Spatio-temporal Variation in Diet and its Association with Parasitic Helminths in *Ameivula pyrrhogularis* (Squamata: Teiidae) from Northeast Brazil

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Abstract.—We investigated the spatial and temporal variation of the diet of the Brazilian whiptail *Ameivula pyrrhogularis* using lizards sampled in four Caatinga locations, during the rainy and dry seasons 2015–2016. We also evaluated the importance of diet in the transmission of helminths, considering that changes in the environment can influence the diet and can be one important factor in the transmission of parasites. The predominant food items consumed were insects of Isoptera, Coleoptera, and Lepidoptera. We observed only spatial diet variations what may be a reflection of changes in the foraging strategies of the lizard influenced by environmental pressures, whether due to local characteristics or human activities. As for parasitism, we found 43% overall prevalence of a helminth, distributed among Cestoda, Acanthocephala, and Nematoda. In the analysis of the association between diet and helminth fauna, there was a positive correlation of adult insects of Coleoptera with the abundance of the cestode *Oochoristica travassosi*. Although the biological cycle of *O. travassosi* is unknown, given this correlation, it is possible that these prey are intermediate hosts of this cestode. The present study can help to understand the relative importance of diet and foraging strategies of *A. pyrrhogularis* in Caatinga environments. In addition, the interaction of invertebrates and parasites is extremely relevant to comprehend the biological cycle of helminths with a heteroxenous cycle and their transmission mechanisms.

Key Words.—Caatinga; feeding habits; helminth fauna; lizard; parasite

Resumo.—Investigamos a variação espacial e temporal da dieta do calango cauda-de-chicote *Ameivula pyrrhogularis*, usando lagartos amostrados em quatro locais na Caatinga, durante as estações chuvosa e seca 2015-2016. Também avaliamos a importância da dieta na transmissão de helmintos, considerando que mudanças no ambiente podem influenciar a dieta e podem ser um fator importante na transmissão de parasitas. Os itens alimentares mais consumidos foram insetos de Isoptera, Coleoptera e Lepidoptera. Observamos apenas variações espaciais na dieta, o que pode ser um reflexo de mudanças nas estratégias de forrageamento do lagarto influenciadas por pressões ambientais, seja devido a características locais ou atividades humanas. Quanto ao parasitismo, encontramos 43% de prevalência total de helmintos, distribuídos em Cestoda, Acanthocephala e Nematoda. Na análise da associação entre dieta e helmintos, houve correlação positiva de adultos de Coleoptera com a abundância do cestóide *Oochoristica travassosi*. Embora o ciclo biológico de *O. travassosi* seja desconhecido, dada essa correlação é possível que essas presas sejam hospedeiras intermediárias desse cestóide. O presente estudo pode ajudar a entender a importância relativa da dieta e estratégias de forrageamento de *A. pyrrhogularis* em ambientes de Caatinga. Além disso, a interação de invertebrados e parasitas é extremamente relevante para compreender o ciclo biológico dos helmintos com o ciclo heteroxênico e seus mecanismos de transmissão.

Palavras-chave.—Caatinga; hábitos alimentares; fauna de helmintos; lagarto; parasita

Introduction

The diet of a species can be associated with ecological aspects of the environment and thus provide information on the ingested items, foraging strategies, and interactions with other coexisting populations (Huey and Pianka 1981). Lizards have phylogenetically defined food patterns and can be classified as active or sedentary foragers (Duffield and Bull 1998; Carvalho et al. 2007). The diet composition may vary depending

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on their behavior and morphological and physiological characteristics (Sartorius et al. 1999; Rocha et al. 2009) and on habitat resources availability (Duffield and Bull 1998; Vitt and Pianka 2007). Spatial and seasonal changes in the environment may also influence the types of prey available for lizards (Pianka 1970; Rocha 1996; Teixeira-Filho et al. 2003); however, continuous consumption of a particular type of food demonstrates that, although there are predisposing factors to changes, little or no difference in diet can also occur (Vrcibradic and Rocha 1995, 1996; Zaluar and Rocha 2000; Teixeira-Filho et al. 2003).

