

# Feeding ecology of *Ameiva ameiva* in a caatinga area of northeastern Brazil

Raul F.D. Sales<sup>1</sup>, Leonardo B. Ribeiro<sup>1,2</sup> & Eliza M.X. Freire<sup>1,2</sup>

<sup>1</sup>Laboratório de Herpetologia, Universidade Federal do Rio Grande do Norte, Brazil

<sup>2</sup>Programa Regional de Pós-graduação em Desenvolvimento e Meio Ambiente, Universidade Federal do Rio Grande do Norte, Brazil

We studied the feeding ecology of the neotropical lizard *Ameiva ameiva* in a semiarid area in the state of Rio Grande do Norte, Brazil. The main food items ingested were insect larvae and pupae, gastropods, beetles, spiders, roaches and orthopterans. The population specialized more in the consumption of larvae and pupae in the rainy season, and consumed different types of prey more evenly in the dry season. The population niche width in the rainy season was narrower, due largely to a lower degree of individual specialization, despite individual niche widths that did not differ significantly between seasons. Individual specialization was stronger in the dry season, causing an expansion in the population niche width. Sexual differences in diet were small, despite sexual dimorphism in body size. Maximum, average and range of prey sizes were positively correlated with lizard body size, but minimum prey size remained constant, resulting in a positive relationship between body size and individual niche width. Despite differences between adult and juvenile lizards in maximum and average prey sizes, the fact that adults continue to feed on small prey suggests that there may be competition for food resources between age classes.

*Key words:* diet, individual specialization, lizard ecology, optimal foraging, seasonality, semiarid, Squamata, Teiidae

## INTRODUCTION

The feeding behaviour and diet composition of lizards are influenced by intrinsic and extrinsic factors (Pianka, 1986). Sex and age are the main intrinsic factors that may influence the type and size of prey, due to differences in morphology and/or behaviour between males and females and between adults and juveniles (Schoener, 1967; Fitch, 1981; Vitt, 2000). Rainfall and resource availability are considered the most important extrinsic factors (Pianka, 1970; Van Sluys, 1995; Rocha, 1996). Historical factors such as phylogeny and further ecological factors such as competition also exert a strong influence on the feeding ecology of lizards (Pianka, 1973; Barbault & Maury, 1981; Vitt & Zani, 1998).

Another type of variation in the use of resources that has increasingly received attention in recent years is individual specialization (Bolnick et al., 2003). In ecology, the idea that individuals in a population would be ecologically equivalent persisted for a long time, ignoring the possible existence of variation among individuals in the exploitation of resources (Costa et al., 2008a). However, some recent studies have suggested that many populations exploiting a wide variety of resources may actually be composed of a collection of individuals specialized in the use of a small portion of the resources used by the entire population (Bolnick et al., 2003, 2007, 2010; Araújo et al., 2007, 2009; Svanbäck & Bolnick, 2007). The phenomenon of individual specialization has been documented in several species in the animal kingdom (Bolnick et al., 2003), and may have important ecological and evolutionary implications.

The teiid lizard *Ameiva ameiva* (Linnaeus, 1758) has one of the largest geographic distributions among liz-

ards of the New World, occurring naturally in southern Mexico, Central America and most of South America (Pianka & Vitt, 2003). In Brazil, this lizard inhabits diverse ecosystems, making it a conspicuous component of most lizard assemblages in different biomes (Vitt & Colli, 1994). The feeding habits of *A. ameiva* have been investigated in autecological (Vitt & Colli, 1994; Zaluar & Rocha, 2000) as well as in community ecological studies (Magnusson & Silva, 1993; Vitt, 1995; Vitt & Zani, 1998; Mesquita et al., 2006a,b). However, the influence of seasonality, sex and ontogeny on the feeding ecology of the species is poorly known (Zaluar & Rocha, 2000; Magnusson & Silva, 1993), and the only thorough ecological study conducted in the Brazilian caatinga was a result of field work carried out in 1977–1978 (Vitt, 1995).

The present study sought to broaden and deepen our knowledge of the life history of *A. ameiva* in northeastern Brazil, in an area characterized by a semiarid climate and remarkable seasonality in rainfall. We addressed the following questions: 1) Is the diet of *A. ameiva* closely related to its foraging mode, and is it similar throughout its vast geographical distribution? 2) Are there sexual and ontogenetic differences in diet? 3) Does seasonality affect the population niche width and the degree of individual specialization in diet? 4) Is the size of prey consumed positively correlated with body size?

## MATERIALS AND METHODS

### Study area

The study was conducted at the Ecological Station of the Seridó (ESEC Seridó, 06°34'36.2"S, 37°15'20.7"W, datum: WGS84, altitude: 192 m), which encompasses a caatinga area of 1,166.38 hectares located in the mu-

*Correspondence:* Raul F.D. Sales, Laboratório de Herpetologia, Departamento de Botânica, Ecologia e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, 59072-970, Natal, Rio Grande do Norte, Brazil. *E-mail:* raulsales17@gmail.com

nicipality of Serra Negra do Norte, Rio Grande do Norte, Brazil. The climate is semiarid, hot and dry (Ab'Sáber, 1974), with a rainy season that predominates between March and May, and rainfall ranging between 500 and 700 mm/year. Mean annual temperatures vary from 28 to 30 °C, with maximum temperatures exceeding 40 °C, while the minimum ranges between 17 and 20 °C. Relative air humidity oscillates around 30–50% in the dry season, reaching 80–90% in the rainy season (Nimer, 1972). The vegetation of ESEC Seridó is arboreal-bushy hyperxerophilous, and in the rainy season the ground is covered with herbaceous extract, which is greatly reduced in the dry season (Varela-Freire, 2002).

