Feeding habits and predator-prey size relationships in the whiptail lizard Cnemidophorus ocellifer (Teiidae) in the semiarid region of Brazil

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FEEDING HABITS AND PREDATOR-PREY SIZE RELATIONSHIPS IN THE WHIPTAIL LIZARD *CNEMIDOPHORUS OCELLIFER* (TEIIDAE) IN THE SEMIARID REGION OF BRAZIL

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Abstract. We studied the diet of the whiptail lizard *Cnemidophorus ocellifer* (Spix, 1825) and the relationships between predator size and prey size in a Caatinga area of northeastern Brazil. Lizards (N = 111) were collected during the day through active search. In the laboratory, we measured them and registered the number of ingested items of each prey category to Order, as well as the dimensions and frequencies of each. The main prey category in the *C. ocellifer* diet was insect larvae and pupae, followed by Orthoptera, Isoptera, Coleoptera and Araneae. Termites (Isoptera) were important only in numeric terms, having negligible volumetric contribution and low frequency of occurrence, an uncommon feature among whiptail lizards. The types and sizes of prey consumed by adult males and females were similar, despite sexual dimorphism in head size. Adults and juveniles ingested similar prey types, but differed in prey size. Maximum and minimum prey sizes were positively correlated with lizard body size, suggesting that in this population individuals experience an ontogenetic change in diet, eating larger prey items while growing, and at the same time excluding smaller ones.

Keywords. Body size; Caatinga; Diet; Lizards; Ontogeny; Prey size.

Introduction

Both intrinsic and extrinsic factors have strong influence on the feeding ecology of lizards (Pianka, 1986). Rainfall and seasonal fluctuations in availability of food are among the most important extrinsic factors (Pianka, 1970; Magnusson and Silva, 1993; Rocha, 1996). Foraging mode, body size, sex, and ontogeny are important intrinsic factors influencing diet composition (Schoener, 1967; Huey and Pianka, 1981; Perry, 1996; Vitt, 2000). The consequences of body size on feeding ecology have been studied in diverse taxonomic groups. In some cases, predators exclude smaller prey items from the diet as they grow and add larger items, in such a way that both minimum and maximum prey size increase at similar rates (*e.g.,* Costa *et al.,* 2008; Costa, 2009). In others cases, the predator adds larger items to its diet as it grows, but continues to eat small prey. A positive relationship between predator body size and maximum prey size occurs, but minimum prey size remains constant or increases with a much slighter slope (*e.g.,* Scharf *et al.,* 2000; Sales *et al.,* 2011). Finally, the predator may not add larger items to its diet as it grows; in this case, minimum and maximum prey sizes are not correlated with body size (dietary specialists; *e.g.,* Vitt *et al.,* 1997a; Colli *et al.,* 2003).

The family Teiidae is composed of actively foraging, sexually dimorphic lizards, distributed throughout the Americas (Vitt and Caldwell, 2009). Within teiids, the Teiinae constitute the most speciose and widespread group, mainly owing to the small-bodied species (less than 100 mm in snout-vent length) until recently united in the single genus *Cnemidophorus* (collectively known as whiptail lizards). In spite of the overall similarity in morphology and ecology among its members, molecular studies have not supported the monophyly of *Cnemidophorus,* and Reeder *et al.* (2002) resurrected the genus *Aspidoscelis* for the North and Central American clade of *"Cnemidophorus".* The South American whiptails (the *lemniscatus* group) currently constitute the genus *Cnemidophorus,* and are more closely related to the large-bodied teiine genera *Ameiva* and *Kentropyx.* These three genera are now known to constitute a monophyletic group that Reeder *et al.* (2002) referred to as "cnemidophorines".

