Using lizards to evaluate the influence of average abundance on the variance of endoparasites in semiarid areas: dispersion and assemblage structure

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Abstract

The distribution of parasites within host populations and communities, and the mechanisms responsible for these patterns, are poorly understood aspects of wildlife parasitology. Here, we evaluate the influence of the average abundance of endoparasite variance, using endoparasites of lizards from the Caatinga domain (semiarid region), north-eastern Brazil. We hypothesized that, due to the high number of generalist endoparasite species, they may occur randomly throughout host populations in an aggregate pattern. In addition, we evaluated the degree to which sample variance is influenced by the average abundance of endoparasite species, patterns of co-occurrence and dominance among endoparasite species and similarities between abundance and the richness of endoparasite infracommunities in several host species. Between September 2015 and February 2016, 2141 lizards (1233 infected) from 16 species were collected from six Caatinga areas. In total, 25,687 endoparasites were collected, which belonged to 13 species including nematodes, pentastomids, cestodes, trematodes and acanthocephalans. Parasite–host associations documented here included 39 newly identified interactions. Endoparasites occurred in a typical aggregate pattern of distribution within their hosts; there was no measurable preference related to the acquisition of hosts by endoparasites. Despite the new records, endoparasites found were commonly associated with lizards in Caatinga environments, which may reflect fauna composed of generalist endoparasite species.

Introduction

Historically, ecological studies have been conducted at different hierarchical scales, such as ecosystems, communities, guilds and populations (Rynkiewicz *et al.*, 2015); this result in the reduction of complexity facilitates comparing these components in different habitats and localities (Thomas *et al.*, 2005). Studies of species abundance, occurrence and fluctuation are considered central themes in Ecology (Holt *et al.*, 2003). Parasites are considered good model organisms for testing ecological hypotheses since they are abundant in natural environments. In addition, their habitat (hosts) have well-defined limits and, depending on the group, can be effectively replicated (Pietrock & Marcogliese, 2003).

The study of parasites does have unique characteristics when compared to that of free-living organisms (Holmes & Price, 1980). Characteristics such as dispersion and recruitment are closely related to the ecology and phylogeny of parasite hosts (Poulin, 2007). Infrapopulations (*sensu* Bush *et al.*, 1997) describe all individuals of a given parasitic species present in a single host specimen at the same time. Host characteristics including size and sex, seasonality, diet and habitat influence the composition and distribution of species within infrapopulations (Esch *et al.*, 1990; Holt *et al.*, 2003; Poulin, 2007).

The component community (all infrapopulations living within a particular host species) is frequently an aggregate of host populations (Shaw & Dobson, 1995). Usually, hosts offer heterogeneous environments for infection by parasites, and individual variations in behaviour, genetics and immune responses may contribute to the aggregation of parasites (Poulin, 2013). The aggregation of parasites is so prevalent with regard to host associations that it has been proposed as a premise to define the ecological relationship between parasite and host (Crofton, 1971; Pacala & Dobson, 1988). An aggregate distribution may provide important information regarding the relationship between parasites and their hosts, and some models have been proposed to identify factors that determine such distribution patterns, such as host

density, mortality rate, size, age and sex (May & Anderson, 1979; Gordon & Rau, 1982; Adjei *et al.*, 1986; Rousset *et al.*, 1996; Combes, 2001).

Some patterns describing models of occurrence and distribution of parasites in wild hosts have been proposed. They include the competitive exclusion (King, 1964), increased prevalence (Janovy *et al.*, 1995) and resource partitioning (Mouillot *et al.*, 2003) models. Additionally, null models (Harvey *et al.*, 1983; Krasnov *et al.*, 2006) can be used to evaluate whether the occurrence of parasites is random in different host species or if it is the result of interspecific interactions (Ulrich & Gotelli, 2010, 2013). The organization of communities may present somewhere along a continuum that extends between randomness and structure (Price, 1987; Poulin, 1996; Leung, 1998; Rolff, 2000; Lacerda *et al.*, 2013), where communities composed of small populations, or an organism with low vagility, are typically randomly organized (Gotelli & Rohde, 2002).

An alternative explanation for the aggregate distribution of parasites regards the relationship between the variance and the mean parasite abundance *per* host, which indicates how aggregation may be regulated by mean infection value (Shaw & Dobson, 1995). This assumption is based on the aggregate distribution of organisms, and follows Taylor's law of species distribution (Taylor, 1961), in which the density of organisms varies proportionally in relation to the mean of the population density. Cooccurrence models can also be used to characterize parasite communities, where pairs of parasites may have positive or negative associations with levels of host infection (Price, 1987). These results may be difficult to interpret, since they reflect competition and/or specialization in the exploitation of a particular host (historical or current). Therefore, it is necessary to test more hypotheses concerning the mechanisms that shape parasite communities, especially those living within terrestrial hosts (Poulin, 1996; Krasnov *et al.*, 2006; Budischak *et al.*, 2012).

In the present study, we evaluate the influence of average abundance on the variance of endoparasites observed within lizards living in semiarid areas of the Caatinga in north-eastern Brazil. Studies on lizard endoparasites from Caatinga have become more frequently produced in recent years (Ávila *et al.*, 2012; Brito *et al.*, 2014a; Araujo Filho *et al.*, 2017; Teixeira *et al.*, 2017; Teles *et al.*, 2017), but our understanding of endoparasite community structures with regard to both the abundance and aggregation patterns of parasites is lacking (Ávila *et al.*, 2012; Araujo Filho *et al.*, 2014). The endoparasitic fauna of Caatinga lizards is composed mainly of generalists, where parasite abundances are positively related to the size, sex and reproductive period of the hosts, as well as with the rainy season, which indicate that multiple factors determine the patterns of resource use by parasitic species (Anjos *et al.*, 2007; Almeida *et al.*, 2008; Ávila *et al.*, 2012; Lima *et al.*, 2017; Oliveira *et al.*, 2017; Teixeira *et al.*, 2017; Teles *et al.*, 2017).

