	4	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Odonata	1	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Opilionidae	9	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Orthoptera	537	8.28	0.2	12.46	0.5	6.65	0.8	5.35	0.5	5.95	0.1	7.55	0.2
Phasmatodea	1	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Pseudoscorpionida	143	0.81	-0.5	2.19	0.8	1.60	0.8	-	-1	0.92	0.2	0.77	-0.0
Psocoptera	107	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Scorpionida	30	0.81	-1	-	-1	-	-1	-	-1	1.72	-1	-	-1
Tysanura	316	3.37	0.1	1.22	0.5	2.41	0.6	-	-1	0.93	-1	0.78	-1
Vertebrates	2	-	-1	-	-1	-	-1	-	-1	1.73	-1	0.62	-1
Zoraptera	10	-	-1	-	-1	-	-1	-	-1	-	-1	-	-1
Empty Stomachs	-	11	-	28	-	10	-	4	-	0	-	1	-
Total niche width	1.96	2.6	-	2.61	-	6.07	-	1.72	-	3.03	-	3.20	-
Niche breadth (dry season)	-	2.92	-	1.63	-	5.27	-	2.28	-	2.31	-	1.98	-
Niche breadth (rainy season)	-	2.29	-	3.59	-	4.02	-	1.43	-	2.91	-	4.36	-
Dmax (dry and wet season)	-	0.9282	-	0.8162	-	0.682	-	0.8995	-	0.7815	-	0.7808	-
Dmax (dry season)	-	0.9029	-	0.7384	-	0.5315	-	0.7671	-	0.6857	-	0.6773	-
Dmax (rainy season)	-	0.8702	-	0.7819	-	0.7616	-	0.9721	-	0.8374	-	0.826	-
Dmax (prey availability)	0.5000	-	-	-	-	-	-	-	-	-	-	-	-

Table 2. Dietary Niche Overlap of lizards in Monumento Natural Grota do Angico, Sergipe, Brazil.

Species	<i>Gymnodactylus geckoides</i>	<i>Lygodactylus Klugei</i>	<i>Brasilincicus heathi</i>	<i>Tropidurus hispidus</i>	<i>Tropidurus semitaeniatus</i>
<i>Ameivula ocellifera</i>	0.85	0.94	0.90	0.56	0.44
<i>Gymnodactylus geckoides</i>		0.71	0.93	0.52	0.52
<i>Lygodactylus klugei</i>			0.78	0.61	0.50
<i>Brasilincicus heathi</i>				0.34	0.30
<i>Tropidurus hispidus</i>					0.94
<i>Tropidurus semitaeniatus</i>					

were compared pairwise by Kolmogorov-Smirnov tests (Zar, 1999).

Four out of the 18 months, of sampling showed rainfall data above the historical average (Fig. 1). There was no significant variation in precipitation between the two seasons in 2012; 2013 was characterised by atypical rainfall peaks in January and from April to June, coinciding with the rainy season (Fig. 1).

RESULTS

A total of 427 stomachs (73 empty) belonging to 11 species of lizards were examined. For prey analysis, we considered prey items found in at least five stomachs, reducing the number of study species to six (Table 1). We recognised 25 categories of prey items with an *IVI* between 0.38 (Acari and Diptera for *T. hispidus*) and 68.53 (Formicidae for *T. semitaeniatus*, Table 1). Overall the most important preys were Isoptera for *A. ocellifera*, *G. geckoides*, *L. klugei* and *B. heathi* and Formicidae for *T. semitaeniatus* and *T. hispidus* (Table 1). Lizards also ingested vertebrates (other lizards) and plant material (leaves, fruit and seeds).

Food niche breadth ranged between 1.72 (*B. heathi*) and 6.07 (*L. klugei*; Table 1). The average niche overlap

was low (0.31) but still higher than expected by chance (0.21 ± 0.001 , $P=0.02$, Fig. 2). Diet overlaps ranged from 0.30 (*B. heathi* and *T. semitaeniatus*) to 0.94 (*A. ocellifera* and *L. klugei* as well as *T. hispidus* and *T. semitaeniatus*). The highest values of diet overlap were found among species that preferentially feed on Isoptera (*L. klugei* and *A. ocellifera*) and Formicidae (*T. hispidus* and *T. semitaeniatus*, Table 2).