### Field work

The field work consisted of monthly sampling over three consecutive days, from October 2008 to September 2010. The dry season extended from October 2008 to January 2009, July to December 2009, and June to September 2010. The rainy season comprised the months of February to June 2009 and January to May 2010. Mean monthly rainfall during the dry and rainy seasons was 11.2 mm and 135.6 mm, respectively. From 0800 to 1700, we walked trails that covered all types of vegetation of the ESEC Seridó, in order to sample all microhabitats locally used by the species. Some lizards were collected with the help of 4.5 calibre air rifles (Urko®).

### Morphometry and sexual dimorphism

For all animals collected, we took the following measures using a digital caliper (precision 0.1 mm) before fixation: snout–vent length from the tip of the snout to the anterior end of cloaca (SVL), head length from the posterior edge of the tympanum to the tip of the snout (HL), jaw length from the tip of the snout to the labial commissure (JL); head width at the widest point on the skull (HW), head height at the maximum height of the skull (HH), tail length (TL), hindlimb length (HLL), and forelimb length (FLL). Body mass (in grams) of each individual was measured using Pesola® scales (precision 0.2 g). All lizards were deposited in the Herpetological Collection of the Department of Botany, Ecology, and Zoology (CHBEZ) of the Universidade Federal do Rio Grande do Norte. The classification of individuals into adult and juvenile categories was done according to Vitt (1995), defining adult males as  $SVL \geq 99$  mm and adult females as  $SVL \geq 102$  mm. The existence of sexual differences in body size (SVL) and body mass was determined through analysis of variance (ANOVA). To assess sexual differences in other body dimensions, analysis of covariance (ANCOVA) was performed for each morphological characteristic, with SVL as a covariate, thus removing the body-size bias.

### Diet analysis

Stomach contents were placed in petri dishes and examined under a stereomicroscope to identify the food items ingested, usually to order level. The length and width of each prey item were measured with the aid of graph paper, and the volume was estimated by the prolate spheroid formula:  $V = 4/3\pi (\text{length}/2) \times (\text{width}/2)^2$  (following Vitt & Zani, 1998). The frequency of occurrence (number

of stomachs containing the prey category  $i$ , divided by the total number of stomachs) and the numerical and volumetric percentages of each prey category were determined for pooled stomachs following Mesquita & Colli (2003). The importance index ( $I$ ) was calculated for each prey category by  $(\text{occurrence} + \text{numerical} + \text{volumetric percentages})/3$  (following Mesquita et al., 2006a).

Numerical and volumetric proportions were used to calculate the niche width for each individual and for the population (pooled stomachs), using the inverse of Simpson's diversity index (Simpson, 1949). We also calculated the standardized values of the Simpson index to remove the effect of number of prey categories used, using Levin's standardized index (Krebs, 1999). An ANCOVA with seasonality as a factor and SVL as a covariate was performed on individual niche widths to investigate differences between seasons corrected for body size.

To analyse the degree of individual variation in diet in each season, we calculated the similarity between each individual's diet and the diet of the population ( $PS_i$ ), using the numerical and volumetric proportions of each prey category, following the equation:

$$PS_i = 1 - 0,5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j)$$

where  $p_{ij}$  is the proportion of prey category  $j$  in the diet of individual  $i$ , and  $q_j$  is the proportion of prey category  $j$  in the diet of the population as a whole (pooled stomachs). The average  $PS_i$  provides a measurement of similarity between the diets of individuals and the diet of the population ( $IS$ ) (Bolnick et al., 2002, 2007). The  $IS$  index ranges from 0 (when each individual uses a unique portion of the resources used by the entire population) to 1 (when all individuals use all the food resources used by the population). The IndSpec1.0 programme (Bolnick et al., 2002) was used in the calculation of  $PS_i$  and  $IS$  values. The  $IS$  values obtained in each season were compared to reveal seasonal differences in diet specialization. An ANCOVA with seasonality as the factor and SVL as a covariate was applied to the  $PS_i$  values to verify differences in the degree of individual specialization between seasons without body-size bias. The  $PS_i$  and  $IS$  values considered in this study represent the average of the  $PS_i$  and  $IS$  indices obtained from the numerical and volumetric proportions of prey.

A disadvantage of calculating the degree of individual specialization through the analysis of stomach contents is that it represents a snapshot of the diet of an individual, and may not necessarily reflect the food preferences and diet composition of the animal in the long run (Araújo et al., 2007). Thus, stomach contents may be underestimating the diversity of prey consumed by the individual, therefore overestimating the degree of individual specialization of the population (Bolnick et al., 2003). To circumvent this problem, we built null models for the population in both seasons in IndSpec 1.0 through the non-parametric Monte Carlo procedure, which generates replications of null matrices of the diet derived from the distribution of the population from which  $P$  values can be computed (Bolnick et al., 2002). Using the distribution of null values from the  $IS$  index, it is possible to determine if

**Table 1.** Diet composition of *Ameiva ameiva* at ESEC Seridó, Rio Grande do Norte, Brazil, from October 2008 to September 2010. F = frequency of occurrence, N = number, V = volume (mm<sup>3</sup>), I = importance index.