The genus *Ameivula* (Teiidae) comprises 11 species (Arias et al. 2018), commonly called Brazilian whiptails, that encompasses the old complex of *Cnemidophorus ocellifer*, distributed from northeast Brazil to northern Argentina (Arias et al. 2011a,b, 2018). *Ameivula pyrrhogularis*, (*phyrros* = flame-colored; *gularis* = throat; Fig. 1), which has no English common name, was recently described in the Brazilian Caatinga (Silva and Ávila-Pires 2013). This *Ameivula* complex is characterized by heliophilous lizards that are active foragers, typical of open vegetation on sandy or rocky soils at forest edges, and are commonly found near human habitation (Mesquita and Colli 2003a,b; Silva and Ávila-Pires 2013). Its diet is diverse and composed predominantly of small prey such as Isoptera and other insect larvae (Magnusson et al. 1985; Mesquita and Colli 2003a,b; Teixeira-Filho et al. 2003; Menezes et al. 2011), usually consuming aggregated or sedentary prey (Huey and Pianka 1981; Magnusson et al. 1985; Bergallo and Rocha 1994). Some recent research related to the spatial and seasonal variation in the *Ameivula* diet indicate the absence of seasonal variation, as described for *A. littoralis* (Teixeira-Filho et al. 2003), or seasonal fluctuations on the types of prey consumed, as in *A. ocellifera* (Sales and Freire 2015). Feeding habits may also be related to the recruitment of many parasites, which contribute with relevant information regarding the interactions between predators and prey (Bush 1990; Lafferty et al. 2008). Parasites represent a hidden diversity within the perceived environment, constitute an important part of biodiversity in all ecosystems, and contribute to the maintenance of local host communities and ecosystems function (Bush et al. 1997; Poulin and Morand 2000; Poulin 2008).

Several factors influence the composition of endoparasitic fauna and determine the presence and abundance of helminths, among them the behavior of a lizard (Aho 1990). For active foragers, which move through larger areas in search of food (Magnusson et al. 1985) and keep the body in constant contact with the substrate, a higher rate of infection may occur, mainly with monoxenous parasites, which do not require intermediate hosts to complete their life cycles (Aho 1990; Bush et al. 2001). On the other hand, the immobile behavior of sit-and-wait foragers (Magnusson et al. 1985) may favor greater interaction with prey infected with heteroxenous parasites (Aho 1990; Bush et al. 2001).

The helminth fauna of herbivorous and carnivorous lizards may also be different (Roca et al. 2005), with the former being more affected by monoxenous parasites (Aho 1990; Martin et al. 2005; Roca et al. 2005). Among these monoxenous parasites, nematodes in the family Pharyngodonidae are commonly reported as parasites of lizards (Avila and Silva 2010), with species of different nematodes genera parasitizing according to the host diet (Roca et al. 2005; Carretero et al. 2006). The structure of the helminth community is more rich and diverse in herbivorous hosts due to the facility of accidentally ingested eggs of these monoxenous nematodes present in fecal material deposited in the environment (Roca et al. 2005; Carretero et al. 2006).

The objective of the study was to verify the existence of spatial and temporal variation in the diet of *A. pyrrhogularis* collected in the Caatinga biome in northeastern Brazil, and its association with helminth parasitism. As the food supply may vary due to changes in the environment, our expectation is that this change will influence the diet of this lizard. In addition, as a carnivorous species, its diet may be a contributing factor in the transmission of parasites, favoring mainly a contamination by heteroxenous parasites.

Material and Methods

Study areas.—We conducted the study in four municipalities, located in Ceará State of Brazil: (1) Aiuaba, in the Ecological Station of Aiuaba (06°36'6.5"S, 40°07'28.5"W); (2) Barro, in the District of Cuncas (07°05'15.0"S, 38°43'19.5"W); (3) Crato, in the District of Dom Quintino (07°04'20.3"S, 39°28'52.1"W); and (4) Lavras da Mangabeira, in the District of Quitaiús (06°54'42.8"S, 39°06'46.5"W). The distance between localities ranges from 49 km (between Barro and Lavras de Mangabeira) to 174 km (between Aiuaba and Barro). These localities have a mean annual rainfall of 562.4 mm, 934.3 mm, 1,090.9 mm, and 866.4 mm, respectively (Instituto de Pesquisa e Estratégia Econômica do Ceará [IPECE]. 2016. Perfil municipal. Available from http://www.ipece.ce.gov.br/index.php/2016-12-16-13-09-40 [Accessed 1 December 2017]). In the Caatinga there is a rainy season (November to April) and a dry season (May to October), with temperatures varying from 26° to 30° C throughout the year, reaching 40° C during dry periods (Leal et al. 2003; IPECE. 2016. *op. cit*.). This region has shallow, rocky soils of crystalline origin, with phytophysiognomies distributed in arboreal and shrubby landscapes, humid or transition forests, pastures and plantations (Leal et al. 2003; IPECE. 2016. *op. cit*.).