Most studied *Cnemidophorus* populations are known to feed predominantly on termites and insect larvae (*e.g.,* Vitt *et al.,* 1997b; Mesquita and Colli, 2003a, b; Dias and Rocha, 2007; Menezes *et al.,* 2006, 2008, 2011). Massive ingestion of small prey can minimize the occurrence of ontogenetic changes in diet and studies on whiptail lizards, where termites constituted a predominant food item, found no association between lizard size and prey size (Mesquita and Colli, 2003b; Teixeira-Filho *et al.,* 2003; Dias and Rocha, 2007; Menezes *et al.,* 2006, 2008).

Herein, we provide data on the feeding habits of a population of *Cnemidophorus ocellifer* (Spix, 1825) from the semiarid Caatinga in northeastern Brazil. This species is widely distributed in Brazil, occurring in the Cerrado, in the Caatinga, and in restingas along the northeastern coast (Vanzolini *et al.,* 1980; Menezes *et al.,* 2011). Our main goals were to (1) determine its diet composition, (2) explore the relationship between lizard body size and prey size; and (3) examine the existence of sexual and ontogenetic variations in diet. We hypothesized that the feeding habits of *C. ocellifer* are similar to that of other whiptail lizards, with predominant consumption of termites and larvae and absence of a relationship between lizard size and prey size. In this case, we would expect weak sexual and ontogenetic differences in diet. Alternatively, if there are ontogenetic and sexual differences in diet, we would expect to find a positive correlation between lizard size and prey size.

Materials and Methods

Study Site

This 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 municipality of Serra Negra do Norte, state of 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 800 mm/year. Mean annual temperatures vary from 28°C to 30°C, and maximum temperatures exceed 40°C on some days of the year, whereas the minimum temperatures range between 17°C 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; the ground is covered with herbaceous extract in the rainy season, which is greatly reduced in the dry season (Varela-Freire, 2002).

Lizard Sampling

The field work consisted of monthly trips for three consecutive days, from September 2008 to August 2010. During this period, from 0800 h to 1700 h, we walked trails that covered all the types of vegetation of the ESEC Seridó in order to sample the different habitats and microhabitats used by the species. Along these trails, some lizards were captured with 4.5 mm air rifles (Urko®). Killing of animals was conducted in accordance with current legislation. All lizards were measured (see below), dissected to remove the stomachs, then fixed in 10% formalin, conserved in 70% ethanol, and deposited in the Herpetological Collection of the Department of Botany, Ecology, and Zoology (CHBEZ) of the Universidade Federal do Rio Grande do Norte.

Data Analysis

In all animals collected, we took the following measures using digital calipers (precision of 0.1 mm) before fixation: snout-vent length (SVL), from the tip of the snout to the anterior end of cloaca; head length (HL), from the posterior margin of the tympanum to the tip of the snout; head width (HW) at the widest point of the skull; head height (HH) at the maximum height of the skull; and jaw length (JL), from the tip of the snout to the labial commissure. The classification of individuals into adult and juvenile categories was done according to Vitt (1995), considering adults those individuals that reached the minimum size of sexual maturity (adult males as SVL $\geq$ 56 mm and adult females as SVL $\geq$ 55 mm). The existence of sexual differences in body size (SVL) was determined through analysis of variance (ANOVA). To assess sexual differences in head and jaw size (HL, HW, HH and JL), analysis of covariance (ANCOVA) was performed with SVL as covariate.

Stomach contents were placed in petri dishes and examined under a stereomicroscope to identify the food items ingested, usually to Order level. Ants (Formicidae) were treated as an exclusive prey category in the Order Hymenoptera, and larval stages of the Orders Lepidoptera, Coleoptera, Diptera and Neuroptera were placed together in one prey category (insect larvae and pupae). The length and width of each prey item was measured with the aid of graph paper, and the volume was estimated by the prolate spheroid formula: $V = 4/3\pi\ (\text{length}/2) \times (\text{width}/2)^2$

Table 1. Summary of morphometric characters (in millimeters) of adult males and females of *Cnemidophorus ocellifer* at the Ecological Station of the Seridó, Rio Grande do Norte, Brazil. See methods for abbreviations and statistical descriptions. *P-values* marked with an asterisk (*) indicate significant differences between the groups.

