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ORIGINAL PAPER

Spatial-temporal variation of parasites in *Cnemidophorus ocellifer* (Teiidae) and *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Tropiduridae) from Caatinga areas in northeastern Brazil

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Abstract Parasites are natural regulators of their host populations. Despite this, little is known about variations in parasite composition (spatially or temporally) in environments subjected to water-related periodic stress such as the arid and semiarid regions. The objective of this study was to evaluate the spatial-temporal variation in endoparasite species' abundance and richness in populations of Neotropical *Cnemidophorus ocellifer*, *Tropidurus hispidus*, and *Tropidurus semitaeniatus* lizards in the semiarid northeast of Brazil. The location influenced the abundance of parasites in all analyzed lizard species, while season (dry and rainy) only influenced the total abundance for *T. hispidus*. In all seasons, males significantly showed more endoparasites than females in all lizard species, although for *T. hispidus*, this difference was only found in the dry season. Seasonal variations affect the abundance patterns of parasites. Likely, variables include environmental variations such as humidity and temperature, which influence the development of endoparasite eggs when outside of the host. Further, the activity of the intermediate hosts and the parasites of heteroxenous life cycles could be affected by an environmental condition. The variation in the abundance of parasites between the sampling areas could be a reflection of variations in climate and physiochemical conditions. Also, it could be due to differences in the quality of the environment in which each host population lives.

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Introduction

Variations in environmental conditions play a significant role in the biology of parasites and their hosts, with the ability to alter the immune system of vertebrates (Møller et al. 2003). More specifically, this applies to ectotherms due to variations in their immune system, mediated by environmental temperature fluctuations in which they are inserted (Le Morvan et al. 1998). In addition, seasonal variations of the environmental conditions also influence the biology of lizards, with evidence of alterations in patterns of foraging, diet, and thermal biology (Rocha 1996; Miranda and Andrade 2003; Sepúlveda et al. 2008). Recent studies have shown that seasonal variations influence the ecology of parasites, affecting abundance and, therefore, their transmission, due to changes in the behavior of hosts, in the biology of the vector and even in the infectious stage of the parasite (Altizer et al. 2006).

Potential spatial-temporal variations in a community structure of parasites, along with the importance of local processes, are generally not considered (Poulin and Valtonen 2002) despite their importance. The patterns found in a community of parasites are not frequently compared to patterns of other communities (Calvete et al. 2004). Studies with spatial-temporal variations in parasite communities are more common in fish (Poulin and Valtonen 2001; Timi et al. 2010), a variation which has not been explored in great depth in studies of parasite communities in lizards. Various factors can affect, individually or together, the composition of parasite communities. However, the pattern of abundance found in a community can vary with changes in climate or physicochemical local conditions, due to the tolerance of species or abiotic factors (Pietrock and Marcogliese 2003; Soininen et al. 2007; Poulin and Krasnov 2010).

The *Cnemidophorus* genus, which is present from lesser antiles to central Argentina (Reeder et al. 2002), has 14 species present in Brazil (Bérnils and Costa 2012). The genus encompasses heliophile lizards that are active foragers with high body temperatures inhabiting open areas and generally using the clean soil, underbush, sandy soils of desert, savanna areas, or forest borders as a substrate (Wright and Vitt 1993; Mesquita and Colli 2003; Pianka and Vitt 2003).

The *Tropidurus* genus which is found in continental South America (Rodrigues 1987; Frost et al. 2001) is made up of heliophile lizards with a "sit-and-wait" foraging strategy. These are predominantly insectivores that mainly inhabit open areas of Caatinga, Cerrado, Chaco, and Restinga (Rodrigues 1987; Van Sluys et al. 2004). For the Caatinga Biome, six species are described with *Tropidurus hispidus* and *Tropidurus semitaeniatus* being the two most abundant and widely distributed species (Rodrigues 2003). In Caatinga, the two species are generally found in sympatry, which is common for *Tropidurus* lizards (Colli et al. 1992).