Thus, our goals were to determine the community composition of lizard endoparasites and test the following hypothesis: (H0) due to interspecific competition, the occurrence of endoparasites within hosts is structured, and is homogeneously distributed; and (H1) due to the abundance of generalist endoparasitic species, they may occur randomly within host populations in an aggregate pattern. In addition, we determined the degree to which sample variance is influenced by the average abundance of endoparasitic species, patterns of cooccurrence and dominance among endoparasitic species and similarities between the

abundance and richness of infracommunities of endoparasites in several host species.

Materials and methods

Study areas

Samples were collected from three areas of Alto Sertão, Sergipe, Northeast Brazil. Each area was composed of two sampling sites, which resulted in a total of six sample units. Area I was located in Porto da Folha (Quilombola settlement of Mocambo) and Poço Redondo (private farm) municipalities; area II was located in the Poço Redondo municipality (Grota do Angico Natural Monument and the Angico Farm); and area III was located in Canindé do São Francisco (Jerimum Farm) and Porto da Folha (Quilombola settlement of Mocambo) municipalities. The most distant areas were approximately 40 km apart.

All sampling sites were located in the Caatinga domain, a semiarid region of north-eastern Brazil with a 'BSh' climate, according to Köppe, which belongs to the Southern Sertaneja Depression (Ab'Saber, 1974; Velloso *et al.*, 2002), in the Alto Sertão region of Sergipe state. The rainfall levels vary in accordance with a four-month rainy season and eight-month dry season. The average annual precipitation level is approximately 500 mm, and the average annual temperature varies between 26 and 28°C. Vegetation within the area is composed of typical plants from the arboreal shrubby of Caatinga, in which cacti and bromeliads are present (Andrade-Lima, 1981; Sá *et al.*, 2004).

Data collection

Sites were visited for 30 days, within dry (April and August 2016) and rainy (September 2015 and February 2016) seasons. Specimens were collected using pitfall traps and by actively searching for animals. After collection, the specimens were euthanized and deposited in the Herpetological Collection of the Federal University of Paraíba (Universidade Federal da Paraíba – CHUFPB).

Lizards were dissected under a stereomicroscope, and lung, stomach, liver, gallbladder and small and large intestine tissues were analysed. Further cavities were searched for endoparasites. Endoparasites were counted and preserved in 70% ethanol for subsequent analyses. Specimens were identified to the lowest possible taxonomic level with the aid of a microscope equipped with an image analyser (Carl Zeiss Microimaging GmbH, Gottingen, Germany) and mounted on temporary slides with the use of either a lactic acid medium (nematodes), Hoyer's medium (pentastomids) or stained with acetic carmine and mounted in Eugenol (acanthocephalans, trematodes and cestodes).

Statistical analysis

Ecological terminology used was in accordance with definitions provided in Bush *et al.* (1997). To determine the distribution pattern of the infrapopulations (all endoparasites of a particular species present in a population of hosts), the dispersion index (DI) was calculated, which ranged from zero to one using Quantitative Parasitology 3.0 software (Rózsa *et al.*, 2000). A DI of zero indicated that all species were uniformly distributed and a DI of one indicated that all endoparasites were found in only one host (Poulin, 1993). In addition, the Morisita index of aggregation was calculated by computing the abundance of

species, which had an associated *P*-value (chi-square), using XLstat software (Addinsoft, 2004).

To test whether the endoparasitic community was randomly distributed across host species, a pseudo community analysis was performed with 10,000 randomizations of a null model. The presence–absence matrix was built with species of endoparasites (rows) and hosts species (columns). We used the algorithm 'R3' because it maintained the specialization of each endoparasitic species, but considered the possibility of using newly available resources (Winemiller & Pianka, 1990).

Linear regression analysis was performed between variance of mean intensity ($\log^{10}$) and the average abundance of endoparasites, to identify a possible degree of restriction in aggregation, although this parameter is influenced by aggregate populations, reflecting possible competition for space (host/site of infection) and/or the 'limit abundance' that a host specimen can support (Shaw & Dobson, 1995).

The normality of abundance and richness was assessed using the Shapiro–Wilk test. The data were not normally distributed (Wald = 0.410, $P < 0.0001$; W = 0.803, $P < 0.0001$, respectively). Therefore, the Spearman and Pearson correlation test was used to evaluate whether pairs of endoparasitic species were correlated. The Bray–Curtis similarity index was performed to evaluate the relationship between the richness and abundance of an endoparasitic infracommunity within each group of hosts analysed. Species assessed included *Gymnodactylus geckoides* Spix, 1825; *Phyllopezus pollicaris* Spix, 1825 (Phyllodactylidae); *Ameivula ocellifera* Spix, 1825 (Teiidae); *Vanzosaura multiscutata* Amaral, 1993 (Gymnophthalmidae); and *Tropidurus hispidus* Spix, 1825 and *T. semitaeniatus* Spix, 1825 (Tropiduridae). At least ten specimens from each of these species were collected in each area studied. A similarity matrix was constructed using the Bray–Curtis method. Analyses were performed using the R program (Core Team, 2019).