	Adult Males (N = 49)	Adult Females (N = 33)	Statistic	P
SVL	69.8 ± 8.6 (56.8 – 91.1)	67.0 ± 6.4 (56.0 – 77.7)	$F_{1,80} = 2.297$	0.134
HL	19.4 ± 3.0 (14.0 – 25.5)	16.7 ± 1.6 (12.5 – 19.6)	$F_{2,79} = 26.325$	< 0.001*
HW	11.6 ± 2.0 (7.8 – 16.2)	9.4 ± 0.9 (7.4 – 12.7)	$F_{2,79} = 73.296$	< 0.001*
HH	9.9 ± 1.6 (7.2 – 14.0)	8.1 ± 0.8 (6.7 – 11.2)	$F_{2,79} = 63.712$	< 0.001*
JL	13.7 ± 1.9 (10.4 – 18.0)	11.7 ± 1.0 (9.6 – 13.2)	$F_{2,79} = 42.318$	< 0.001*

(Dunham, 1983). 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. The importance index (I) was calculated for each prey category by adding up the occurrence, numerical and volumetric percentages, and dividing by three (Mesquita and Colli, 2003b). We calculated the importance index for the total sample, and separately for adult males, adult females, all adults, and juveniles.

The degree of qualitative similarity in the diet of adult males and females and adults and juveniles was examined with the Pianka's Overlap Index – O_{jk} (Pianka, 1973), in which values range from 0 (no similarity) to 1 (complete similarity). We calculated overlap values using the Niche Overlap Module of EcoSim v.7 (Gotelli and Entsminger, 2004), and compared the observed overlap values with simulated values generated from 1000 randomizations of the original matrix (Randomization Algorithm 3).

For each individual, we calculated prey size (maximum, minimum and mean prey volume). Lizards that ingested fewer than two prey items were excluded from prey-size analyses due to incompatibility of estimating both maximum and minimum prey sizes. The Mann-Whitney U test (Zar, 1999) was applied to verify the existence of sexual and ontogenetic differences in diet for the number of food items ingested, total stomach volume, mean, maximum and minimum prey volume. Linear regressions (Zar, 1999) were performed to test the relationship between the body size of lizards (SVL) and prey size, with all variables $\log_{10}$-transformed to meet the requirements of normality.

All statistical analyses were performed using PASW Statistics 18.0 software for Windows, with α set at 0.05. Before performing all the parametric tests, all variables were tested for normality and homoscedasticity of variances. Throughout the text, the descriptive statistics are represented as a mean ± standard deviation (SD).

Results

We collected 111 specimens of *C. ocellifer,* 60 males (49 adults and 11 juveniles), 44 females (33 adults and 11 juveniles), and seven individuals (one adult and six juveniles) in which it was not possible to determine the sex. The mean SVL of adult males did not differ significantly from that of adult females, but head and jaw size measurements (HL, HW, HH and JL) were significantly higher in adult males (Table 1).

Of the 111 stomachs examined, 98 (88.3%) contained at least one food item. We identified a total of 811 food items in the analyzed stomachs and recognized 20 prey categories, mostly arthropods (Table 2). Based on importance indexes, the diet of *C. ocellifer* was composed mainly of insect larvae and pupae, Orthoptera, Isoptera, Coleoptera and Araneae (Table 2). The most important prey category in frequency, number, and volume was insect larvae and pupae, present in 54.0% of the stomachs, representing 33.0% of the total number of prey, 26.2% of total volume and with a notably higher importance index compared to other prey categories. Orthoptera, Araneae and Coleoptera had a good representation in volume and frequency of occurrence, and Isoptera was well represented in number, but had low frequency of occurrence and negligible importance in volume (Table 2). The plant material ingested had little significance in the diet, and was composed mainly of leaf fragments, most likely ingested accidentally while capturing prey. Cannibalism was registered in one occasion; we found a whole neonate conspecific (32.5 mm SVL) in the stomach of an adult female (70.7 mm SVL).