Field and laboratory work.—We conducted fieldwork in two months of the rainy season (February and March) and two of the dry season (September and October) of two consecutive years (2015 and 2016), with 5 d of collection in each locality per month/year. To collect lizards, we used the active search method. In the laboratory, we euthanized the lizards with Sodium Thiopental, necropsied and fixed them in 10% formalin, and kept specimens in 70% alcohol. We identified the specimens according to Silva and Ávila-Pires (2013) and removed and preserved the stomach contents in 70% alcohol. We deposited the lizards in the Herpetological Collection of the Universidade Regional do Cariri (URCA-H), Campus Crato (See Acknowledgments for catalog numbers).

For diet analysis, we used a methodology adapted from studies of freshwater invertebrates (Carvalho and Uieda 2009) and fishes (Motta and Uieda 2005). We opened each stomach separately in a Petri dish, screened the contents, and separated the consumed items on slides with glycerin. For each food category, we identified items under a binocular stereomicroscope and determined the area (mm2) occupied by items using a millimeter paper placed under the slide. We identified prey to class and order using Ruppert et al. (2005) and Triplehorn and Johnson (2011). We grouped the very fragmented exoskeleton of Hexapoda into the category Exoskeleton and leaves and sticks into Plant Fragments.

In the parasitological analyzes, we examined organs and body cavities and processed the recovered helminths according to Amato et al. (1991), with acanthocephalans and cestodes stained in carmine and diaphanized in creosote, and nematodes cleared in lactophenol. We based the identifications on Yamaguti (1963), Rêgo and Ibañez (1965), Vicente et al. (1993), and Anderson et al. (2009). We preserved the specimens in 70% alcohol and deposited them in the Coleção Helmintológica do Instituto de Biociências de Botucatu (CHIBB), Universidade Estadual Paulista, Campus de Botucatu (CHIBB 8189 to 8457).

Data analysis.—We used the food items consumed by the lizards in the four localities and two seasons to characterize the diet and to verify the existence of spatial and seasonal variations. For each lizard with stomach content (considered a replicate), we calculated the richness of food items consumed and the alimentary niche breadth. The Levins' measure of alimentary niche breadth gives more weight to resources used in greater abundance, the value of the measure being standardized for a scale of 0 (maximum specialization) to 1 (more generalist; Krebs 1999).

We used the diet data (area of each food category consumed), richness, and alimentary niche breadth data transformed in log (x+1) to construct three matrices of similarity (Bray-Curtis coefficient). We applied a Permutation Multivariate Analysis of Variance (PERMANOVA) and a Permutation Multivariate Dispersion (PERMDISP), considering 9,999 permutations, to those matrices to test for spatial (four localities) and seasonal (rainy and dry) differences. A significant value of PERMANOVA ($P \leq 0.05$) indicates that there are disparities between the groups, but this difference can be due to the factor analyzed or to the dispersion of data. Thus, to understand the origin of this difference, we applied the PERMDISP, where a non-significant value ($P > 0.05$) indicates that the difference is due to the analyzed factor (Anderson et al. 2008), in which case a PERMANOVA pairwise test was applied. We performed analyses using the software Primer version 6.1.12 & Permanova version 1.0.2 (Anderson et al. 2008).

We calculated the eco-parasitological descriptors of prevalence (percentage), abundance (mean and standard error), and intensity of infection (mean, standard error, and range of variation) according to Bush et al. (1997). The prevalence is the number of infected hosts divided by the number of lizards examined, while mean abundance is the ratio of total helminths recovered in the host population by the total number of hosts analyzed (parasitized or not). The mean intensity of infection is the ratio of total helminths found in the host population by the number of parasitized hosts.

To verify the association of the parasitic fauna with the diet found in the collected lizards, first we performed partial Mantel tests, with 9,999 random permutations and missing values treated with pairwise deletion, to verify if there was spatial or seasonal influence on the parasites in lizards versus its diet. We performed the analyzes using a parasites distance matrix (Bray-Curtis) made with the parasite abundance of each lizard, a diet distance matrix (Bray Curtis) made with the alimentary items area ingested by each lizard, and a spatial/season distance matrix (Euclidean distance) made with the geographic coordinates/season where each lizard was collected. The partial Mantel test showed no spatial ($P = 0.109$) and seasonal ($P = 0.116$) differences. Therefore, using all the lizards analyzed, we applied multiple Spearman rank correlations (rs), with significance value corrected by the Holm-Bonferroni method, between each food item consumed and the abundance of the parasites that presented a prevalence higher than 10% (Bush et al. 1990). We performed these analyses with only the heteroxenous cycle parasites.