Prey category	F	F%	N	%	V	V%	I
Araneae	24	39.3	39	2.9	12092.5	8.5	16.9
Blattodea	21	34.4	63	4.8	8286.0	5.8	15.0
Chilopoda	2	3.2	2	0.1	99.4	<0.1	1.1
Coleoptera	36	59.0	91	6.9	12727.2	8.9	24.9
Diplopoda	7	11.4	8	0.6	167.9	0.1	4.0
Gastropoda	37	60.6	116	8.8	12838.9	9.0	26.1
Hemiptera	12	19.6	36	2.7	4369.0	3.0	8.5
Homoptera	8	13.1	10	0.7	908.5	0.6	4.8
Hymenoptera							
Formicidae	10	16.3	17	1.3	1033.9	0.7	6.1
Others	5	8.1	7	0.5	3653.7	2.5	3.7
Isopoda	1	1.6	1	<0.1	1.0	<0.1	0.5
Isoptera	5	8.1	151	11.5	844.9	0.5	6.7
Insect larvae and pupae	47	77.0	714	54.6	41998.3	29.6	53.7
Lepidoptera	2	3.2	2	0.1	11.2	<0.1	1.1
Plant material	12	19.6	–	–	1569.8	1.1	–
Mantodea	2	3.2	2	0.1	388.5	0.2	1.2
Oligochaeta	1	1.6	1	<0.1	402.7	0.2	0.6
Orthoptera	18	29.5	25	1.9	17664.8	12.4	14.6
Ootheca	1	1.6	1	<0.1	126.6	<0.1	0.5
Insect eggs	1	1.6	–	–	41.8	<0.1	–
Scorpiones	3	4.9	3	0.2	1190.0	0.8	1.9
Vertebrata							
Anurans	3	4.9	3	0.2	7824.2	5.5	3.5
Lizards	2	3.2	2	0.1	1150.0	0.8	1.4
Lizard eggs	1	1.6	11	0.8	12343.0	8.7	3.7
Fishes	1	1.6	1	<0.1	31.6	<0.1	0.5
Miscellaneous fragments	31	50.8	–	–	–	–	–

the degree of individual specialization is higher than expected by chance. We used 10,000 randomizations in the Monte Carlo bootstrap simulations to obtain the *P* values, which indicate the percentage of randomizations where the null value of *IS* was lower than the observed value.

The Mann–Whitney *U* test (Zar, 1999) was applied to verify the existence of seasonal, sexual and ontogenetic differences in diet for the number of food items ingested, total stomach volume, average and maximum prey length, and average and maximum prey volume. Differences in body size (SVL) in the sample across seasons were accounted for by applying the Mann–Whitney *U* test on regression residuals between SVL and diet variables.

The degree of similarity in numerical and volumetric proportions of prey categories used for adult males, adult females and juveniles in both seasons was examined with the symmetric overlap index  $O_{jk}$  (Pianka, 1973). Values range from 0 (no similarity) to 1 (complete similarity). Throughout the text,  $O_{jk}$  values shown represent the average between the numerical and volumetric similarities.

Linear regressions were performed to assess the relationship between the body size of lizards and the size of prey, with all variables  $\log_{10}$ -transformed to meet the requirements of normality. All statistical tests were performed using SPSS 16.0 software for Windows, with a

significance level of 5%. Before performing parametric tests, all variables were tested for normality and homoscedasticity of variances. Throughout the text, the descriptive statistics are represented as mean  $\pm$  standard deviation (SD).

## RESULTS

### Morphometry and sexual dimorphism

We collected 68 specimens of *Ameiva ameiva*: 35 adults (15 females and 20 males) and 33 juveniles (18 females, eight males and seven individuals of undetermined sex). The average SVL of adult males (143.4 $\pm$ 20.5 mm, range 106.7–177.8) was non-significantly higher than that of adult females (131.2 $\pm$ 13.3 mm, range 109.6–155.0;  $F_{1,33}=3.976$ ,  $P=0.054$ ). The average SVL of young males (67.7 $\pm$ 15.5 mm, range 51.8–89.2) was similar to that of young females (75.3 $\pm$ 18.1 mm, range 49.0–101.5;  $F_{1,24}=1.038$ ,  $P=0.318$ ). Body mass was significantly higher in adult males (90.7 $\pm$ 37.4 g, range 34.0–162.0) compared to adult females (63.9 $\pm$ 18.7 g, range 31.5–72.0;  $F_{1,33}=4.680$ ,  $P=0.038$ ). Young males and females did not differ significantly in body mass (males: 9.8 $\pm$ 6.9 g, range 3.7–20.5; females: 13.2 $\pm$ 3.9 g, range 2.7–28.0;  $F_{1,24}=0.593$ ,  $P=0.449$ ).

**Table 2.** Importance indices obtained from the pooled stomachs of *Ameiva ameiva* collected in different seasons at ESEC Seridó, Rio Grande do Norte, Brazil, from October 2008 to September 2010. ♂ = adult males (20 in the rainy season and one in the dry season), ♀ = adult females (11 in the rainy season and four in the dry season), J = juveniles (nine in the rainy season and 17 in the dry season), Σ = total individuals collected in a particular season.