To quantify the availability of invertebrates in the environment, we sampled 100,615 specimens divided into 29 categories, with the most abundant being Collembola (70.15%), Formicidae (8.65%) and Acari (7.38%, Table 1). The most frequent categories present in each of the 12 months of sampling were Acari, Araneae, Blattaria, Collembola, Coleoptera, Diptera, Formicidae, insect larvae, Orthoptera, Pseudoscorpiones and Thysanura; the least common potential prey items present only in a single month were Dermaptera, Ephemeroptera, Mecoptera, Odonata, Phasmatodea and Zoraptera. The diversity (*B*) of prey available in the environment was 1.96. Collembola was the most abundant prey available during both the rainy season (75.01% of all trapped invertebrates) and the dry season (56.84%). Opiliones and Diplopoda were found only during the rainy season and Dermaptera, Diplura, Ephemeroptera, Mecoptera, Odonata, Phasmatodea and Zoraptera only in the dry season (Table 3).

Prey consumption did not markedly differ between seasons with regards to the main categories (Fig. 3), although the most commonly consumed order differed between rainy and dry periods (except for *B. heathi* which consumed preferably Isoptera in both periods Fig. 4). The widths of the trophic niche ranged from 1.43 (*B. heathi*) to 4.36 (*T. hispidus*) in the rainy season (Table 1). During the dry period it ranged from 1.63 (*G. geckoides*) to 5.27 (*L. klugei*; Table 1).

Several classes showed the lowest possible electivity indices (-1.00), such as Acari for *A. ocellifera*, Blattaria for *G. geckoides*, Opiliones for *L. klugei*, Diptera for *B. heathi* and Thysanura for *T. hispidus* and *T. semitaeniatus*. Three categories showed the maximum electivity index (+1.00): Gastropoda for *A. ocellifera*, *L. klugei*, *T. hispidus* and *T. semitaeniatus*, Homoptera for *A. ocellifera* and *T. hispidus* and plant material for *A. ocellifera*, *B. heathi*, *T. hispidus* and *T. semitaeniatus*. Lizard electivity for other available prey categories such as Chilopoda, Diplopoda, Formicidae, Hemiptera, wasps, Isoptera, insect larvae, Lepidoptera, Orthoptera and Pseudoscorpiones were

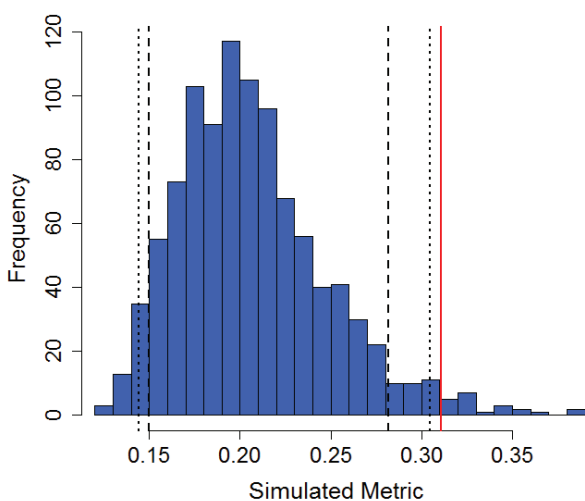
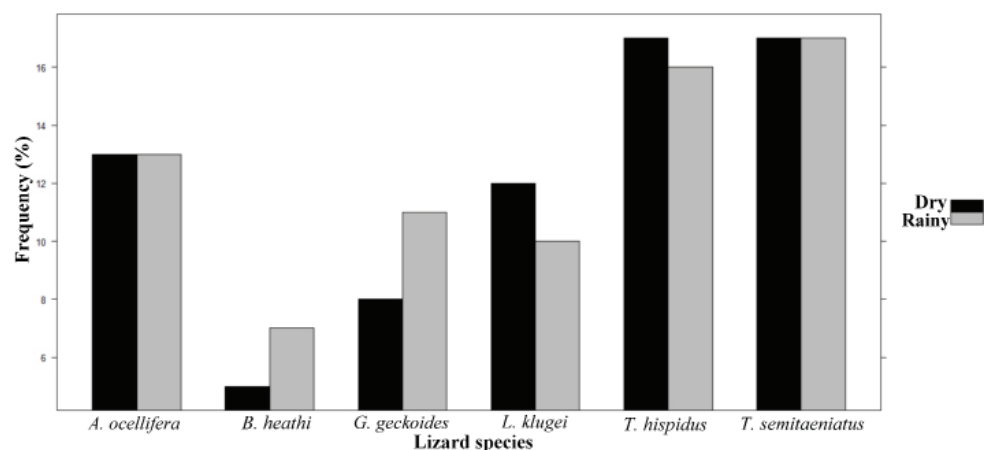