Dominance (*d*) of endoparasitic species was calculated according to the Berger–Parker index (Magurran, 2013). Later, the Kruskal–Wallis test was performed to determine whether differences in the dominance of the component community among host species and within each host species were significant (only endoparasitic species with prevalence greater than 5% were considered).

Results

A total of 2141 lizards were dissected, which belonged to 16 different species. Species identified included *Acratosaura mentalis* (number of specimens (*n*) = 62; mean snout-vent length ± standard deviation (SVL) = 48.1 ± 9.5); *Ameiva* (*n* = 12; SVL = 77.6 ± 38.5); *Ameivula ocellifera* (*n* = 541; SVL = 65.7 ± 10.1); *Coleodactylus meridionalis* (*n* = 1; SVL = 17.1); *G. geckoides* (*n* = 477; SVL = 38.7 ± 2.4); *Hemidactylus brasilianus* (*n* = 1; SVL = 39.1); *Hemidactylus mabouia* (*n* = 1; SVL = 59.7); *Iguana* (*n* = 2; SVL = 124.3); *Lygodactylus klugei* (*n* = 65; SVL = 27.5 ± 2.1); *Brasiliscincus heathi* (*n* = 25; SVL = 63 ± 5.7); *Phyllopezus pollicaris* (*n* = 173; SVL = 60.6 ± 9.3); *Polychrus acutirostris* (*n* = 1; SVL = 126.8); *Tropidurus hispidus* (*n* = 354; SVL = 71.1 ± 16.2); *T. semitaeniatus* (*n* = 307; SVL = 67.6 ± 10.2); *Tupinambis merianae* (*n* = 7; SVL = 90 ± 5.1); and *V. multiscutata* (*n* = 112; SVL = 32.4 ± 2.1). A total of 25,687 endoparasites were collected and identified, which included nematodes, pentastomids, acanthocephalans, trematodes and cestodes, from a total of 13 taxa (table 1) from 1233 host organisms.

Of the total number of hosts analysed, 57.58% were parasitized by at least one species, and an average of 20.8 ± 15.5 parasites were found in each infected host. A total of 39 new host records were identified (table 1). Within the host population, 23.76% were infected by two species of endoparasites; 6.40% were infected by three species; 1.54% were infected by four species; 0.24% were infected by five species; and only two specimens of *T. hispidus* (0.16%) were each infected by six endoparasitic species.

Nematodes were the most highly prevalent type of endoparasitic organism identified. Of the seven species that were found at a prevalence greater than 5%, five were nematodes, and one species of Pentastomida and Cestoda were also found (table 1). All endoparasitic species exhibited a typical aggregate distribution patterns (table 2). Although subtle variations were observed between monoxenic and heteroxenic species, the latter type produced slightly higher discrepancy values.

The occurrence of endoparasites in the host community did not differ significantly from that which would be expected to occur at random, and the observed index value of 0.617 was not smaller than the simulated index of 0.497, which indicated the absence of community structure ($P > 0.9$). Variance observed was strongly explained by mean value observed (F_{942}; $R^2 = 0.98$; $P < 0.001$) (fig. 1). In other words, there was a regulatory effect that affected the average number of parasites per host, and this restriction generated the aggregation limit observed.

The species of endoparasites possessing the greatest correlation values were congeners *Physaloptera lutzi* and *P. retusa* (table 3). Similarly, monoxenic species were positively correlated, but the only species that was associated with others was *Parapharyngodon alvarengai*. Similarity analysis revealed that phylogenetically similar hosts, or those with similar foraging habits, possessed similar endoparasitic fauna (table 4). Sympatric lizards *T. hispidus* and *T. semitaeniatus* had endoparisitic fauna that were the most similar.

Endoparasitic species exhibited different levels of dominance within each host species (table 5). Similarly, dominance was significantly variable among host species (Shannon index H' = 19.67; Degrees of freedon GL = 11; $P < 0.001$). For the teiid species *A. ocellifera*, the dominant species was the monoxenic nematode *Pharyngodon cesarpintoi*. For the lizards, *G. geckoides*, *Brasiliscincus heathi* and *T. semitaeniatus*, the dominant species was the monoxenic nematode *Parapharyngodon alvarengai*. *Phlopezpezus pollicaris* exhibited a high degree of dominance, and the monoxenic species, *Spauligodon oxkutzcabiensis*, was the most important. For the *T. hispidus* host, the heteroxenic species, *P. lutzi*, and the monoxenic species, *P. alvarengai*, had the highest dominance values.

Discussion

Thirteen endoparasitic species were determined to be associated with lizards. Monoxenic nematodes were the most prevalent, which included *P. alverengai*, *P. cesarpintoi* and *S. oxkutzcabiensis* (Pharyngodonidae) species. These species were most prevalent within *T. hispidus*, *T. semitaeniatus*, *A. ocellifera* and *P. pollicaris* hosts. The absence of intermediate hosts, coupled with the habit of some lizards of 'tasting' the environment with their tongue (personal observation), may contribute to high infection rates of endoparasites with direct cycles (Anderson, 2000). However, foraging mode, contact between susceptible hosts and population density may also contribute to increases observed within this category. *Pharyngodon* were prevalent within lizards (Gupta *et al.*, 2009; Anjos *et al.*, 2012; Brito *et al.*, 2014a; Teles *et al.*, 2017).

Table 1. Endoparasites associated with the lizards collected in the Caatinga environment, a semiarid region of the Alto Sertão of Sergipe, Northeast Brazil.