Prey categories	Rainy season (n=39)				Dry season (n=22)			
	♂	♀	J	Σ	♂	♀	J	Σ
Araneae	10.7	19.3	29.7	14.8	10.3	28.6	27.1	24.9
Blattodea	17.2	26.9	4.3	17.4	–	–	15.4	10.2
Chilopoda	1.8	3.1	–	1.7	–	–	–	–
Coleoptera	22.7	29.0	26.6	25.3	19.2	25.1	23.9	25.3
Diplopoda	5.5	9.4	4.1	6.2	–	–	–	–
Gastropoda	30.0	34.0	18.3	28.9	1.5	10.9	20.3	18.8
Hemiptera	5.6	7.3	–	4.9	–	47.5	11.5	19.3
Homoptera	1.8	3.1	4.2	3.5	10.1	–	8.3	8.1
Hymenoptera								
Formicidae	5.9	6.1	10.8	6.6	–	26.9	–	5.0
Others	7.2	3.1	4.1	5.4	–	–	–	–
Isopoda	–	–	–	–	–	–	2.2	1.6
Isoptera	–	–	–	–	58.7	12.0	17.8	25.1
Insect larvae and pupae	59.7	70.3	67.3	64.6	–	39.8	24.0	23.9
Lepidoptera	–	–	4.1	0.8	–	–	2.2	1.6
Mantodea	–	–	–	–	–	–	5.8	3.9
Oligochaeta	2.0	–	–	0.9	–	–	–	–
Orthoptera	23.6	13.7	–	16.1	–	19.4	10.5	12.2
Ootheca	1.8	–	–	0.9	–	–	–	–
Scorpiones	4.1	–	–	2.0	–	–	2.8	1.9
Vertebrata								
Anurans	6.6	–	–	3.6	–	13.6	–	3.3
Lizards	–	7.1	–	2.0	–	–	–	–
Lizard eggs	8.0	–	–	4.5	–	–	–	–
Fishes	–	3.1	–	0.8	–	–	–	–

Accounting for body size, we found sexual differences in head length (ANCOVA,  $F_{2,58}=22.478$ ,  $P<0.001$ ), jaw length (ANCOVA,  $F_{2,58}=12.068$ ,  $P=0.001$ ), head width (ANCOVA,  $F_{2,58}=9.127$ ,  $P=0.004$ ), head height (ANCOVA,  $F_{2,58}=16.030$ ,  $P<0.001$ ), forelimb length (ANCOVA,  $F_{2,57}=14.477$ ,  $P<0.001$ ), hindlimb length (ANCOVA,  $F_{2,58}=12.659$ ,  $P=0.001$ ) and body mass (ANCOVA,  $F_{2,58}=7.570$ ,  $P=0.008$ ), with higher values for males. Only tail length showed no significant differences between males and females (ANCOVA,  $F_{2,50}=2.910$ ,  $P=0.094$ ). Thus, males are heavier and have larger heads and limbs than females of the same body size.

## Diet

Of the 68 stomachs examined, 61 (89.7%) contained at least one food item. The seven individuals with empty stomachs were all juveniles collected during the dry season. We identified 1306 food items in the stomachs analysed and recognized 25 prey categories (Table 1). The diet of *A. ameiva* was mainly composed of insect larvae and pupae, gastropod molluscs, beetles, spiders, roaches and orthopterans (Table 1). The most important prey category was insect larvae and pupae, which were

present in 77.04% of the stomachs analysed; they represented 54.67% of the total number of prey and 29.62% of the total volume consumed, and had a notably higher importance index than all other prey categories. We also detected the presence of small vertebrates in six of the 68 stomachs analysed (8.82%), representing two individual *Vanzosaura rubricauda*, three anurans (including a juvenile *Scinax signatus*), eleven *Tropidurus* eggs, and fish fragments (scales). The plant material ingested had little significance in the diet, and was mainly composed of leaf fragments probably ingested accidentally while capturing prey.

When analysing the composition of diet in relation to seasonality (Table 2), we found variations in the proportion of certain prey categories. In the rainy season, insect larvae and pupae represented the most important prey category in all groups. In the dry season, this category was less prevalent, with termites, beetles, spiders, hemipterans and orthopterans gaining in importance. The  $O_{jk}$  index showed a 43.8% population similarity between the seasons.

The population niche width, both numerically and volumetrically, was narrower in the rainy season (Table 3).

**Table 3.** Indices of niche width of *Ameiva ameiva* in the dry season ( $n=22$ ) and rainy season ( $n=39$ ) at ESEC Seridó, Rio Grande do Norte, Brazil, from October 2008 to September 2010.

Niche width indices	Dry season		Rainy season	
	Individual	Population	Individual	Population
Numeric Simpson	2.33±1.20	3.625	2.37±1.12	2.144
Numeric Levins	0.50±0.37	0.187	0.43±0.29	0.06
Volumetric Simpson	2.12±0.89	7.218	2.06±1.06	6.228
Volumetric Levins	0.38±0.28	0.414	0.29±0.22	0.261

However, the individual niche widths did not differ significantly between seasons, either numerically (ANCOVA,  $F_{2,58}=0.256$ ,  $P=0.615$ ) or volumetrically (ANCOVA,  $F_{2,58}=3.913$ ,  $P=0.053$ ).