Fig. 2. Histogram of the simulated index values, the observed index value (red vertical line), and the one- and two-tailed 95% confidence intervals (the pairs of black vertical thin-dashed and thick-dashed lines, respectively).

Table 3. Resource availability by periods (dry and rainy) in the Monumento Natural Grota do Angico, Sergipe, Brazil, between 2012 and 2013. Values correspond to (N) abundance and (F) Frequency.

Taxon	Rainy Season				Dry Season			
	N	N%	F	F%	N	N%	F	F%
Acari	6479	8.79	5	100.00	948	3.53	7	100.00
Araneae	525	0.71	5	100.00	698	2.60	7	100.00
Blattaria	50	0.07	5	100.00	142	0.53	7	100.00
Chilopoda	22	0.03	3	60.00	8	0.03	3	42.86
Collembola	55303	75.01	5	100.00	15281	56.84	7	100.00
Coleoptera	2368	3.21	5	100.00	2162	8.04	7	100.00
Dermoptera	0	0.00	0	0.00	1	0.00	1	14.29
Diplopoda	5	0.01	3	60.00	0	0.00	0	0.00
Diplura	0	0.00	0	0.00	6	0.02	2	28.57
Diptera	4282	5.81	5	100.00	1556	5.79	7	100.00
Ephemeroptera	0	0.00	0	0.00	1	0.00	1	14.29
Hemiptera	20	0.03	4	80.00	9	0.03	4	57.14
Formicidae	3375	4.58	5	100.00	5330	19.83	7	100.00
Wasps	57	0.08	5	100.00	33	0.12	6	85.71
Isopoda	4	0.01	2	40.00	8	0.03	1	14.29
Isoptera	66	0.09	5	100.00	9	0.03	4	57.14
Insect Larvae	423	0.57	5	100.00	113	0.42	7	100.00
Lepidoptera	123	0.17	5	100.00	36	0.13	4	57.14
Mantodea	5	0.01	3	60.00	7	0.03	3	42.86
Mecoptera	0	0.00	0	0.00	4	0.01	1	14.29
Odonata	0	0.00	0	0.00	1	0.00	1	14.29
Opiliones	9	0.01	3	60.00	0	0.00	0	0.00
Orthoptera	259	0.35	5	100.00	278	1.03	7	100.00
Phasmatodea	0	0.00	0	0.00	1	0.00	1	14.29
Pseudoscorpionida	52	0.07	5	100.00	91	0.34	7	100.00
Psocoptera	38	0.05	5	100.00	69	0.26	6	85.71
Scorpionida	12	0.02	4	80.00	18	0.07	6	85.71
Thysanura	252	0.34	5	100.00	64	0.24	7	100.00
Zoraptera	0	0.00	0	0.00	10	0.04	1	14.29
Total	73729	100.00			26884	100.00		

**Fig. 3.** Consumption of prey by each species in both periods (dry and rainy) in the Monumento Natural Grota do Angico, Sergipe, Brazil, between 2012 and 2013. Axis (Y) corresponds to number of Orders of invertebrate consumed.