Regarding *Cnemidophorus ocellifer*, there is no available data for the influence of temporal variations in environmental conditions on the diet and behavior of this lizard. However, the variations directly influence the foraging strategy of *T. hispidus* and *T. semitaeniatus*. During the dry season, both species live with a limited amount of resources, therefore displaying similar foraging strategies. In the rainy season, due to characteristic changes in vegetation, the species adopt different foraging strategies (Kolodiuk et al. 2009). With regard to how seasonal variations affect diet, Ribeiro and Freire (2011) observed that in the dry season, ants and termites are the most important items for both species. However, in the rainy season (despite the fact that ants continue to be the most important items), both species display opportunistic predation of arthropods that have a seasonal reproductive cycle, e.g., Lepidoptera, Coleoptera, Orthoptera, and others Hymenoptera (not Formicidae). The variations in environmental conditions also exert a strong influence on reproduction in the two species in Caatinga, both reproducing predominantly in the dry season with some instances during the first months of the rainy season (Vitt and Goldberg 1983; Vitt 1992).

The objectives of this study were to describe the influence of the spatial, temporal, and sexual variation of the lizards on the abundance of parasites in Teiidae and Tropiduridae lizards in the Caatinga Biome.

Materials and methods

Study areas

The lizards were collected in four locations: (1) Aiuaba-CE (AIA) (06° 36′ S, 40° 07′ W), with an average rainfall of 562.6 mm per year and an annual temperature of 26 °C (Jacomine et al. 1973); (2) João Câmara-RN (JCA) (05° 33′ S, 35° 56′ W), with an average rainfall of 648.6 mm per year and a temperature of 24.7 °C (IDEMA 2008); (3) Santa Quitéria-CE (STQ) (04° 19′ S, 40° 09′ W), with an average rainfall of 799.8 mm per year and a temperature of around 26 °C (IPECE 2011); and (4) Várzea Alegre-CE (VAA) (06° 52′ S, 39° 13′ W), with an average rainfall of 965.3 mm per year and a temperature of around 26 °C (IPECE 2005), all within the Caatinga Biome, in the ecoregion of the "Depressão Sertaneja Setentrional" (Fig. 1).

Sampling of lizards

In each area, two samplings were made: one in the dry season between October and November and the other in the rainy season between April and May. The collections were made with active searches and through the use of "pit fall" traps coupled with interception fences, where in each sample area, 30 traps in a Y shape were installed, each one made up of four 30-L buckets (one in the middle and one in each extremity) interlinked by a plastic drift fence. Sampling period was 10 days per season, and the lizards were then fixed with 10 % formalin, conserved in 70 % alcohol, and housed in the herpetological collection of the Universidade Federal da Paraíba (CHUFPB). Later, all specimens were dissected under a magnifying glass, the sexes were determined, and the respiratory and gastrointestinal tracts were analyzed in the search of endoparasites. When present, the parasites were counted, assembled in slides with lactophenol, and analyzed by light microscopy. After identification, the prevalence indexes (percent of hosts infected) and the mean intensity of infection (Bush et al. 1997) were calculated, considering the lizard species collected in the two seasons.

Statistical analysis

In order to confirm variations in the abundance of endoparasites of the three lizard species in the sampling areas (between the dry and rainy seasons, between the sexes, and the interaction between the sampling area with the season), we used a