Parasite	Host	%	I_F	I_S	Abu	H	L_C
NEMATODA							
Pharyngodonidae							
Parapharyngodon alvarengai	*Acratosaura mentalis*[a]	3.5	2	LI	2	1	
	Ameiva ameiva	20	3	LI	6	2	
	Ameivula ocellifera	3.5	3.7 ± 0.9	SI, LI	71	19	
	Gymnodactylus geckoides	28.5	1.9 ± 1	LI	261	136	
	Lygodactylus klugei[a]	2.1	2	LI	2	1	
	Brasiliscincus heathi	48	2.8 ± 1.8	LI	34	12	
	Phyllopezus pollicaris	6.3	4.1 ± 1.5	LI	46	11	
	Tropidurus hispidus	52.8	5.4 ± 5.4	SI, LI	1017	187	
	Tropidurus semitaeniatus	46.9	7.4 ± 7.3	SI, LI	1072	144	
	Vanzosaura multiscutata[a]	6.2	1	LI	1	1	
	Total	42.2	4.9		2512	514	M
Pharyngodon cesarpintoi	*Ameiva ameiva*	3.5	102	LI	102	1	
	Ameivula ocellifera	63.2	44 ± 67.5	S, SI, LI	15,061	342	
	Lygodactylus klugei[a]	5.8	3	S	3	1	
	Phyllopezus pollicaris[a]	4	14.7 ± 4	LI	103	7	
	Tropidurus hispidus[a]	1.4	19 ± 3.1	S, LI	95	5	
	Tropidurus semitaeniatus[a]	4.5	6.4 ± 2.2	S, LI	90	14	
	Tupinambis merianae[a]	14.2	15	LI	15	1	
	Vanzosaura multiscutata[a]	1.7	3	LI	3	1	
	Total	30	42.5		15,472	372	M
Spauligodon oxkutzcabiensis	*Acratosaura mentalis*[a]	32.2	3.4 ± 2.3	LI	68	20	
	Ameivula ocellifera[a]	2	4.4 ± 1.4	LI	49	11	
	Gymnodactylus geckoides	2.7	6.3 ± 2.8	LI	82	13	
	Lygodactylus klugei	2.1	1	LI	1	1	
	Phyllopezus pollicaris	75.1	28 ± 32.3	SI, LI	3651	130	
	Tropidurus hispidus[a]	1.9	5.7 ± 1.1	LI	40	7	
	Tropidurus semitaeniatus[a]	0.8	1	LI	1	1	
	Vanzosaura multiscultata[a]	2.6	1	LI	1	1	
	Total	14.5	22.2		3893	184	M
Heterakidae							
Strongyluris oscari	*Ameivula ocellifera*	2.5	1.6 ± 0.6	L, LI	23	14	
	Gymnodactylus geckoides[a]	0.5	10	LI	10	1	
	Ligodactylus klugei[a]	5.8	2	S	2	1	
	Tropidurus hispidus	12.1	10.8 ± 5.8	L, SI, LI	467	43	
	Tropidurus semitaeniatus	57.6	12.7 ± 10.8	L, OES, S, SI, LI	1487	117	
	Total	13.4	12.2		1989	176	M
Physalopteridae							
Physaloptera lutzi	*Ameivula ocellifera*	1.4	6.5 ± 1	S, CAV	52	8	
	Ameiva ameiva	8.3	2	S	2	1	
	Gymnodactylus geckoides	2.3	1.2 ± 0.2	S	14	11	
	Lygodactylus klugei	9.2	5 ± 2.1	S	30	6	

(*Continued*)

Table 1. (*Continued.*)

Parasite	Host	%	I_F	I_S	Abu	H	L_C
	Tropidurus hispidus	46	6.5 ± 5.7	S, SI, LI, CAV	1063	163	
	Tropidurus semitaeniatus	3.9	1.5 ± 0.3	S	18	12	
	Vanzosaura multiscutata	0.9	3	S	3	1	
	Total	9.5	5.8		1182	202	H
Physaloptera retusa	*Ameivula ocellifera*[a]	0.5	5.6 ± 0.4	S, LI	17	3	
	Tropidurus hispidus	6.2	5.2 ± 3.3	S, SI, LI, CAV	116	22	
	Tropidurus semitaeniatus[a]	1.6	5	CAV	5	5	
	Tupinambis merianae	14	1	S	1	1	
	Total	2.5	3.6		139	31	H
⬜⬜⬜Onchocercidae							
Piratuba sp.	*Acratosaura mentalis*[a]	1.6	1	CAV	1	1	
	Ameivula ocellifera[a]	1.8	4.7 ± 1	CAV, OVA	47	10	
	Gymnodactylus geckoides	0.8	2.7 ± 0.3	CAV	11	4	
	Lygodactylus klugei[a]	1.5	1	CAV	1	1	
	Tropidurus hispidus	2.5	8.4 ± 2.1	CAV	76	9	
	Tropidurus semitaeniatus[a]	0.6	2	CAV	2	2	
	Total	1.3	5.4		138	27	H
Cosmocercidae	*Gymnodactylus geckoides*[a]	0.4	2	S, L	4	2	
	Tropidurus semitaeniatus[a]	0.9	1.3	S, CAV	4	3	
	Vanzosaura multiscutata[a]	0.8	1	CAV	1	1	
	Total	0.3	2.4		9	6	M
Rhabdochonidae							
Trichospirura sp.	*Phyllopezus pollicaris*	1.6	2	GB	6	3	
	Tropidurus semitaeniatus[a]	0.3	1	GB	1	1	
	Total	0.3	2.4		7	4	H
PENTASTOMIDA							
Raillietiellidae							
Raillietiella mottae	*Acratosaura mentalis*[a]	12.9	2.3 ± 1.2	L	19	8	
	Ameivula ocellifera[a]	2.9	4.3 ± 0.9	L	70	16	
	Gymnodactylus geckoides	2.9	1.7 ± 0.4	L	25	14	
	Hemidactylus mabouia	100	1	L	1	1	
	Lygodactylus klugei[a]	1.5	1	L	1	1	
	Phyllopezus pollicaris	11.5	1.8 ± 0.7	L	37	20	
	Tropidurus hispidus	10.7	6.1 ± 4.2	L	234	38	
	Tropidurus semitaeniatus	1.9	2.6 ± 0.4	L	16	6	
	Vanzosaura multiscutata[a]	3.5	1.5 ± 0.3	L	6	4	
	Total	8.4	3.9		409	108	H
ACANTOCEPHALA							
Oligacanthorhynchidae							
Oligacanthorynchus sp.	*Ameivula ocellifera*[a]	1.1	8 ± 1.3	F, SI, CAV	48	6	
	Gymnodactylus geckoides[a]	0.2	1	F	1	1	
	Phyllopezus pollicaris[a]	2.3	2.7 ± 0.4	F, SI, LI	11	4	
	Tropidurus semitaeniatus	0.3	1	LI	2	1	