RESULTS

Diet.—In total, we captured 496 lizards, and determined the diet of 452 individuals who presented digestive content, of which we sampled 215 in the

Figure 1. *Ameivula pyrrhogularis* (no common name) photographed during the wet season of 2015 in Barro municipality, State of Ceará, Brazil. (Photographed by Lidiane A. F. da Silva).

rainy season (56, 51, 56, and 52 from Aiuaba, Barro, Crato and Lavras da Mangabeira, respectively) and 237 in the dry season (62, 54, 59, and 62 from Aiuaba, Barro, Crato and Lavras da Mangabeira, respectively). All individuals we analyzed were adults because the gonads of the evaluated lizards were developed when we examined during the necropsy. We recognized 24 types of food items, including one item of plant origin (leaves and sticks) and the others of animal origin. From the 23 animal food items, five were identified to class (Gastropoda, Oligochaeta, Arachnida, Chilopoda, and Diplopoda), 17 to order (Isopoda, Squamata, and 13 Hexapoda orders, of which only Coleoptera and Lepidoptera were discriminated in larva and adult), and one we considered a fragmented exoskeleton of Hexapoda. In general, there was a predominant consumption of Lepidoptera larvae for lizards from all locations in the rainy season and of Isoptera in the dry season, except in the dry season of Barro locality, where fragments of exoskeleton and Coleoptera larvae were consumed in a percentage higher than Isoptera (Table 1). Although in the two seasons there was a high consumption of fragmented exoskeleton of Hexapoda, the same pattern remained when we excluded this item from the analysis (Table 2; Fig. 1). A spatial and temporal difference was also evident when we considered only the items with consumption of 10–20% (Table 2; Fig. 1).

The PERMANOVA test applied to the diet data (area of each food category consumed) indicated a significant difference for locality (Pseudo-$F_{3,444}$ = 7.895, $P <$ 0.001), season (Pseudo-$F_{1,444}$ = 33.07, $P <$ 0.001), and their interaction (Pseudo-$F_{3,444}$ = 3.180, $P <$ 0.001). The PERMDISP verified a difference due to the effect of the analyzed factor, however, not due to the dispersion of data, only for locality (Pseudo-$F_{3,448}$ = 0.562, $P =$ 0.689). There were significant differences (PERMANOVA pair-wise test, $P <$ 0.001) for most combination of localities, except between Aiuaba and Lavras da Mangabeira ($P =$ 0.224).

The highest value for the richness of food items consumed was for the rainy season in Crato and the dry season in Aiuaba, while the alimentary niche breadth values ranged from 0.35 to 0.44, indicating a diet specialization (Table 1). For richness, there was a significant difference (Pseudo-$F_{3,444}$ = 4.453, $P =$ 0.004) only for the interaction (locality × season), and this difference was due to the effect of the analyzed factor (Pseudo-$F_{7,444}$ = 2.802, $P =$ 0.109). There was a significant difference (PERMANOVA pair-wise test, $P <$ 0.001) in the rainy season of Crato with Aiuaba ($P =$ 0.011), Barro ($P =$ 0.022) and Lavras da Mangabeira ($P =$ 0.012), and in the dry season of Crato with Aiuaba ($P =$ 0.023). For the alimentary niche breadth, there were no significant differences for the three analyzed factors (locality, season, and their interaction).

Helminth fauna and diet association.—From the 496 lizards analyzed, we found 212 infected with at least one parasite taxa (overall prevalence of 42.7%). The parasites comprised 1,911 helminths (Table 3), distributed in Cestoda (adults of *Oochoristica travassosi*), Acanthocephala (cysthacanth), and Nematoda (encysted larvae; larvae of *Cruzia* sp., *Oswaldofilaria* sp. and *Physaloptera* sp.; adults of *Parapharyngodon* sp., *Pharyngodon cesarpintoi* and *Physalopteroides venancioi*). The highest values of prevalence, mean abundance, and mean intensity of infection (Table 3) occurred for the monoxenous nematode *P. cesarpintoi* and the heteroxenous nematode *O. travassosi*. Thus, the analysis of the association between diet and helminth fauna was performed only for *O. travassosi*, indicating correlation only with adult Coleoptera (r_s = 0.27, $P <$ 0.001).