When comparing qualitatively the diet of adult males and females, and adults and juveniles, we verified that the prey types consumed were basically the same, which is evidenced by the importance indexes shown in Table 1. According to the O_{jk} index, the qualitative similarity between the diet of adult males and females was 0.882 (numeric) and 0.860 (volumetric), both indices significantly higher than expected by chance (*p-values* of 0.004 and 0.026). The

TABLE 2. Diet composition of *Cnemidophorus ocellifer* (N = 111) at the Ecological Station of the Seridó, Rio Grande do Norte, Brazil. F = frequency of occurrence, N = number, V = volume (mm^3), I = importance index (T = total sample, M = adult males, F = adult females, A = all adults, J = juveniles). U.A.R. = Unidentified arthropod remains.

Prey category	F (%)	N (%)	V (%)	I_T	I_M	I_F	I_A	I_J
Acari	2 (1.8)	2 (0.2)	23.9 (< 0.1)	0.6	—	—	—	2.8
Araneae	23 (20.7)	38 (4.6)	5328.0 (11.5)	12.3	10.6	17.1	13.9	8.7
Blattodea	10 (9.0)	11 (1.3)	1326.8 (2.8)	4.4	2.6	7.5	4.7	2.8
Coleoptera	31 (27.9)	66 (8.1)	4487.9 (9.7)	15.2	9.7	24.7	16.1	11.4
Diplopoda	4 (3.6)	4 (0.4)	105.9 (0.2)	1.4	0.8	2.3	1.4	1.4
Diptera	3 (2.7)	4 (0.4)	22.8 (< 0.1)	1.0	—	1.1	0.4	2.9
Gastropoda	13 (11.7)	16 (1.9)	128.6 (0.2)	4.6	3.2	5.7	4.2	5.9
Hemiptera	17 (15.3)	33 (4.0)	3493.6 (7.5)	8.9	6.9	11.1	8.6	10.5
Homoptera	13 (11.7)	25 (3.0)	638.2 (1.3)	5.3	1.7	8.0	4.3	8.8
Hymenoptera								
Formicidae	7 (6.3)	9 (1.1)	391.3 (0.8)	2.7	3.8	3.6	3.6	—
Others	6 (5.4)	9 (1.1)	422.6 (0.9)	2.4	2.2	2.5	2.2	3.0
Isoptera	15 (13.5)	256 (31.5)	805.9 (1.7)	15.6	15.6	17.1	15.9	14.5
Insect larvae and pupae	60 (54.0)	268 (33.0)	12060.0 (26.2)	37.7	43.6	33.5	38.7	35.1
Lepidoptera	3 (2.7)	4 (0.4)	279.9 (0.6)	1.2	—	2.4	1.0	2.3
Mantodea	9 (8.1)	12 (1.4)	1622.8 (3.5)	4.3	3.7	4.5	4.6	2.9
Odonata	3 (2.7)	3 (0.3)	472.0 (1.0)	1.3	0.9	1.2	1.0	3.5
Orthoptera	31 (27.9)	49 (6.0)	8883.4 (19.3)	17.7	14.5	20.5	17.2	19.7
Insect eggs	1 (0.9)	—	1.2 (< 0.1)	—	—	—	—	—
Vertebrata								
Lizards	2 (1.8)	2 (0.2)	1227.4 (2.6)	1.5	—	4.1	1.9	—
Plant material	15 (13.5)	—	562.2 (1.2)	—	—	—	—	—
U.A.R.	33 (29.7)	—	3701.1 (8.0)	—	—	—	—	—

TABLE 3. Average values of the quantitative variables analyzed for the diet of adult males and females, and for adults and juveniles of *Cnemidophorus ocellifer* at the Ecological Station of the Seridó, Rio Grande do Norte, Brazil. The volume scale is in mm^3. *Z-values* refer to the Mann-Whitney U test, and *p-values* marked with an asterisk (*) indicate significant differences between the groups.