Table 1. (*Continued.*)

Parasite	Host	%	I_F	I_S	Abu	H	L_C
	Total	0.6	5.2		62	12	H
Cystacanto	*Ameivula ocellifera*[a]	0.7	1.2 ± 0.2	S, CAV	5	4	
	Gymnodactylus geckoides[a]	0.4	3	S, CAV	6	2	
	Phyllopezus pollicaris	0.5	2	S	2	1	
	Tropidurus hispidus[a]	0.2	6	S	6	1	
	Tropidurus semitaeniatus	0.6	5	S	10	2	
	Total	0.5	3.9		29	10	H
CESTODA							
Linstowiidae							
Oochorystica sp.	*Acratosaura mentalis*[a]	3.2	1.5	S, SI	3	2	
	Ameiva ameiva	16.6	1.5	SI	3	2	
	Ameivula ocellifera	6.2	3.3 ± 1.3	S, SI	114	34	
	Brasiliscincus heathi	28	1.5 ± 0.9	SI	11	7	
	Tropidurus hispidus	2.8	2.7 ± 0.6	SI, CAV	27	10	
	Tropidurus semitaeniatus	7.8	4.1 ± 2.7	S, SI, CAV	99	24	
	Total	6.4	3.3		257	79	H
TREMATODA							
Dicrocoeliidae							
Euparadistomum paraenses	*Tropidurus hispidus*[a]	1.69	4.16 ± 0.5	GB	25	6	
	Total	0.3	4.1		25	6	H

[a]New records of hosts. Prevalence (%). I_F, mean intensity of infection; I_S, infection site; Abu, abundance; H, number of hosts; L_C, life cycle; M, monoxenic; He, heteroxenic; L, L; S, stomach; SI, small intestine; LI, large intestine; GB, gallbladder; CAV, cavity; OES, oesophagus; OVA, ovary.

Table 2. Morisita aggregation index.

Taxa	Imor	Mclu	Muni	Imst	P	D
Physaloptera lutzi	2.11	1.10	0.89	0.50	P < 0.001	0.95
Physaloptera retusa	21.39	1.64	0.37	0.55	P < 0.001	0.98
Raillietiella mottae	9.21	1.32	0.68	0.52	P < 0.001	0.96
Strongyluris oscari	2.66	1.06	0.93	0.50	P < 0.001	0.94
Parapharyngodon cesarpintoi	2.39	1.00	0.99	0.50	P < 0.001	0.89
Spauligodon oxkutzcabiensis	3.45	1.03	0.96	0.50	P < 0.001	0.94
Parapharyngodon alvarengai	1.05	1.05	0.95	0.50	P < 0.001	0.80
Oochorystica sp.	10.86	1.52	0.49	0.52	P < 0.001	0.97

Imor, index value; Mclu, upper values; Muni, lower values; Imst, standardized index value; *P*, chi-square test value for each distribution; D, Poulin's discrepancy index. When Imor is >Mclu, the distribution is considered aggregate. Values of Imst >0.5 indicate aggregated distribution.

The genus is composed of monoxenic species, which are parasites of vertebrates, with a wide global distribution pattern (Ávila & Silva, 2010; Campião *et al.*, 2014; Goldberg *et al.*, 2016).

The most important hosts (prevalence > 45%) for *P. alvarengai* were *T. hispidus* (52.82%) and *T. semitaeniatus* (46.90%). Previous studies (Anjos *et al.*, 2012; Brito *et al.*, 2014a) reported high prevalence values for *P. alverengai* within the same host species in different regions of Caatinga. Concerning the host *A. ocellifera*, the prevalence of the nematode *P. cesarpintoi* was high (63.21%). In addition, the nematode, *S. oxkutzcabiensis*, was highly prevalent (75.14%) within the host *P. pollicaris*, which was a finding that

was similar to that which was reported previously in Caatinga (Lima *et al.*, 2017). Despite being considered generalists, these species were more prevalent in particular hosts than others. This variation may be associated with undescribed cospeciation mechanisms, as well as with the specific microhabitat and diet of the hosts (Esch *et al.*, 1990; Hamann *et al.*, 2006; Brito *et al.*, 2014b).