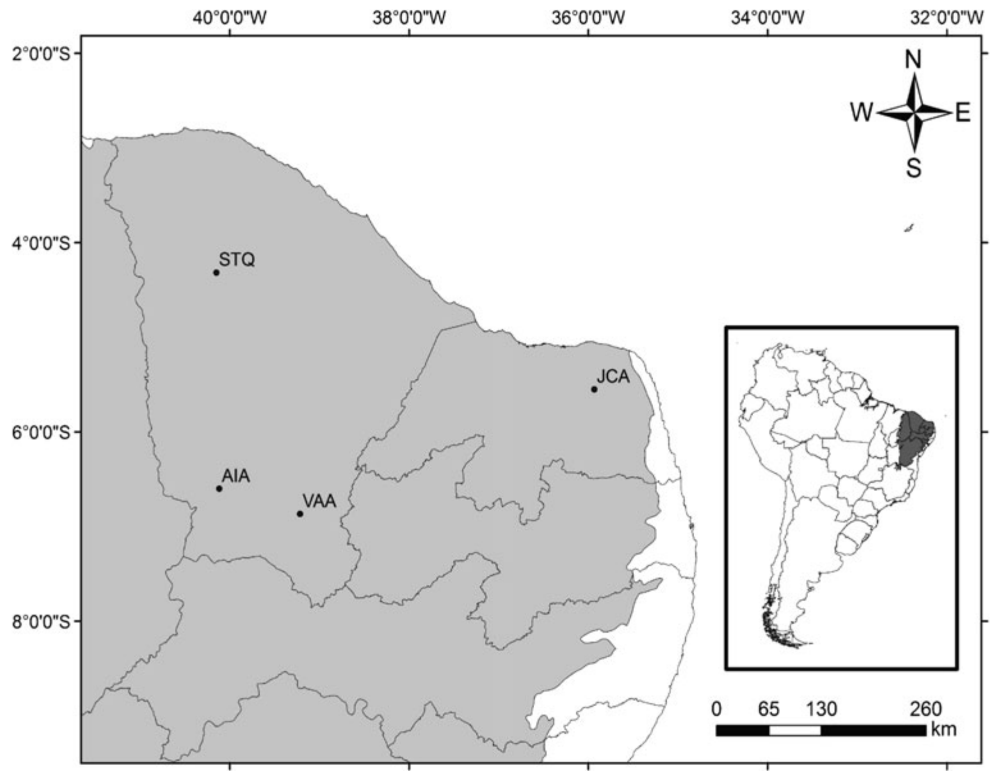

Fig. 1 Sampling sites: Estação Ecológica de Aiuaba-CE (*AIA*); Fazenda Cauaçu, João Câmara-RN (*JCA*); Santa Quitéria-CE (*STQ*); and Várzea Alegre-CE (*VAA*)

generalized linear model (GLM)/nonlinear model, in the logarithmic function, taking on a distribution of the Poisson type, using the Statistica software, version 8.0 (StatSoft 2007). To do the GLM, we used the residuals of the regression between the snout-vent length (SVL) of the lizards and the total number of parasites. This treatment was done to remove the confounding effect of host size, as this can strongly influence the abundance of endoparasites (Poulin 1997).

Results

In total, 302 *C. ocellifer* (132 males, 122 females, and 48 juveniles), 288 *T. hispidus* (84 males, 153 females, and 51 juveniles), and 120 *T. semitaeniatus* (32 males, 75 females, and 13 juveniles) were collected. *C. ocellifer* and *T. hispidus* were recorded in the four sampling areas, while *T. semitaeniatus* did not occur in ESEC Aiuaba (AIA).

Seven species of endoparasites were found in *C. ocellifer* (one Cestoda and six Nematoda) (Table 1). Nine species were found in *T. hispidus*, with six being Nematoda, one Acanthocephala, one Cestoda, and one Pentastomida (Table 1). In *T. semitaeniatus*, four were recorded (three Nematoda and one Cestoda) (Table 1).

Abundance of parasites in relation to the sex of lizards

For both *C. ocellifer* and *T. semitaeniatus*, a significant difference in the abundance of endoparasites regarding the sex was found, with males showing greater mean intensity of infection than females, irrespective of season (Table 2).

There was no significant difference in the abundance of parasites between the sexes in *T. hispidus* (Table 2); however, it was observed that males displayed greater infection during the dry season (Wald=5.35; Gl=1; $P<0.01$).

Spatial and temporal variation in the abundance of endoparasites

In the cases of *C. ocellifer* and *T. semitaeniatus*, the location influenced the abundance of endoparasites, whereas the season did not, although the interaction between area and season was significant when considering the abundance of parasites (Table 2, Figs. 2 and 3).

For *T. hispidus*, the area, season, and interaction between these two factors influenced the total abundance of endoparasites (Table 2, Fig. 4).