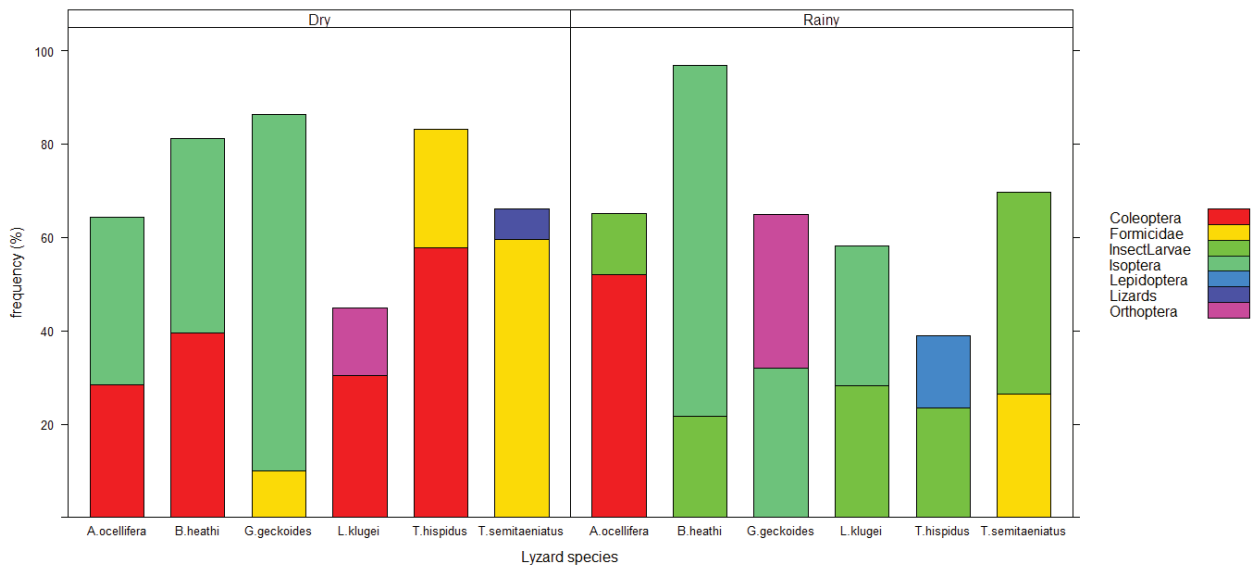


Fig. 4. Consumption of the two Orders of invertebrate most important by each species in both periods (dry and rainy). The axis (Y) correspond the frequency in percentages.

also high (Table 1). The proportions of available prey did not differ from consumed prey for all species and seasons (Kolmogorov-Smirnov $p > 0.05$, Table 1). Prey availability did not vary seasonally ($D_{max} = 0.5000$; Table 1).

DISCUSSION

This study showed that lizard species in MNGA were mainly insectivorous. Isoptera was the most important item in the diets of *A. ocellifera*, *G. geckoides*, *L. klugei* and *B. heathi* and Formicidae for *T. hispidus* and *T. semitaeniatus*, demonstrating that these species select a few categories among all available prey. Preference for such prey categories is often reported in the diet of congeners of lizards studied here (Colli et al., 1992; Vitt, 1995; Dias & Silva, 1998; Meira et al., 2007; Kolodiuk et al., 2009), suggesting niche conservatism with respect to diet. We observed that all species consumed sedentary and active prey. The lowest niche breadth values among the species assessed were observed for *A. ocellifera*, *G. geckoides* and *B. heathi*, and the highest for *L. klugei*, *T. hispidus* and *T. semitaeniatus*. Therefore, we confirm that ambush foragers generally have wider diet niches than active foragers (Schoener, 1971; Huey & Pianka, 1981). A sit-and-wait foraging strategy had already been suggested for *Phyllopezus pollicaris* (Dias & Silva, 1998), *T. hispidus*, *T. itambere*, *T. oreadicus*, *T. torquatus* and *T. semitaeniatus* (Colli et al., 1992; Rocha & Bergallo, 1994; Dias & Silva, 1998; Fialho et al., 2000; Meira et al., 2007; Kolodiuk et al., 2009), and active foraging for *A. abaetensis*, *A. ocellifera*, *A. ameiva* (Vitt & Colli, 1994; Silva et al., 2003; Dias & Rocha, 2007) and *V. rubricauda* (Dias & Silva, 1998). These two foraging strategies represent the extremes of a continuum, and wide variation within and among lizard species complicates their classification (Cooper, 1994; Werner et al., 1997; Werner, 1998).