The most prevalent heteroxenic endoparasites were *P. lutzi* in *T. hispidus* (46.04%) and *P. retusa* in *T. merianae* (14.02%) (Physalopteridae). Physalopterids are endoparasites of several vertebrates (Goldberg *et al.*, 1998; Campião *et al.*, 2014) and can be found in 38 omnivorous lizards in Brazil (Ávila &
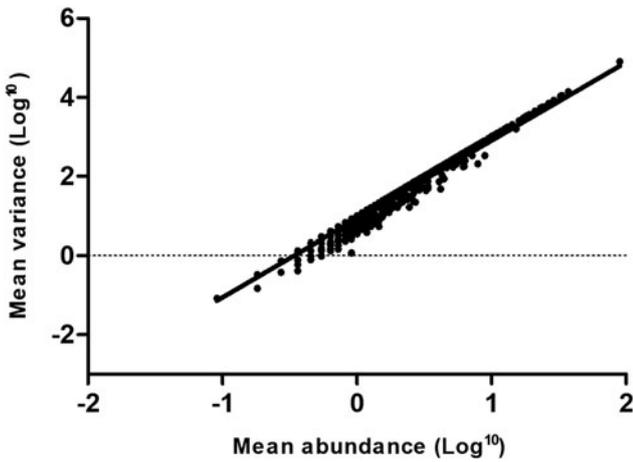
Fig. 1. Relationship between variance and mean abundance (log[10]; F_{942}; $R^2 = 0.98$; $P < 0.001$) of endoparasites associated with lizards, collected in a semiarid Caatinga environment, Northeast Brazil.

Silva, 2010; Araujo Filho *et al.*, 2014; Lima *et al.*, 2017). The prevalence of these endoparasites varies according to the area considered (Brito *et al.*, 2014a; Lima *et al.*, 2017), and it may be related to changes in intermediate host communities and seasonality (Narayanan *et al.*, 1961; Vasconcellos *et al.*, 2010).

The pentastomid genus *Raillietiella* (Raillietiellidae) infects a wide variety of insectivorous lizards in Brazil (Vrcibradic *et al.*, 2002; Almeida *et al.*, 2008; Ribeiro *et al.*, 2012; Brito *et al.*, 2014a; Sousa *et al.*, 2014; Lima *et al.*, 2017). Herein, the genus was most highly prevalent in *A. mentalis* (12.9%), *P. pollicaris* (11.56%) and *T. hispidus* (10.73%) lizards. As demonstrated by Lima *et al.* (2017), species of *Raillietiella* were prevalent in gecko hosts (Gekkonidae and Phyllodactylidae), and their high degree of prevalence within *A. mentalis* (Gymnophthalmidae) and their newly discovered association with *Raillietiella mottae* may be a result of the species' flexibility, in the infection of new hosts, variations in host use and the availability intermediates. These variations have also been found in several other *Raillietiella* species (Kelehear *et al.*, 2011, 2012).

Trichospirura nematodes occur in amphibians (Moravec & Kaiser, 1994), lizards (Goldberg *et al.*, 1998) and mammals (Bain & Junker, 2013) and were first recorded to infect lizards in South America by Lima *et al.* (2017) in Caatinga. We found few specimens of *Trichospirura* sp. that were associated with the gallbladder of *P. pollicaris* (1.69%) and *T. semitaeniatus* (0.32%), the latter of which is a new record. The trematode *Euparadistomum paraenses* was found in the gallbladder of the lizard *T. hispidus*, which was the first record of that genus of endoparasite infecting lizards globally. Typically, they parasitize marsupial mammals (Betterton, 1980), and the low prevalence determined (1.69%) may indicate an accidental infection by the parasitic species. Other new host records (table 1) indicate the potential for the exploration of host lizard assemblages, since endoparasitic species of intermediate prevalence values may not have been found to date due to either their absence or insufficient host population samples in certain areas.

Regarding distribution patterns, all component communities considered in this study exhibited aggregate distribution patterns and high discrepancy values. Endoparasite populations of lizards are aggregated even when the hosts lived in different microhabitats and have different diets and foraging activities (Anjos *et al.*, 2012; Barreto-Lima *et al.*, 2012; Macedo *et al.*, 2017; Cabral

Table 3. Spearman correlation between pairs of endoparasite species (prevalence >5%) and Pearson correlation (P-values) associated with lizards from an environment in Caatinga, north-eastern Brazil. Statistically significant p-value (bold).

	Physaloptera lutzi	Physaloptera retusa	Raillietiella mottae	Strongyluris oscari	Parapharyngodon cesarpintoi	Spauligodon oxkutzcabiensis	Parapharyngodon alvarengai	Oochoristica sp.	P-value
Physaloptera lutzi	1								
Physaloptera retusa	0.150	1							0.502
Raillietiella mottae	0.098	0.074	1						0.568
Strongyluris oscari	0.059	0.032	0.064	1					0.763
Parapharyngodon cesarpintoi	−0.126	−0.042	−0.014	−0.119	1				0.092
Spauligodon oxkutzcabiensis	−0.076	−0.027	0.099	−0.075	−0.132	1			0.112
Parapharyngodon alvarengai	0.324	0.157	0.087	0.211	−0.230	−0.118	1		**0.0001**
Oochoristica sp.	0.003	0.016	0.025	0.066	0.076	−0.024	0.015	1	0.610

Table 4. Similarity between the lizard species grouped according to the composition of the endoparasites fauna, using the Bray–Curtis index.