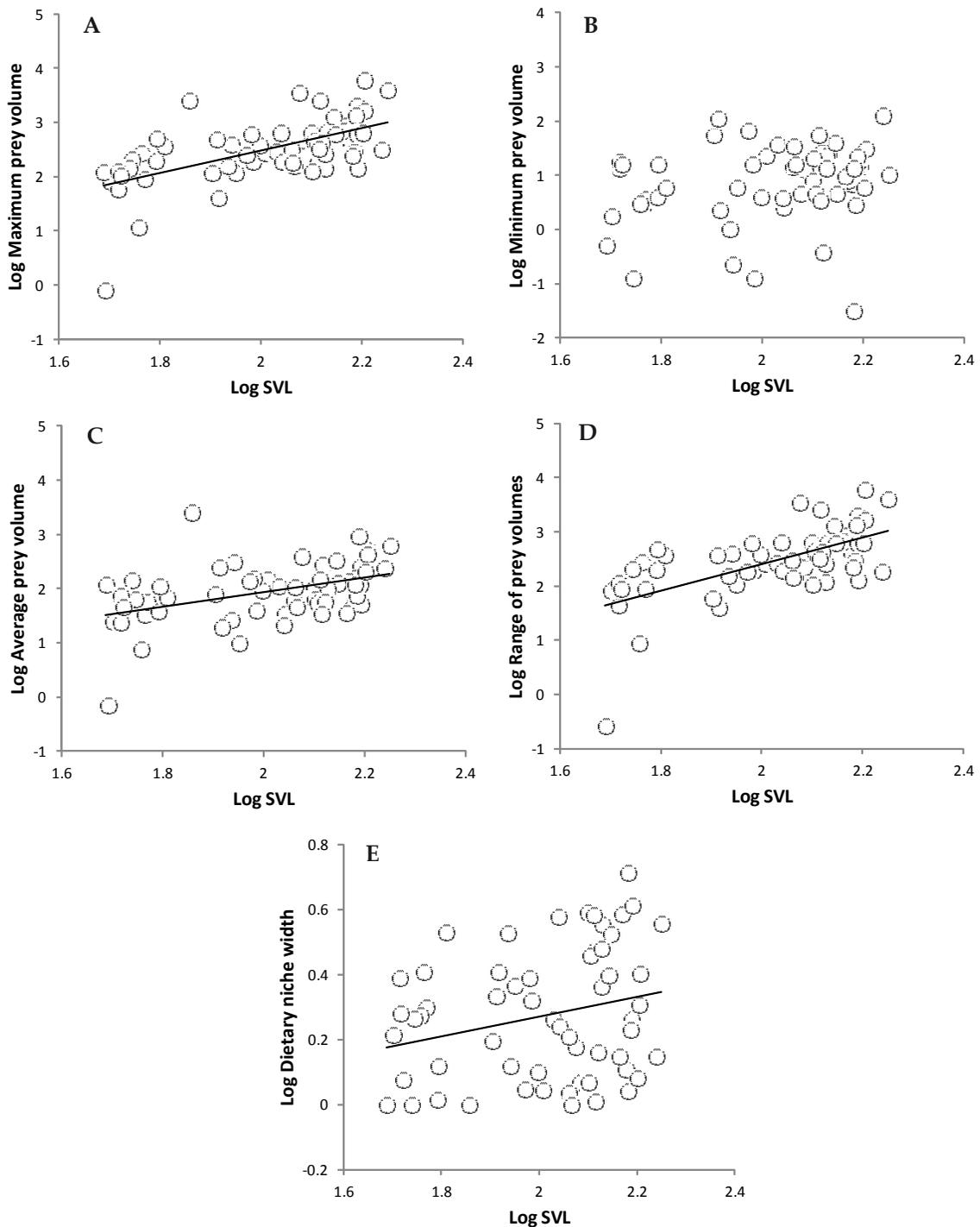
The  $IS$  index values were lower in the dry season ( $IS=0.2903$ ) compared to the rainy season ( $IS=0.4934$ ), indicating a higher degree of individual specialization in the dry season. In fact, the mean  $O_{jk}$  index (obtained by averaging the pairwise overlaps between all individuals in the sample) was lower in the dry season ( $O_{jk}=0.179$ ) than in the rainy season ( $O_{jk}=0.413$ ), and the  $PS_i$  values were significantly lower for individuals in the dry season (ANCOVA,  $F_{2,58}=21.663$ ,  $P<0.001$ ). In addition, the  $IS$  values were significantly lower than the null values provided by the Monte Carlo simulations ( $P<0.001$  in both seasons), showing that the degree of individual specialization was higher than expected by chance.

In the quantitative analysis of diet, none of the variables measured differed between seasons (number of food items ingested:  $Z=-0.796$ ,  $P=0.426$ ; total stomach volume:  $Z=-0.391$ ,  $P=0.696$ , maximum prey length:  $Z=-1.772$ ,  $P=0.076$ ; average prey length:  $Z=-1.757$ ,  $P=0.079$ ; maximum prey volume:  $Z=-0.466$ ,  $P=0.642$ ; average prey volume:  $Z=-0.015$ ,  $P=0.988$ ). Adult males and females differed significantly only in the number of food items ingested (higher in females), and in the average prey volume (higher in males, Table 4). However, when comparing adults and juveniles, we observed significantly higher values for adults in all variables (Table 4). The  $O_{jk}$  index showed 86.7% qualitative similarity between the diet of adult males and adult females, and 74.0% similarity between the diet of adults and juveniles.

The snout-vent length of lizards (SVL) showed positive correlations with maximum prey volume ( $R^2=0.354$ ,

**Table 4.** Average values of the quantitative variables analysed for the diet of adult males and females, and for adult and juvenile *Ameiva ameiva* at ESEC Seridó, Rio Grande do Norte, Brazil, between October 2008 and September 2010. The length scale is in mm, the volume scale in  $\text{mm}^3$ .  $P$ -values marked with an asterisk (\*) indicate significant differences between the groups analysed.