Variables	Adult Males (N = 29)	Adult Females (N = 26)	Z	P	Adults (N = 56)	Juveniles (N = 15)	Z	P
Number of prey items ingested	9.7 ± 9.3	11.5 ± 14.6	-0.676	0.499	10.6 ± 11.9	13.7 ± 15.2	-0.847	0.397
Total stomach volume	595.0 ± 633.3	752.3 ± 589.3	-1.163	0.245	665.9 ± 607.4	284.7 ± 164.0	-2.233	0.026*
Maximum prey volume	312.7 ± 488.7	282.3 ± 267.4	-0.801	0.423	297.4 ± 392.9	122.4 ± 133.8	-2.599	0.009*
Minimum prey volume	21.0 ± 29.2	13.4 ± 19.7	-1.181	0.238	17.3 ± 25.0	4.9 ± 5.9	-2.910	0.004*
Mean prey volume	89.1 ± 88.1	82.0 ± 60.8	-0.455	0.649	85.2 ± 75.2	35.6 ± 54.6	-3.226	0.001*

similarity in diet of adults and juveniles was 0.853 (numeric) and 0.786 (volumetric), both also significantly higher than expected by chance (*p-values* of 0.003 and 0.004). In the quantitative analyses of the diet, adult males and females did not differ in any of the variables analyzed (Table 3). However, when comparing adults and juveniles, in most of the variables we observed significantly higher values for adults (Table 3).

The body size of lizards (SVL) showed positive correlations with maximum prey volume ($R^2 = 0.114$, $F_{1,69} = 8.862$, $P = 0.004$, Figure 1A), minimum prey volume ($R^2 = 0.128$, $F_{1,69} = 10.155$, $P = 0.002$, Figure 1B) and mean prey volume ($R^2 = 0.235$, $F_{1,69} = 21.147$, $P < 0.001$, Figure 1C). Head and mouth dimensions (HL, HW, HH, JL) also showed positive correlations with prey size (R^2 values from 0.058 to 0.067 for maximum prey volume, from 0.095 to 0.102 for minimum prey volume, and from 0.131 to 0.170 for mean prey volume; *p-values* < 0.05), except for HL and HH against maximum prey volume ($P = 0.051$ in both cases).

DISCUSSION

Teiids are considered extreme active foragers inside the spectrum of foraging intensity (Magnusson *et al.,* 1985; Perry, 1999). These lizards move around searching for food almost constantly, and use, besides vision, a highly developed chemoreception (vomeronasal) to detect and discriminate prey (Cooper, 1990, 1995). As chemically-oriented, active foragers, teiids frequently capture prey that are sedentary (*e.g.,* larvae), clumped in the environment (*e.g.,* termites), or hidden in the substrate (*e.g.,* nocturnal arthropods) (Huey and Pianka, 1981; Anderson, 1993). The diet of *C. ocellifer* in the ESEC Seridó was mainly composed of sedentary prey (insect larvae and pupae), but also contained a high proportion of mobile and evasive prey (orthopterans, beetles and spiders). Termites were also important, but only in numeric terms. These five prey categories constitute the most important ones in the diets of most cnemidophorines (*e.g.,* Vitt *et al.,* 1995, 1997b, 2000; Mesquita and Colli, 2003a, b; Menezes *et al.,* 2006, 2008, 2011; Sales *et al.,* 2011). Thus, the feeding habits of *C. ocellifer* from ESEC Seridó are similar to the general feeding pattern of this lizard clade. However, the relatively low importance of termites is an uncommon feature among whiptails (see below).