	Ameivula ocellifera	Gymnodactylus geckoides	Phyllopezus pollicaris	Tropidurus hispidus	Tropidurus semitaeniatus
Ameivula ocellifera	1				
Gymnodactylus geckoides	0.022	1			
Phyllopezus pollicaris	0.025	0.073	1		
Tropidurus hispidus	0.044	0.207	0.064	1	
Tropidurus semitaeniatus	0.036	0.191	0.047	0.567	1

Table 5. Berger–Parker dominance index and Kruskal–Wallis test (H = 19.67; GL = 11) corresponding to variation in dominance within each host species. Statistically significant *p*-value (bold).

Host	P. lu	P. re	R. mo	St. os	Ph. ce	Sp. ox	Pir. sp	Pa. al	Ooc. sp	E. pa	Oli. sp	Tri. sp	P-value
(Am. oc)	0.3	0.1	0.4	0.1	96.7	0.3	0.3	0.4	0.7	0	0.3	0	**0.012**
(Ac. me)	0	0	20.4	0	0	73.1	1	2.1	3.2	0	0	0	0.340
(Aa. am)	1.7	0	0	0	90.2	0	0	5.3	2.6	0	0	0	0.601
(G. ge)	3.4	0	6.1	2.4	0	20.2	2.7	64.6	0	0	0.2	0	**0.005**
(L. kl)	75	0	2.5	5	7.5	2.5	2.5	5	0	0	0	0	0.780
(B. he)	0	0	0	0	0	0	0	75.5	24.4	0	0	0	**0.001**
(P. po)	0	0	0.9	0	2.6	94.7	0	1.1	0	0	0.2	0.1	**0.007**
(T. hi)	30.2	4.6	6.6	13.3	2.7	9.7	2.1	29	0.7	0.5	0	0.1	**0.004**
(T. se)	0.6	0.2	0.5	53.4	3.2	0.03	0.07	38.1	3.5	0	0.07	0.03	**0.008**
(T. me)	0	6.2	0	0	93.7	0	0	0	0	0	0	0	0.530
(V. mu)	20	0	40	0	20	6.6	0	13.3	0	0	0	0	0.360

Lizards: *Am. oc, Ameivula ocellifera*; *Ac. me, Acratosaura mentalis*; *Aa. am, Ameiva*; *G. ge, Gymnodactylus geckkoides*; *L. kl, Ligodactylus klugei*; *B. he, Brasiliscincus heathi*; *P. po, Phyllopezus pollicaris*; *T. hi, Tropidurus hispidus*; *T. se, T. semitaeniatus*; *T. me, Tupinambis merianae*; *V. mu, Vanzosaura multiscutata*. Endoparasites: *P. lu, Physaloptera lutzi*; *P. re, P. retusa*; *R. mo, Raillietiella mottae*; *St. os, Strongyluris oscari*; *Ph. ce, Pharyngodon cesarpintoi*; *Sp. ox, Spauligodon oxkutzcabiensis*; *Pir.* sp, *Piratuba* sp.; *Pa. al, Parapharyngodon alvarengai*; *Ooc.* sp, *Oochorystica* sp.; *E. pa, Euparadistomum paraenses*; *Oli.* sp, *Olygachantharynchus* sp.; *Tri. sp, Trichospirura* sp.

et al., 2018; Ribeiro *et al.*, 2018). Individual susceptibility, food specificity and variability with regard to exposure to infective parasitic forms are responsible for the distribution of parasites among hosts (Anderson & May, 1979; Anderson & Gordon, 1982). Heteroxenic endoparasites have higher discrepancy values than monoxenic species; and infective forms can occur in environmental 'pockets' and accumulate in individuals used as intermediate hosts, which may contribute to the aggregation of endoparasitic populations (Anderson & May, 1979; Anderson & Gordon, 1982).

Anjos *et al.* (2012) identified depauperate fauna dominated by generalist endoparasites in *T. hispidus* and determined intermediate values of discrepancy (D = 0.51) in Caatinga areas in Ceará (CE) state. Ribeiro *et al.* (2012) determined that discrepancy values were high for the nematode genus, *Rhabdias* sp. (D = 0.83), in a population of the *Anolis brasiliensis* lizard species in the same area. Cabral *et al.* (2018) determined that values of discrepancy were high for *P. alvarengai* (0.68), *Physalopteroides venacioi* (0.97), *Physaloptera* sp. (0.98) and *Strongyluris oscari* (0.98) nematodes associated with the *Mabuya arajara* lizard species in the humid forest within the Araripe Plateau (as 'brejo de altitude'), CE.

In the Atlantic Forest, the nematode species *S. oscari* and *Oswaldocruzia burseyi* exhibited intermediate discrepancy values (D = 0.57 and D = 0.62, respectively), which were associated with the population of the lizard, *Enyalius perditus*, in the state of Minas Gerais (Barreto-Lima *et al.*, 2012). For teiid lizards in the Amazon region, Macedo *et al.* (2017) found determined intermediate (D = 0.52) to high (D = 0.92) discrepancy values for endoparasitic nematodes. In addition to aggregation, we determined that average abundance strongly influenced the number of endoparasites per host observed, and determined the variance of samples (fig. 1). Due to the nature of the parasite/host relationship, an interpretation of these values can clarify aspects of the acquisition and establishment of infrapopulations (Shaw & Dobson, 1995).

Infrapopulations may be directly influenced by host species and, thus, be distributed according to their genetic predisposition (Schad & Anderson, 1985; Quinnell, 2003), immune response (Galvani, 2003) and duration of exposure of the host to infective forms (Gordon & Rau, 1982). As a result, older hosts tend to be more highly infected than juvenile hosts, which may result in higher mortality rates within the age category (Rousset *et al.*, 1996).