Discussion

Abundance of parasites in relation to gender

The males from the three lizard species showed greater infection than females, although in *T. hispidus*, this difference only occurred in the dry period. For the males of *T. hispidus*, this seasonal variation in the abundance of parasites could be associated with its reproductive period, which occurs in the

Table 1 Values of prevalence (Prev.) and mean intensity of infection (MII) in the three lizard species studied in four locations of Caatinga: (1) Estação Ecológica de Aiuaba-CE (AIA), (2) João Câmara-RN (JCA), (3) Santa Quitéria-CE (STQ), and (4) Várzea Alegre-CE (VAA)

Taxon/family/specie	AIA		JCA		STQ		VAA	
	Prev. (%)	MII (range)	Prev. (%)	MII (range)	Prev. (%)	MII (range)	Prev. (%)	MII (range)
Cnemidophorus ocellifer								
Cestoda								
Linstowiidae								
Oochoristica sp.	–	–	5.76	1.16 (1–2)	–	–	–	–
Nematoda								
Heterakidae								
Strongyluris oscari	–	–	–	–	–	–	0.99	4 (4)
Kathlaniidae								
Cruzia sp.	–	–	–	–	2.38	22 (22)	–	–
Pharyngodonidae								
Parapharyngodon alvarengai	1.72	1 (1)	–	–	2.38	3 (3)	–	–
Pharyngodon sp.	20.68	7.16 (1–19)	15.38	29.56 (3–119)	9.52	16.75 (5–30)	4.95	10.4 (3–24)
Spauligodon okxcutzcabiensis	1.72	1 (1)	0.96	42 (42)	–	–	–	–
Physalopteridae								
Physaloptera lutzi	3.44	5.5 (1–10)	–	–	11.92	6 (1–19)	2.97	2.33 (1–5)
Tropidurus hispidus								
Acanthocephala								
Oligacanthorhynchidae								
Oligacanthorhyrchus sp.	–	–	–	–	–	–	3.5	(2–5)
Cestoda								
Linstowiidae								
Oochoristica sp.	1.04	5 (5)	–	–	–	–	5.08	2.33 (1–3)
Nematoda								
Heterakidae								
S. oscari	44.79	5.13 (1–39)	10.52	2.5 (1–4)	2.63	28 (1–55)	35.59	4.14 (1–16)
Onchocercidae								
Oswaldofilaria sp.	–	–	–	–	1.31	2 (2)	–	–
Pharyngodonidae								
P. alvarengai	35.41	3.44 (1–22)	40.35	3.73 (1–18)	15.78	4.66 (1–12)	15.25	3.11 (1–6)
Pharyngodon sp.	4.16	11.5 (2–37)	1.75	20 (20)	–	–	–	–
Physalopteridae								
P. lutzi	47.91	9.65 (1–60)	10.52	2.66 (1–7)	18.42	3 (1–8)	32.2	3.63 (1–9)
Rhabdiasidae								
Rhabdias sp.	1.04	3 (3)	–	–	–	–	–	–
Pentastomida								
Raillietiellidae								
Raillietiella mottae	2.08	1 (1)	1.75	2 (2)	–	–	–	–
Tropidurus semitaeniatus								
Cestoda								
Linstowiidae								
Oochoristica sp.	–	–	1.88	1 (1)	–	–	4.76	2.5 (2–3)
Nematoda								
Heterakidae								
S. oscari	–	–	–	–	16.66	2 (1–3)	19.04	7.25 (2–21)
Pharyngodonidae								
P. alvarengai	–	–	50.94	11.25 (1–36)	41.66	7.6 (3–13)	16.66	3.42 (1–6)
Physalopteridae								
P. lutzi	–	–	–	–	6.25	1 (1)–	–	–

Table 2 GLM of the variations in the abundance of parasites between the sampling areas of the lizards, dry and rainy seasons, interaction area, and season and between the sexes of the lizards

	Wald	Degrees of freedom	*P*
Cnemidophorus ocellifer			
Area	142.4	3	*<0.01*
Season	1.06	1	>0.30
Area × season	9.23	3	*<0.05*
Sex	95.80	1	*<0.01*
Tropidurus hispidus			
Area	14.73	3	*<0.001*
Season	5.39	1	*<0.01*
Area × season	137.3	3	*<0.0001*
Sex	0.07	1	>0.78
Tropidurus semitaeniatus			
Area	7.79	2	*<0.02*
Season	1.03	1	>0.30
Area × season	13.66	2	*<0.001*
Sex	26.60	1	*<0.0001*

Values presented in italics are statistically significant

dry season (Vitt and Goldberg 1983). The males become more aggressive due to sexual selection, therefore increasing the levels of stress, favoring a higher infestation rate by parasites (DeNardo and Sinervo 1994; Salvador et al. 1996).