Table 1. Percentage of food items consumed by *Ameivula pyrrhogularis* (no common name) collected in four localities and two seasons in the state of Ceará, Brazil. Localities are Aiuaba (Ai), Barro (Ba), Crato (Cr), Lavras da Mangabeira (La), seasons are rainy (R) and dry (D). Larval stage is indicated by L and adult by A. Plant corresponds to plant fragments. Mean and standard deviation is presented for richness of items consumed and for alimentary niche breadth (standardized), calculated for the total of lizards analyzed by locality and season.

| Items	Ai-R	Ba-R	Cr-R	La-R	Ai-D	Ba-D	Cr-D	La-D
Gastropoda	0.30	0.38	0.54	0.38	0.30	0.45	0.64	0.15
Oligochaeta	1.09	-	0.38	1.04	-	-	-	-
Arachnida	4.79	5.99	3.39	7.32	13.23	9.75	10.38	4.97
Isopoda	-	-	0.27	0.01	-	0.50	0.33	0.15
Chilopoda	0.22	0.98	1.07	1.28	-	0.22	0.13	0.22
Diplopoda	-	0.52	0.07	-	-	-	-	-
Blattodea	-	3.38	0.17	-	-	-	-	0.06
Coleoptera-L	1.42	2.91	1.41	3.49	3.79	15.45	4.71	0.47
Coleoptera-A	1.09	1.88	14.91	2.16	3.36	13.36	15.07	6.51
Diplura	-	-	-	0.33	-	-	-	-
Diptera	-	0.30	1.89	1.13	1.77	-	0.49	0.06
Embioptera	1.24	0.13	1.18	0.19	1.62	0.67	1.45	0.46
Hemiptera	0.91	1.44	0.60	0.31	0.48	2.99	4.03	1.62
Homoptera	2.79	1.70	2.86	0.55	1.48	0.69	0.60	0.39
Hymenoptera	0.85	0.16	1.05	0.40	1.28	0.67	0.37	0.74
Isoptera	19.70	9.98	22.66	13.47	47.85	14.53	29.82	51.63
Lepidoptera-L	26.11	35.02	26.13	31.35	0.47	5.15	0.54	1.81
Lepidoptera-A	2.82	1.65	1.77	7.63	0.57	-	0.66	0.19
Neuroptera	0.46	0.89	0.66	1.73	0.80	0.75	0.32	0.58
Odonata	-	-	-	2.93	-	0.64	-	-
Orthoptera	13.44	10.49	1.98	8.17	2.82	5.13	5.77	9.12
Squamata	-	0.25	-	-	-	-	-	-
Exoskeleton	20.77	20.12	14.58	15.63	16.17	28.22	21.88	18.48
Plant	2.00	1.82	2.43	0.48	4.01	0.85	2.80	2.40
Richness	3.89 ± 2.13	4.08 ± 2.45	5.18 ± 2.49	3.94 ± 2.34	4.23 ± 1.89	3.81 ± 1.71	3.56 ± 1.97	3.79 ± 1.55
Niche breadth	0.35 ± 0.26	0.40 ± 0.26	0.39 ± 0.25	0.42 ± 0.26	0.44 ± 0.30	0.43 ± 0.28	0.41 ± 0.32	0.38 ± 0.24

DISCUSSION

Diet.—*Ameivula pyrrhogularis* consumed predominantly insects of the orders Lepidoptera, Isoptera and Coleoptera, but also had a high percentage of Arachnida and Orthoptera in its diet. The high percentage of exoskeleton fragments in the digestive content also reinforces the importance of hexapods in the diet of this lizard. Similar diet was reported for congeneric species inhabiting the Cerrado (Vitt 1991; Mesquita and Colli 2003a,b), the Restinga (Bergallo and Rocha 1994; Dias and Rocha 2007; Menezes et al. 2008; Santana et al. 2010) and the Caatinga (Santana et al. 2010; Menezes et al. 2011; Sales et al. 2012; Sales and Freire 2015; Ferreira et al. 2017).

Active foragers usually detect their prey through chemical signals picked up by the tongue when they move for long distances (Cooper 1990). These lizards tend to identify and choose to ingest grouped or sedentary prey, while sit-and-wait foragers consume prey that are more mobile (Huey and Pianka 1981; Magnusson et al. 1985; Bergallo and Rocha 1994; Zaluar and Rocha 2000). Apparently, *A. pyrrhogularis* shows an active foraging behavior, indicated by the considerable consumption of Coleoptera larva and adult, Lepidoptera larva and Isoptera, most with low mobility and that live aggregated in the substrate (Pianka 1986; Menezes et al. 2011), of high nutritive value, and that assists in the energetic and hydric balance of the lizard (Nagy et al. 1984; Anderson and Karasov 1988). Among the five main food items observed in the diet of other species of *Ameivula*, Arachnida and Orthoptera are also reported (Vitt 1995; Mesquita and Colli 2003a,b; Menezes et al. 2008; Sales et al. 2012).