Variables	Among adults		$Z$	$P$
	Males ( $n=20$ )	Females ( $n=15$ )		
Total number of prey items	24.7±27.3	40.0±45.4	-2.319	0.020*
Total stomach volume	3984.0±4198.2	2960.5±2003.9	-0.300	0.764
Average prey length	12.7±4.1	10.5±2.7	-1.733	0.083
Maximum prey length	31.2±21.1	25.1±10.4	-0.685	0.494
Average prey volume	251.1±240.7	94.7±61.0	-2.167	0.030*
Maximum prey volume	1258.4±1578.4	578.3±605.7	-1.117	0.264
Variables	Among age classes		$Z$	$P$
	Adults ( $n=35$ )	Juveniles ( $n=26$ )		
Total number of prey items	31.2±36.4	8.1±8.3	-4.661	<0.001*
Total stomach volume	3545.3±3430.3	679.9±900.7	-5.381	<0.001*
Average prey length	11.8±3.7	8.6±4.8	-3.303	0.001*
Maximum prey length	28.6±17.4	14.4±6.6	-4.931	<0.001*
Average prey volume	184.1±200.2	180.4±492.1	-2.129	0.033*
Maximum prey volume	966.9±1288.3	306.1±488.4	-4.025	<0.001*



**Fig. 1.** Relationship between snout–vent length (SVL) and size of prey consumed and individual niche width of *Ameiva ameiva* at ESEC Seridó, Rio Grande do Norte, Brazil. A) SVL versus maximum prey volume, B) SVL versus minimum prey volume, C) SVL versus average prey volume, D) SVL versus range of prey volumes, E) SVL versus dietary niche width.

$F_{1,59}=32.327$ ,  $P<0.001$ ), average prey volume ( $R^2=0.213$ ,  $F_{1,59}=15.923$ ,  $P<0.001$ ) and range of prey volumes ( $R^2=0.385$ ,  $F_{1,56}=35.014$ ,  $P<0.001$ ), but there was no significant association with minimum prey volume ( $R^2=0.062$ ,  $F_{1,56}=3.673$ ,  $P=0.060$ ). A weak but significant positive correlation was found between SVL and individual niche width ( $R^2=0.071$ ,  $F_{1,59}=4.517$ ,  $P=0.038$ ) (Fig. 1).

## DISCUSSION

### Morphometry and sexual dimorphism

Male *A. ameiva* had larger heads and limbs than females of the same body size. Sexual dimorphism is widespread in most bisexual species of the family Teiidae (Anderson & Vitt, 1990; Vitt, 1991; Censky, 1995; Herrera & Robin-

son, 2000). The main cause of sexual dimorphism is seen as sexual selection favouring larger body size and larger heads for males (Anderson & Vitt, 1990). Larger males generally win aggressive intra-sexual interactions and gain access to a larger number of females, thus achieving higher reproductive success (Censky, 1995, 1997; Lewis et al., 2000).

### General diet composition

The diet of *A. ameiva* at the ESEC Seridó was mainly composed of sedentary prey (insect larvae and pupae and gastropod molluscs) and mobile prey that are inactive and hidden in the substrate when lizards forage (all roaches and a high percentage of beetles, spiders and orthopterans consumed were nocturnal species). These types of prey are more likely to be found and consumed by active foragers, which, besides vision, use chemical cues in the detection and discrimination of prey (Huey & Pianka, 1981; Cooper, 1995). The diet composition of *A. ameiva*, therefore, is closely linked to its foraging mode, confirming previous studies on other teiid lizards (e.g. Mesquita & Colli, 2003; Teixeira-Filho et al., 2003; Dias & Rocha, 2007). In other populations of *A. ameiva* studied, insect larvae and pupae, orthopterans, beetles, spiders, gastropods and termites were also the main food items reported (Vitt & Colli, 1994; Vitt & Zani, 1998; Zaluar & Rocha, 2000; Mesquita et al., 2006a,b), suggesting a strong influence of phylogeny on feeding ecology, with each population additionally reflecting local prey availability. We verified the occasional presence of small vertebrates in the diet of *A. ameiva*, revealing the opportunistic predatory behaviour of this species. Several other vertebrates have already been reported as prey for other populations of *A. ameiva*, including lizards (e.g. Zaluar & Rocha, 2000; Gogliath et al., 2010), lizard eggs (Lieberman, 1980), anurans (Rocha & Vrcibradic, 1998), amphibiaenids (Ubaid et al., 2009) and bats (Connors, 2010).

### Seasonal variations in diet

According to models of optimal foraging theory (MacArthur & Pianka, 1966; Schoener 1971; Cody, 1974; Eastbrook & Dunham, 1976), limited food supply leads to a generalization in the use of food resources, whereas higher abundance of food allows for increased selectivity towards more profitable prey. In environments with strong seasonality, such as the Brazilian caatinga, local productivity is subject to cycles of rainfall (Janzen & Schoener, 1968; Ballinger & Ballinger, 1979), and abundance of arthropods tends to be higher in the rainy season (e.g. Vasconcellos et al., 2010). In this context, we predicted that seasonality of the ESEC Seridó would influence the diet composition of *A. ameiva*.

The results supported our prediction, as population-wide seasonal differences in the diet were evident. The analysis of population niche width confirmed this trend, with a narrower niche in the rainy season. Seasonal variations in the diet of lizards are commonly related to seasonal variation in prey availability in the environment (Dunham, 1981; Van Sluys, 1995; Kolodiuk et al., 2010), which also seems to be the case for *A. ameiva* in the ESEC Seridó. The results indicated that the narrower niche width of the

population in the rainy season was a consequence of the smaller inter-individual variation in niches in this period. Conversely, in the dry season, individual specialization was stronger. The niche expansion of the *A. ameiva* population in the dry season, due to the increase in individual specialization without increasing individual niches, corresponds to the second niche expansion scenario suggested by Bolnick et al. (2007). One explanation for our results is that in the dry season, when the abundance of arthropods is more limited in the caatinga (Vasconcellos et al., 2010), individual diets might increasingly be linked to the availability of prey in the environment. In the rainy season, on the other hand, individuals might tend to target more profitable prey as predicted by optimal foraging models, thus decreasing the degree of individual specialization and increasing diet overlap.