Seasons and abundance of endoparasites

The season influenced the abundance of endoparasites only for *T. hispidus.* A higher abundance in the rainy period could be a reflection of the humidity. Parasites, which mainly have direct life cycles such as *Strongyluris oscari* and *Parapharyngodon alvarengai*, depend on the surrounding environment as their eggs remain on the soil until ingested by the host (Anderson 2000). In addition, a lizard's biology can also be cited as a determining factor in this difference, for example, when *T. hispidus* changes its strategy (due to seasonal change), widening its foraging area, and the diversity of food items consumed during the rainy season (Kolodiuk et al. 2009). This expansion in foraging area could favor a greater number of encounters with the endoparasites.

For *C. ocellifer* and *T. semitaeniatus,* a season by itself did not influence the abundance of parasites. However, its interaction with the sampling area was significant. At the same time, we observed distinct patterns in the abundance of parasites in the dry and rainy seasons in different locations (Figs. 2 and 3). Seasonality can alter behavioral patterns in lizards, such as living space, thermal biology, as well as proportion and

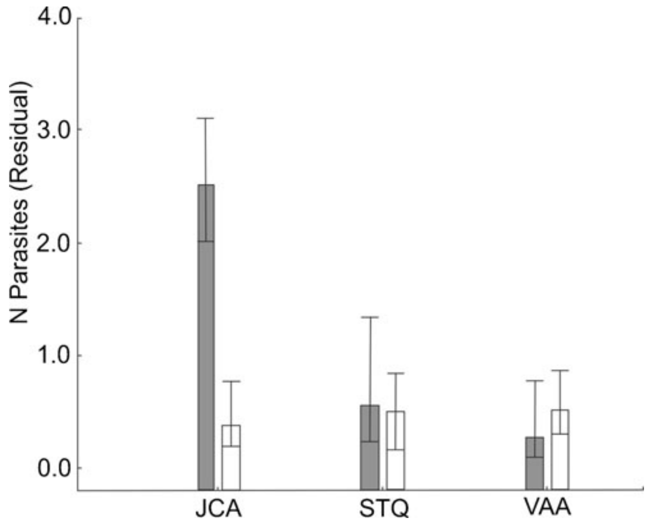

Fig. 3 Average residual in the relationship between SVL and the abundance of endoparasites in *T. semitaeniatus* in the three recorded areas. The *gray columns* represent the dry season and the *white* ones the rainy season, while the *lines* across them represent standard error

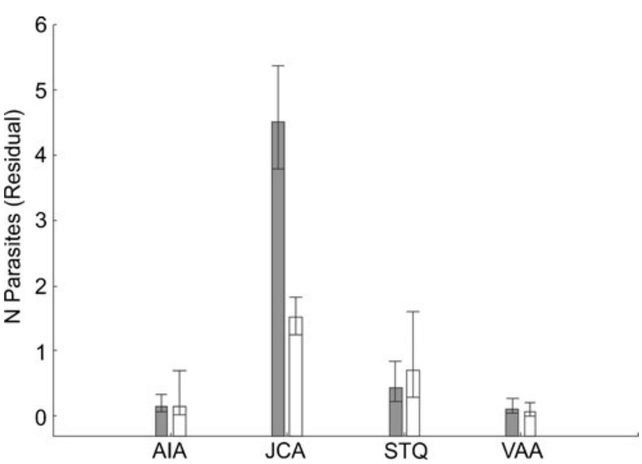

Fig. 2 Average residual of the relationship between SVL and the abundance of endoparasites in *C. ocellifer* in the four recorded areas. The *gray columns* represent the dry season and the *white* ones the rainy season, while the *lines* across them represent standard error