It is common for carnivorous lizards to consume plants, which act as food complement and are an
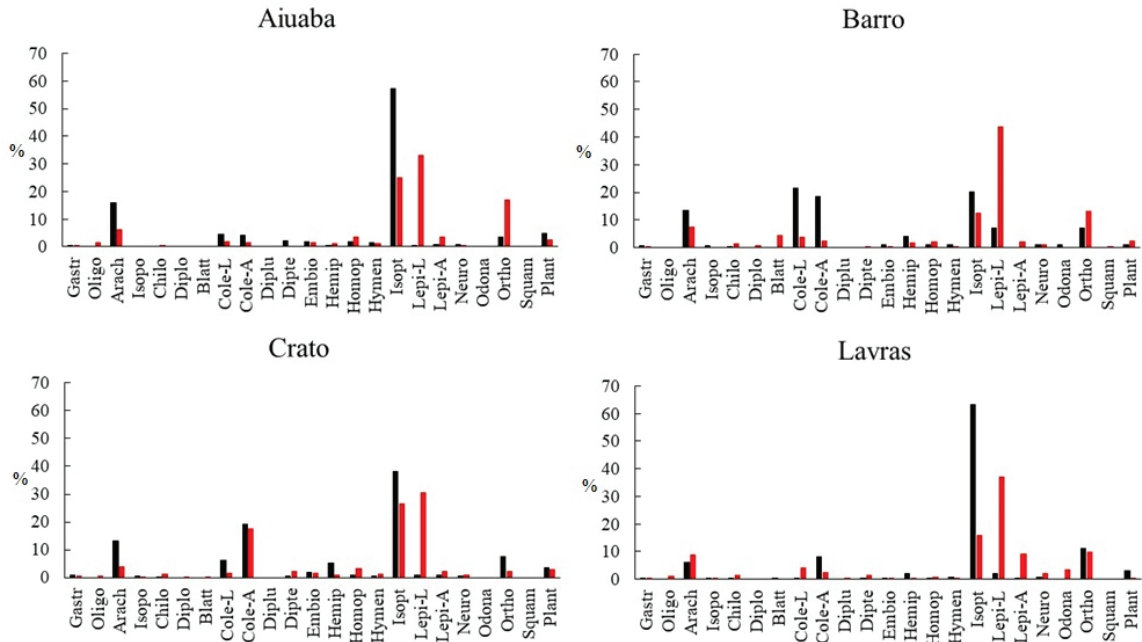
Figure 2. Percentage of food items consumed by *Ameivula pyrrhogularis* (no common name) collected in four locations and in two seasons (black-dry, red-rainy). Abbreviations are Gastr- Gastropoda, Oligo- Oligochaeta, Arach- Arachnida, Isopo- Isopoda, Chilo- Chilopoda, Diplo- Diplopoda, Blatt- Blattodea, Cole- Coleoptera, Diplu- Diplura, Dipte- Diptera, Embio- Embioptera, Hemip- Hemiptera, Homop- Homoptera, Hymen- Hymenoptera, Isopt- Isoptera, Lepi- Lepidoptera, Neuro- Neuroptera, Odona- Odonata, Ortho- Orthoptera, Squam- Squamata, Plant- Plant fragments, L- larvae, A- adult.

important water source in environments with water scarcity (Schall and Ressel 1991; Rocha 1996). In some cases, plants may also be linked to zoochory processes (Magnusson and Silva 1993; Vitt and Carvalho 1995; Vrcibradic and Rocha 1996; Vitt et al. 1997; Passos et al. 2013). The small amount of leaves and sticks found in the *A. pyrrhogularis* diet, however, suggests an accidental intake.

According to Siqueira and Rocha (2008), saurophagia is common for lizards of the families Gekkonidae, Gymnophtalmidae, Liolaemidae, Phyllodactylidae, Scincindae, Teiidae, and Tropiduridae. The fragment of a tail of a lizard found in the digestive contents of an individual of *A. pyrrhogularis* (in Barro locality) suggests the possibility of cannibalism for this species, which has been reported for *A. ocellifera* (Mesquita and Colli 2003b; Sales et al. 2010, 2012; Sales and Freire 2015). Cannibalism is an opportunistic predatory behavior in species of generalist habits and a way of gaining nutritional benefits by catching smaller lizards of the same or phylogenetically similar species (Vitt 2000; Mayntz and Toft 2006). According to Vitt (2000), the capture of one vertebrate can provide a daily portion much larger than a single capture of a small arthropod prey, and this event just appears to be rare because it is rarely noted.