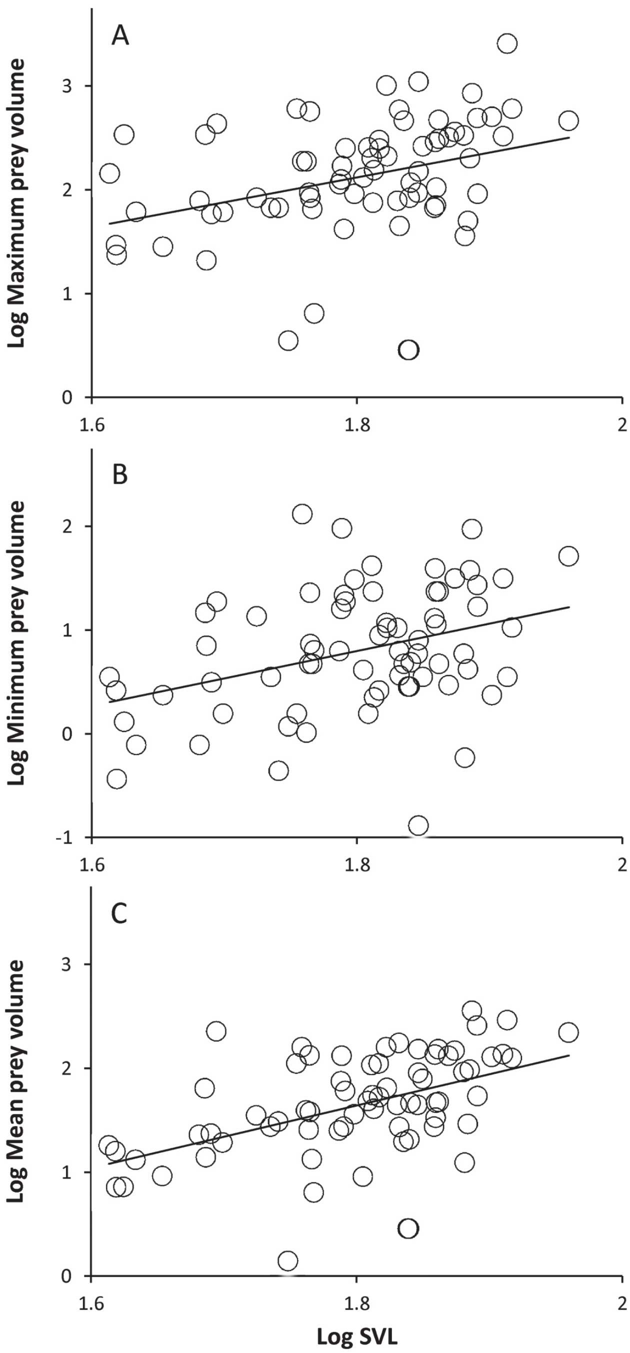

Figure 1. Relationship between snout-vent length – SVL (mm) and prey size (mm^3) in *Cnemidophorus ocellifer* at the Ecological Station of the Seridó, Rio Grande do Norte, Brazil. (A) SVL against maximum prey volume (slope = 2.398, P = 0.004), (B) SVL against minimum prey volume (slope = 2.646, P = 0.002), (C) SVL against mean prey volume (slope = 3.011, P < 0.001).