Studies addressing the influence of seasonality on the degree of individual specialization in reptiles and amphibians are still scarce. In a study conducted by Araújo et al. (2007) with four species of anurans in the Brazilian cerrado, seasonality influenced the degree of individual specialization in *Leptodactylus* sp. and *Proceratophrys* sp. However, contrary to our results, a higher degree of individual specialization was observed in the rainy season, probably due to the narrowing of individual niches in this period (Araújo et al., 2007).

### Sexual and ontogenetic variations in diet

Although males have a relatively larger body and head than females, the qualitative similarity in diet between the sexes was high, while quantitative differences were small, similar to the results of a previous study by Zaluar & Rocha (2000).

The most plausible explanation for the quantitative differences found between the diets of juvenile and adult *A. ameiva* in the ESEC Seridó lies in the fact that juveniles are limited by their smaller body, head and mouth, resulting in a narrower range in the size of potential prey available (Peters, 1983; Vézina, 1985; Vitt, 2000). However, despite differences in prey size, the preferred prey categories consumed by juveniles and adults were very similar. The relationships between prey size and predator size support the second scenario of ontogenetic changes in diet proposed by Costa et al. (2008b). Despite adding larger prey to their diet, adults continue to consume small prey consistently, leaving minimum prey size constant and influencing individual niche width (positively correlated with body size). This suggests that there may be competition between age classes for food resources.

Our results contrast with evidence from a range of terrestrial and marine predators, for which body size is positively correlated with maximum and minimum prey sizes (Costa et al., 2008b; Costa, 2009; but see also e.g. Scharf et al., 2000; Menard et al., 2006). In addition, some studies with teiid lizards of the genus *Cnemidophorus* also found no association between predator size and prey size, due to feeding specialization for termites, prey with little variation in body size (Mesquita & Colli, 2003; Teixeira-Filho et al., 2003). Thus, as suggested by Costa (2009), different predator species can display different ontogenetic changes in diet.

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## REFERENCES

- Ab'Sáber, A.N. (1974). O domínio morfoclimático semiárido das caatingas brasileiras. *Geomorfologia* 43, 1–139.
- Anderson, R.A. & Vitt, L.J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84, 145–157.
- Araújo, M.S., Bolnick, D.I., Martinelli, L.A., Giaretta, A.A. & Reis, S.F. (2009). Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology* 78, 848–856.
- Araújo, M.S., Reis, S.F., Giaretta, A.A., Machado, G. & Bolnick, D.I. (2007). Intrapopulation diet variation in four frogs (Leptodactylidae) of the Brazilian savannah. *Copeia* 2007, 855–865.
- Ballinger, R.E. & Ballinger, R.A. (1979). Food resource utilization during periods of low and high food availability in *Sceloporus jarrovi* (Sauria: Iguanidae). *Southwestern Naturalist* 24, 347–363.
- Barbault, R. & Maury, M.E. (1981). Ecological organization of a Chihuahuan desert lizard community. *Oecologia (Berlin)* 51, 335–342.
- Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L. & Paull, J.S. (2010). Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B* 277, 1789–1797.
- Bolnick, D.I., Svanbäck, R., Araújo, M.S. & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the USA* 104, 10075–10079.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161, 1–28.
- Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology* 83, 2936–2941.
- Censky, E.J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva plei*. *Behaviour* 132, 529–557.
- Censky, E.J. (1997). Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). *Behavioral Ecology and Sociobiology* 40, 221–225.
- Cody, M.L. (1974). Optimization in ecology. *Science* 183, 1156–1164.
- Connors, J.S. (2010). *Ameiva ameiva* (giant ameiva). Diet. *Herpetological Review* 41, 215.
- Cooper, W.E., Jr. (1995). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behaviour* 50, 973–985.
- Costa, G.C. (2009). Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90, 2014–2019.
- Costa, G.C., Mesquita, D.O., Colli, G.R. & Vitt, L.J. (2008a). Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages? *American Naturalist* 172, 868–877.
- Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O. & Colli, G.R. (2008b). Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17, 670–677.
- Dias, E.J.R. & Rocha, C.F.D. (2007). Niche differences between two sympatric whiptail lizards (*Cnemidophorus abaetensis* and *C. ocellifer*, Teiidae) in the restinga habitat of northeastern Brazil. *Brazilian Journal of Biology* 67, 41–46.
- Dunham, A.E. (1981). Populations in a fluctuating environment: the comparative population ecology of *Sceloporus merriami* and *Urosaurus ornatus*. *Miscellaneous Publications of the University of Michigan Museum of Zoology* 158, 1–62.
- Eastbrook, G.F. & Dunham, A.E. (1976). Optimal diet as a function of absolute abundance, relative abundance and relative prey value of available prey. *American Naturalist* 110, 401–413.
- Fitch, H.S. (1981). Sexual size differences in reptiles. *University of Kansas Museum of Natural History Miscellaneous Publications* 70, 1–72.
- Gogliath, M., Ribeiro, L.B. & Freire, E.M.X. (2010). *Cnemidophorus ocellifer* (Spix's whiptail). Predation. *Herpetological Bulletin* 114, 36–38.
- Herrera, E.A. & Robinson, M.C. (2000). Reproductive and fat body cycles of the tegu lizard, *Tupinambis teguixin*, in the llanos of Venezuela. *Journal of Herpetology* 34, 598–601.
- Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Janzen, D.H. & Schoener, T.W. (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49, 96–110.
- Kolodiyuk, M.F., Ribeiro, L.B. & Freire, E.M.X. (2010). Diet and foraging behavior of two species of *Tropidurus* (Squamata, Tropiduridae) in the caatinga of northeastern Brazil. *South American Journal of Herpetology* 5: 35–44.
- Krebs, C.J. (1999). *Ecological Methodology*. Menlo Park: Addison Wesley Longman.
- Lewis, A., Tirado, G. & Sepulveda, J. (2000). Body size and paternity in a teiid lizard (*Ameiva exsul*). *Journal of Herpetology* 34, 110–120.
- Lieberman, A. (1980). Nesting of the basilisk lizard (*Basiliscus basiliscus*). *Journal of Herpetology* 14, 103–105.
- MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. *American Naturalist* 100, 603–609.
- Magnusson, W.E. & Silva, E.V. (1993). Relative effects of size, season and species on the diets of some Amazonian savanna lizards. *Journal of Herpetology* 27, 380–385.
- Menard, F., Labruno, C., Shin, Y., Asine, A. & Bard, F. (2006). Opportunistic predation in tuna: a size-based approach. *Marine Ecology Progress Series* 323, 223–231.
- Mesquita, D.O. & Colli, G.R. (2003). The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a neotropical savanna. *Journal of Herpetology* 37, 498–509.
- Mesquita, D.O., Colli, G.R., França, F.G.R. & Vitt, L.J. (2006a).