In environments with marked seasonality, such as the Caatinga, seasonal variations in the diet are expected because local productivity depends on the humidity

and precipitation cycles of a site (Janzen and Schoener 1968; Ab'sáber 1974; Dunham 1981). For *A. ocellifera*, Sales and Freire (2015) observed a seasonal variation in diet, with Coleoptera and Orthoptera predominant in the rainy season and Hemiptera, Araneae, and Orthoptera in the dry season. In our study, however, despite the small differences in the items consumed in greater quantity in each season, there was a seasonal

Table 2. Synthesis of the results of *Ameivula pyrrhogularis* (no common name) diet analysis, collected at four localities and two seasons, not considering the exoskeleton fragments in this calculation and indicating the items consumed in percentage > 20% and between 10–20% (decreasing order of importance). Larval stage is indicated by L and adult by A.

Locality	Season	> 20%	10–20%
Aiuaba	rainy	Lepidoptera-L, Isoptera	Orthoptera
	dry	Isoptera	Arachnida
Barro	rainy	Lepidoptera-L	Orthoptera, Isoptera
	dry	Coleoptera-L, Isoptera	Coleoptera-A, Arachnida
Crato	rainy	Lepidoptera-L, Isoptera	Coleoptera-A
	dry	Isoptera	Coleoptera-A, Arachnida
Lavras	rainy	Lepidoptera-L	Isoptera, Orthoptera
	dry	Isoptera	Orthoptera

Table 3. Prevalence (%), abundance (mean ± SE) and intensity of infection (mean ± SE and range of variation) of parasitic helminths found in *Ameivula pyrrhogularis* (n = 496) collected in the State of Ceará, Brazil. An asterisk (*) indicates parasites with monoxenous cycles.

Helminth	Prevalence	Abundance	Intensity of infection
CESTODA			
Oochoristica travassosi	19.35	0.49 ± 0.07	2.54 ± 0.25 (1–15)
ACANTHOCEPHALA			
Cistacanth	4.64	0.08 ± 0.02	1.83 ± 0.37 (1–8)
NEMATODA			
Encysted larvae	0.20	0	1
Cruzia sp. *	0.20	0	1
Oswaldofilaria sp.	0.20	0	2
Parapharyngodon sp. *	0.20	0	1
Pharyngodon cesarpintoi *	21.57	3.26 ± 0.52	15.09 ± 2.05 (1–128)
Physaloptera sp.	0.81	0.01	1
Physalopteroides venancioi	0.20	0	1

difference only for the richness of items consumed and depending on the locality analyzed. These results suggest that the availability and accessibility of some prey may be related to the season, leading to a variation only in the richness of available items. A predominance of Isoptera consumption as observed in our study has also been reported for *A. littoralis* and *A. nativo* sampled in Restinga (Teixeira-Filho et al. 2003; Menezes et al. 2008).

The localities we studied show differences in some environmental characteristics, like soil type, number of open areas and stretches of forest, and extension with the development of agriculture and livestock (Leal et al. 2003, 2005; Chiang and Koutavas 2004; IPECE. 2016. *op. cit.*). Spatial differences in the diet are possibly conditioned by environmental differences among localities, which may be limiting the occurrence of some arthropods and, thus, interfering with the abundance and availability of prey according to the microhabitat used (Mesquita and Colli 2003b; Siqueira et al. 2013). Changes in food composition due to geographical variations were also described for *A. ocellifera* (Mesquita and Colli 2003b) and for other lizard species (Pianka 1970; Parker and Pianka 1975; Siqueira et al. 2013). The diet similarity only between the lizards of Aiuaba and Lavras da Mangabeira suggests that forest stretches observed near the reservoirs that supplies those two areas could be generating similar conditions that favor the availability of prey.