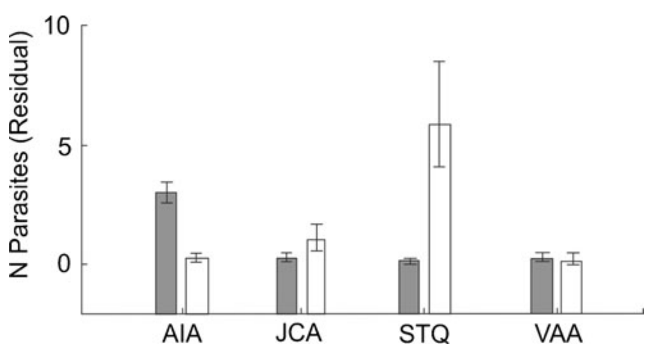

Fig. 4 Residual of the relationship between SVL and the abundance of parasites in *T. hispidus* in the four recorded areas. The *gray columns* represent the abundance of parasites in the dry season and the *white* represent the rainy season, while the *lines* across the columns represent standard error

diversity of consumed prey (Rocha 1996; Miranda and Andrade 2003; Sepúlveda et al. 2008). Moreover, there is interference in the biology of parasites (making the infection more or less efficient) which depends on their interaction with local factors such as humidity, rainfall, temperature, and even the interaction with the soil fauna of the area (Grønvold 1987; Thieltges et al. 2008).

Abundance in relation to area

Area influenced the total patterns of abundance of endoparasites in all three lizard species. Parasite-host relationships are very dynamic, and the environmental variables can be related to this spatial variation in their abundance. We can cite three among the probable causes: (1) variations in abiotic factors in different areas; as during the stages outside the host, the propagules are exposed to environmental factors that modify their success of transmission, affecting their survival and rate of infectivity (Thieltges et al. 2008), and these factors are varied but include local biochemistry (pH, temperature, and ultraviolet radiation) to pollutants from anthropic actions (Thieltges et al. 2008; Tinsley et al. 2011); (2) biotic factors such as predation and hyperparasitism (a parasite whose host is a parasite). Many species of nematodes suffer from pressure due to the presence of predators which leads to a decrease in the quantity of eggs or larvae during their stages of outside the host. The *Cooperia onchophora* parasite, for instance, has their population halved in environments where Oligochaetes are present (Grønvold 1987). Moreover, we can highlight groups of invertebrates such as collembolas, mites, tardigrades, and beetles that predate the eggs/larvae of nematode parasites during the stages outside the host (Thieltges et al. 2008). Thus, the abundance of endoparasites in their final host can be directly influenced by the composition of the local soil fauna. Hyperparasitism can also influence the abundance of nematodes in a given region where bacteria and fungi target nematode eggs, decreasing the chance of these eggs infecting their hosts (Waller and Thamsborg 2004; Ketzis et al. 2006). Therefore, various biotic and abiotic factors of an area can exert an important influence over the patterns of abundance of the endoparasite species in their respective hosts. (3) Spatial variation in the virulence of parasites (as both the parasites and their hosts display variations in their genotypes) results in modifications in the way the hosts defend themselves against the parasites' attack. This could lead to variations in methods of avoiding the hosts' immune system (Dybdahl and Storfer 2003). It is expected that the parasites become well adapted (locally) to their hosts due to their shorter life cycle. However, it is to be expected that the fitness of a parasite species is weakened when the distance from the main host population is increased (Ebert 1994; Dybdahl and Storfer 2003).

Conclusions

Sex exerted influence on the abundance of endoparasites, where males were more infected than females, being this difference possibly due the reproductive season.

The area influenced the overall patterns of endoparasite abundance in all three studied lizard species, probably due to the influence of biotic and abiotic factors from each location. The season influenced the abundance of endoparasites only in *T. hispidus*, being the parasites more abundant in rainy season; this seasonal variation is probably due the fact that the parasites with direct life cycle achieve better environmental conditions and, therefore, can infect more efficiently during this period.

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