Brasiliscincus heathi consumed few food items (ten categories of prey including plant material) and Isoptera was the dominant prey; it showed the lowest niche breadth over the entire study period and in the rainy

season. Therefore, this species was the more specialist lizard in the study area. This result does not correspond with other studies on scincid lizards conducted globally (Huey & Pianka, 1977; Vitt, 1995; Castanzo & Bauer, 1998; Rocha et al., 2004), which document then to be.

Generalist arthropod predators adopted the mixed foraging strategy of the genus. However, this result should be cautiously interpreted, especially because of the relatively small sample size of 16 individuals. Although phylogeny plays an important role in the foraging mode of lizards (Schoener, 1971; Cooper, 1995), each species can modulate its hunting strategies according to the pressures imposed by the environment (Huey & Pianka, 1981; Stamps et al., 1981; Rocha, 1994). Additionally, individuals within a species may specialise in certain food items or display a particular foraging mode (Pough et al., 1998).

The average food niche overlap was relatively low, but higher than expected by chance what indicating a lack of structuring in the diets of the studied species. The coexistence of species even with a high overlap in resource can be related to high prey availability in the environment. However, competitive relationships are more evident when resources are limited (Colwell & Futuyma, 1971; Schoener, 1975) which apparently seems not to have occurred at the studied site during the study period. Eight available prey categories (Diplura, Ephemeroptera, Mecoptera, Odonata, Opiliones, Phasmatodea, Psocoptera and Zoraptera) were not consumed by any species of lizard. Failure to consume these prey might be due to the low frequency of these categories in the environment (Stamps et al., 1981). Despite high availability, other prey categories (Acari, Collembola and Diptera) were not important for the diet of the lizards. Stamps et al. (1981) suggested that this fact is related to optimal foraging models, whose assumptions include optimisation of nutritional values of prey and predict that the selectivity for nutritionally important items may be inversely related to the abundance of these items in the environment. Moreover, the consumption

of prey with small body mass and consequently lower protein could expose lizards to predators, because lizards would need to forage for longer amounts of time to offset energy expenditure (Rocha, 1988; Guix, 1993). Besides external factors (previous experiences, limited availability and small tangible masses of prey) feeding behavior of lizards may be individually mediated through sensory systems (Feder & Lauder, 1986; Pough et al., 1998). The preference for a certain type of prey is usually manifested before the individual has had any exposure to potential prey, indicating that the selectivity of food items is an innate behaviour (Pough et al., 1998).

During the rainy season, lizards did not predominantly consume prey that were most common in the environment (Acari and Collembola). In the dry season, the most abundant categories (Collembola, Formicidae and Coleoptera) were the most important for *L. klugei* and *T. hispidus* (Coleoptera) and *T. semitaeniatus* (Formicidae), except for *A. ocellifera*, *G. geckoides* and *B. heathi* for which Isoptera were most important. Variation in diet composition can vary according to sex, or morphological differences, and can be a function of seasonal changes in prey availability and accessibility (Pianka, 1970; Fitch, 1978; Schoener et al., 1982; Van Sluys, 1995; Rocha, 1996; Fialho et al., 2000).

Small prey composed of soft structures may be underestimated because of the speed at which they are digested. We believe we did not underestimate the abundance of small prey items, such as Acari and Collembola because they were detected for *G. geckoides*, *T. hispidus*, *T. semitaeniatus*, *B. heathi* and *L. klugei*. Our results however differ from Ramos (1981) and Vitt et al. (2005) who showed a clear preference for Collembola and Acari for *Coleodactylus amazonicus*.