The highest richness of prey consumed by lizards collected in Crato during the rainy season may be related

to the highest rainfall index observed in this municipality (Brito and Silva 2012; IPECE. 2016. *op. cit.*), which contributes to a better structuring and maintenance of the vegetation (Kolodiuk et al. 2009; Moro et al. 2015). On the other hand, the highest richness of prey consumed by lizards collected in Aiuaba during the dry season may be related to the better habitat preservation of this locality. These results suggest that prey richness may be related to the conditions of the phytophysiognomy (Hernández 2007; Vasconcellos et al. 2010; Moro et al. 2015), probably influenced by particularities of each locality (vegetation cover, soil, temperature, rainfall, and human disturbance, among others).

The highest consumption of sedentary (Coleoptera and Lepidoptera larvae) and grouped prey (Isoptera) is probably related to the specialized diet of *A. pyrrhogularis*, differing from *A. ocellifera* for which a less selective behavior was reported in the Caatinga (Sales and Freire 2015; Ferreira et al. 2017). According to the theory of optimal foraging, the behavior of the organism is conditioned to locate, capture, and ingest foods that maximize the energy return and that predators usually increase the variety of food items consumed as a reduction in food supply occurs (Emlen 1966; MacArthur and Pianka 1966). With a shortage of prey, predators usually have a generalist diet, whereas when the abundance and variety of prey increases, the diet tends to become more specialized, possibly explaining the fluctuations in the richness and composition of the explored food items (MacArthur and Pianka 1966; Janzen and Schoener 1968; Siqueira et al. 2013; Ferreira et al. 2017). Thus, the spatial differences observed in the *A. pyrrhogularis* diet may be a reflection of changes in their foraging strategies and, in turn, may be influenced by environmental pressures, whether due to local characteristics or human activities.

Helminth fauna and diet association.—The diet is commonly associated with mechanisms by which parasites with heteroxenous life cycle infect their hosts (Martin et al. 2005). A wide variety of helminths occurs in lizards due to coprophagy, geophagy, ingestion of contaminated plant material and infected prey, or by transcutaneous infection (Anderson 2000). Based on data described by Anderson (2000) for other congeneric species, we suggest that *Cruzia* sp., *Parapharyngodon* sp., and *P. cesarpintoi* have a direct life cycle, with the infection in lizards occurring by ingestion of parasite eggs from contaminated substrates. Ants or other invertebrates can transport these eggs adhered to their bodies and lizards ingest them at the time the prey is taken as food (Bursey et al. 1996). Thus, it is possible that the presence of monoxenous cycle parasites in lizards occurs during the capture of their prey or by consumption of mechanical vectors, as fragments of

exoskeleton and contaminated plant material, which may contain eggs and cysts (Aho 1990; Neves et al. 2005; Roca et al. 2005).

The presence of unidentified larval stages of acanthocephalans and nematodes strongly suggests that lizards act as intermediate or paratenic hosts in the biological cycle of these helminths (Bush et al. 2001). *Oochoristica* spp. use cockroaches, beetles (Hickman 1963; Schmidt and Allison 1985), grasshoppers (Widmer and Olsen 1967) and other insects (Conn 1985) in their life cycle. Although the life cycle of *O. travassossi* is unknown, given the positive correlation between its occurrence in *A. pyrrhogularis* and adult insects of Coleoptera in the diet of this lizard, it is possible that these prey act as intermediate hosts in the life cycle of this cestode (Yamaguti 1959).

Some arthropods previously described as possible hosts of *Physaloptera* sp. and *P. venancioi* (Goldberg and Bursey 1989; Jones 1995; Bursey et al. 1996) occurred in the diet of the lizard we studied, such as centipedes, cockroaches, beetles, termites, crickets, and grasshoppers. Thus, although we did not test the correlation between food items and the abundance of *Physaloptera* sp. and *P. venancioi* due to their low prevalence in the lizards analyzed, it is possible to associate the infection of the hosts with the ingestion of these preys. The transmission of *Oswaldofilaria* sp., also with low prevalence, occurs through the inoculation by mosquito vectors, which are probably responsible for the presence of this helminth, because the lizards are exposed in environments where dipterans are present (Mackerras 1953; Pereira et al. 2010).

Our study reports on the types of food items consumed by *A. pyrrhogularis* and can help to understand the relative importance of diet and foraging strategies of *A. pyrrhogularis*, as well as directing further investigations on invertebrate fauna in Caatinga environments. In addition, the interaction of invertebrates and parasites is extremely relevant to understanding the life cycle of heteroxenous helminths and their transmission mechanisms. Certainly, this aspect deserves further investigation, with not only larger sample sizes but also using experimental procedures.

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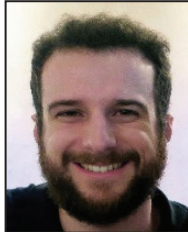
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