- Ecology of a cerrado lizard assemblage in the Jalapão region of Brazil. *Copeia* 2006, 460–471.
- Mesquita, D.O., Costa, G.C. & Colli, G.R. (2006b). Ecology of an Amazonian savanna lizard assemblage in Monte Alegre, Pará state, Brazil. *South American Journal of Herpetology* 1, 61–71.
- Nimer, E. (1972). Climatologia da região Nordeste do Brasil. Introdução à climatologia dinâmica. *Revista Brasileira de Geografia* 34, 3–51.
- Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Pianka, E.R. (1970). Comparative autoecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51, 703–720.
- Pianka, E.R. (1973). The structure of lizard communities. *Annual Reviews of Ecology and Systematics* 4, 53–74.
- Pianka, E.R. (1986). *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure*. Princeton: Princeton University Press.
- Pianka, E.R. & Vitt, L.J. (2003). *Lizards: Windows to the Evolution of Diversity*. London: University of California Press.
- Rocha, C.F.D. (1996). Seasonal shift in lizard diet: the seasonality in food resources affecting the diet of *Liolaemus lutzae* (Tropiduridae). *Ciência e Cultura* 48, 264–269.
- Rocha, C.F.D. & Vrcibradic, D. (1998). Reptiles as predators of vertebrates and as preys in a restinga habitat of southeastern Brazil. *Ciência e Cultura* 50, 364–368.
- Scharf, F.S., Juanes, F. & Rountree, R.A. (2000). Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208, 229–248.
- Schoener, T.W. (1967). The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155, 474–477.
- Schoener, T.W. (1971). Theory on feeding strategies. *Annual Review of Ecology and Systematics* 2, 369–404.
- Simpson, E.H. (1949). Measurement of diversity. *Nature* 163, 688.
- Svanbäck, R. & Bolnick, D.I. (2007). Intraspecific competition drives increased resource use diversity in a natural population. *Proceedings of the Royal Society B* 274, 839–844.
- Teixeira-Filho, P.F., Rocha, C.F.D. & Ribas, S.C. (2003). Relative feeding specialization may depress ontogenetic, seasonal, and sexual variations in diet: the endemic lizard *Cnemidophorus littoralis* (Teiidae). *Brazilian Journal of Biology* 63, 321–328.
- Ubaid, F.K., Nascimento, G.R. & Maffei, F. (2009). *Ameiva ameiva*. Attempted predation of amphibiaenian. *Herpetological Review* 40, 339.
- Van Sluys, M. (1995). Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. *Ciência & Cultura* 47, 61–65.
- Varela-Freire, A.A. (2002). *A Caatinga Hiperxerófila Seridó: A sua Caracterização e Estratégias para sua Conservação*. São Paulo: Academia de Ciências do Estado de São Paulo.
- Vasconcellos, A., Andreazze, R., Almeida, A.M., Araujo, H.F.P., Oliveira, E.S. & Oliveira, U. (2010). Seasonality of insects in the semi-arid caatinga of northeastern Brazil. *Revista Brasileira de Entomologia* 54, 471–476.
- Vézina, A.F. (1985). Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* 67, 555–565.
- Vitt, L.J. (1991). Ecology and life history of the wide-foraging lizard *Kentropyx calcarata* (Teiidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69, 2791–2799.
- Vitt, L.J. (1995). The ecology of tropical lizards in the caatinga of northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History* 1, 1–29.
- Vitt, L.J. (2000). Ecological consequences of body size in neonatal and small-bodied lizards in the neotropics. *Herpetological Monographs* 14, 388–400.
- Vitt, L.J. & Colli, G.C. (1994). Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72, 1986–2008.
- Vitt, L.J. & Zani, P.A. (1998). Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. *Journal of Tropical Ecology* 14, 63–86.
- Zaluar, H.L.T. & Rocha, C.F.D. (2000). Ecology of the wide-foraging lizard *Ameiva ameiva* (Teiidae) in a sand dune habitat of southeastern Brazil: ontogenetic, sexual and seasonal trends in food habits, activity, thermal biology and microhabitat use. *Ciência e Cultura* 52, 101–107.
- Zar, J.H. (1999). *Biostatistical Analysis*, 4<sup>th</sup> edn. New Jersey: Prentice-Hall, Inc.

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