During the dry season, the vegetation of the Caatinga largely dies off, as a hypothesis resulting in lizards expanding their home ranges to access resources for their daily needs. The widest dietary niches for the dry season were found for *A. ocellifera*, *L. klugei* and *B. heathi*. During the rainy season the Caatinga vegetation attracts more beetles (Kolodiuk et al., 2009), and the biggest niche widths were estimated for *G. geckoides*, *T. hispidus* and *T. semitaeniatus*. Thus it is suggested that the variation of the niche widths of the different species between the two periods is a reflection of the high availability of the preferred prey of each species in the respective periods (Toft, 1985, Rocha, 2000). In addition, the food habit is directly linked to trophic morphology and the type of foraging strategy adopted by each species (Huey & Pianka, 1981; Lima & Moreira, 1993).

The Orders that showed the most abrupt seasonal fluctuations in availability were Acarina, Collembola, Diptera and Formicidae. In environments with climatic fluctuations, seasonal variation in diet composition is common, and related to changes in moisture which reflects the abundance of prey. However, resource availability in the environment did not vary significantly between the rainy and dry seasons (see also Vrcibradic & Rocha, 1995). The lack of variation in the diet of lizards in MNGA may be related to the high availability of prey in the area, which may reduce variation in diet (Vrcibradic

& Rocha, 1995, but see also Rocha, 1996). The absence of seasonal variation in the diet of lizards in MNGA may be related to the rainfall recorded in 2012 which was unusually constant across the year.

The consumption of plant material was common, and may be associated with anthelmintic effects, provision of water and aid in digestion. Omnivorous species tend to consume the soft parts of plants (Fialho et al., 2000; Rocha, 2000; Rocha & Siqueira, 2008) or sap, which may not be detectable in stomach content analyses (Teixeira et al., 2013). The consumption of plants can also help to eliminate intestinal parasites and may aid in the digestion of exoskeletons of invertebrates (Lima & Rocha, 2006; Ribeiro et al., 2008).

Saurophagy was observed in *T. hispidus* and *T. semitaeniatus*, which fed on *Vanzosaura rubricauda* and *T. hispidus*, respectively. Cannibalism and saurophagy has previously been reported in lizards (e.g., Anderson, 1960; Bowie, 1973; Polis, 1981; Blanco et al., 2012), and appears to be linked to common predatory behaviours (Polis & Myers, 1985). Previous records of cannibalism and saurophagy exist for in *A. ameiva* (Rocha & Vrcibradic, 1998), *A. ocellifera* (Sales et al., 2010), *H. mabouia* (Bonfiglio et al., 2006; Pombal & Pombal, 2010), *P. macrorhyncha* and *T. torquatus* (Teixeira, 2001).

Taken together, we show that lizards consumed a wide variety of prey, which is well reflected in the abundance of most potential prey items with the exception of Acari and Collembola. In contrast to our expectation we observed an absence of seasonality in diet and prey availability during the study period, and a specialised diet of *B. heathi*. The assemblage of lizards studied does not appear to be trophically structured, and the high prey availability allows a large overlap and use of shared resources.

ACKNOWLEDGEMENTS

The Secretaria de Estado do Meio Ambiente e dos Recursos Hídricos (SEMARH) approved the work (license nº 032.000-01143/2012-7). It was deemed necessary to collect specimens for new information on the diet of lizards and for contributing specimens to the herpetological collection of the UFS for ongoing research. The methodology was designed to not cause any substantial impact on MNGA lizard communities. No lizard sacrificed in this study is threatened with extinction according to the IUCN criteria, and all ethical standards for collecting and sacrifice of wild animals were strictly followed. We would like to thank Adam J. Stow for English review and helpful suggestions, Diana Patricia Rojas for help with the graphics. The Universidade Federal de Sergipe for logistical support. To the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the scholarship grants. The Laboratório de Cordados: Herpetology/ Ichthyology, Universidade Federal de Sergipe by the research and materials provided. To FAPITEC for the resources that allowed the execution of this research.

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Accepted: 22 June 2016