The positive association in *C. ocellifer* between body size and prey size contrasts with most studies on *Cnemidophorus,* which reported a lack of relationship between these variables (*e.g.,* Mesquita and Colli, 2003b; Teixeira-Filho *et al.,* 2003; Dias and Rocha, 2007; Menezes *et al.,* 2006, 2008). As pointed out by these authors, the massive consumption of termites (small prey items with little variation in body size) by most lizards of all ages in these studies contributed to this trend. Termites are usually among the most frequent and important prey in the diet of most species of *Cnemidophorus* in South America (see Ariani *et al.,* 2011 – Table 4 for a review), and also for most whiptail lizards of the genus *Aspidoscelis* in Central and North America (*e.g.,* Pianka, 1970; Vitt *et al.,* 1993; Paulissen *et al.,* 2006; Rodríguez and Casas-Andreu, 2011). In *C. ocellifer* from ESEC Seridó, termites were important in number, but only for few individuals (low frequency of occurrence), and had a negligible volumetric contribution (less than 2%). This does not seem to be an artifact of season/time of the year, since the lizards were sampled year-round. Apparently the infrequent consumption of termites accounted for a significant relationship between prey size and lizard body size in this population. Similar to our results, Ariani *et al.* (2011) verified absence of termites in the diet composition of a population of *C. lacertoides* in a restinga habitat in southern Brazil, despite the local availability of termite mounds. It is not yet clear why some *Cnemidophorus* populations ingest termites massively while others do not, but certainly local variations in the availability of termites and larger prey types that offer more profitability (*e.g.,* insect larvae, orthopterans) are a determinant factor.

Although *C. ocellifer* adult males had relatively larger heads and jaws than adult females, both sexes consumed similar prey types and did not differ in maximum and minimum prey sizes. The occurrence of dietary differences between sexes was expected, because the larger sex has the potential to consume larger prey (*e.g.,* Schoener, 1967; Preest, 1994). Nevertheless, sexual differences may be difficult to be detected in some studies if they represent a small effect size, requiring a large sample size to become statistically significant (Jennions and Møller, 2003). Similar to our results, some studies with sexually dimorphic lizards have not found sexual differences in the types and size of prey (*e.g.,* Zaluar and Rocha, 2000; Kolodiuk *et al.,* 2010; Sales *et al.,* 2011). On the other hand, dietary differences between adults and juveniles, chiefly in prey size as occurred in our study, are widely reported in lizards, and one plausible explanation for such differences lies in the fact that juvenile lizards 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). Other limiting factors to juveniles include bite force (Erickson *et al.,* 2003; Herrel and O'Reilly, 2006) and prey handling performance (Mehta, 2003).

We conclude that *C. ocellifer* in the ESEC Seridó is a carnivorous lizard that consumes mainly insect larvae and pupae, sedentary prey items common in the diet of active foragers. Termites are infrequent in the diet and have negligible volumetric importance, contrasting with the feeding habits of most whiptails, including other populations of *C. ocellifer* in Brazil (Vitt, 1995; Mesquita and Colli, 2003b; Dias and Rocha, 2007; Menezes *et al.,* 2011). The positive association between body size and both minimum and maximum prey sizes suggests that lizards in this population experience an ontogenetic change in the diet, adding larger prey items while growing, and at the same time excluding smaller ones.

Resumo

Nós estudamos a dieta e a relação entre o tamanho do predador e o tamanho das presas no lagarto *Cnemidophorus ocellifer* (Spix, 1825) em uma área de Caatinga do nordeste do Brasil. Os lagartos (N = 111) foram coletados durante o dia através de busca ativa. No laboratório, nós os medimos e registramos o número de itens ingeridos de cada categoria de presa ao nível de Ordem, bem como suas dimensões e frequências. A principal categoria de presa na dieta de *C. ocellifer* foi larvas e pupas de insetos, seguido de Orthoptera, Isoptera, Coleoptera e Araneae. Térmitas (Isoptera) foram importantes apenas em termos numéricos, com contribuição volumétrica desprezível e baixa frequência de ocorrência, uma característica incomum entre lagartos do gênero *Cnemidophorus.* Os tipos e tamanhos das presas consumidas por machos e fêmeas adultos foram similares, apesar do dimorfismo sexual no tamanho da cabeça. Adultos e juvenis ingeriram tipos de presa similares, mas diferiram no tamanho. Os tamanhos máximo e mínimo das presas foram positivamente correlacionados com o tamanho corporal dos lagartos, sugerindo que nesta população os indivíduos experimentam uma mudança ontogenética na dieta, consumindo itens alimentares maiores à medida que crescem, e ao mesmo tempo excluindo presas menores.

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