Small differences in the niche occupied by individuals from the same population facilitate the occurrence of encounters different from the infective forms present in the environment (Janovy & Kutish, 1988), thus increasing the aggregate pattern of infection with parasitic species. Lizard populations may exhibit individual variations with respect to niche use, especially in communities that have few species (Costa et al., 2008); unfortunately, there is a lack of knowledge regarding subpopulation distributions in lizard hosts, making it difficult to compare and understand the distribution patterns of parasites.

Regarding the pseudo community analysis, for parasite species, assemblages are likely structured as a result of nesting (González & Oliva, 2009), temporal variation (Krasnov et al., 2006) and aggregation (Leung, 1998). However, there have also been reports of assemblages of various groups of hosts including fish, amphibians, birds and mammals with no apparent structure (Gotelli & Rohde, 2002; González & Oliva, 2009; Ulrich & Gotelli 2010, 2013; Delfino et al., 2011; Lacerda et al., 2013).

According to our model, host infection occurs randomly, and endoparasite occurrence is randomly distributed across hosts. When intraspecific interactions between endoparasites does not significantly shape the component community, it does not differ significantly from the community predicted by the null model (Poulin, 1996). Communities composed of few species or those that are generalists are typically not structured (Gotelli & Rohde, 2002; González & Oliva, 2009). With regard to lizards, especially those living in Caatinga environments, few endoparasite species are specific to lizard hosts, such as the nematodes Ozolaimus cirratus and O. megatyphlon. Alaeuris caudatus and A. vogelsangi are, however, specific parasites of iguanas, and Gynaecometra bahiensis specifically parasitizes Polychrus acutirostris. These specificities are probably related to arboreal habits and the herbivorous and omnivorous diets of hosts, respectively (Ávila & Silva, 2010; Araujo Filho et al., 2014; Teles et al., 2017).

The resources sought by parasites may occur in hosts of distinct taxa, which may contribute to the formation of random communities. This does not necessarily indicate a low degree of richness, competitive exclusion or lack of interaction among species (Brooks et al., 2006). For the Caatinga domain, historical and ecological factors, and seasonality and geographic variations have a greater influence on the establishment of endoparasite communities (Brito et al., 2014a, b; Araujo Filho et al., 2017; Lima et al., 2017; Teixeira et al., 2017; Teles et al., 2017).

According to Jaenike (1996), to understand the effects of variance on average abundance, the following premise must be considered: (1) the parasite has the ability to regulate host fitness; and (2) average abundance depends on parasite frequency within the host population. Thus, the greater the degree of parasite aggregation, the greater the fitness of the host population. If the degree of aggregation is low, the fitness of the host population is also low (Shostak & Dick, 1987; Jaenike, 1996). Similarly, aggregation is associated with increased fitness of the parasite population.

In contrast, aggregation can facilitate meeting potential partners for reproduction. Heavily infected hosts may have high mortality rates (Adjei et al., 1986), compromising the maintenance of infrapopulations (provided the life cycle of the species does not depend on the death of its host). The restriction of variance on the average abundance of parasitic species provides a balance between aggregation and infrapopulation viability, which can be evolutionarily established (Wilson et al., 2002). This mechanism may be especially prominent in parasitic species and may be

one of the primary ecological forces shaping infrapopulation distribution (Shaw & Dobson, 1995; Lagrue et al., 2015). This association has been found in several studies of aggregated populations of parasites (Anderson & Gordon, 1982; Shaw & Dobson, 1995; Wilson et al., 2002; Poulin, 2013).

It is widely accepted that variance dominated by the mean indicates that there is a restriction in the level of aggregation within a population. This results in a trade-off between a high degree of aggregation of endoparasites, which can cause high mortality rates in their hosts (Rousset et al., 1996), and low levels of aggregation, which may cause difficulties in finding partners for reproduction. As a result, populations of parasites are produced that have optimal levels of aggregation (Poulin, 2007). We found that 98% of the variance observed was explained by mean abundance, a value that was unexpectedly high. Shaw & Dobson (1995) reviewed the relationship between mean variance and abundance in 269 populations of hosts (amphibians, birds and mammals) and found that 87% of observed variance is related to average abundance. However, there was a lack of research on reptiles, especially in semiarid areas, so comparisons with this work are not straightforward.

In the endoparasitic species P. lutzi and P. retusa, a positive correlation between abundance and the use of intermediate and definitive hosts was observed (Anderson, 2000). Parapharyngodon alvarengai was positively correlated with P. lutzi, P. retusa and S. oscari species. Pharyngodon cesarpintoi and S. oxkutzcabiensis exhibited a negative (or low degree of) correlation with all other species. These species may be considered generalist when infecting lizards, but their abundance and prevalence were greater in teiid and gecko hosts, respectively (Ávila & Silva, 2010; Brito et al., 2014a; Lima et al., 2017). Taxonomic proximity and life cycle may contribute to associations found; however, competition, density-dependence and use of resources by endoparasites may also be important, but these features are difficult to measure in natural populations. Nevertheless, P. alvarengai was the only species that presented a statistically significant association with the other species. This relationship was likely enhanced by the generalist habit and monoxenic cycle of P. alvarengai. The species has been present in nearly all studies that have included lizards of South America (Ávila & Silva, 2010; Brito et al., 2014a; Galdino et al., 2014).

The hosts of endoparasite species that were most similar were T. hispidus and T. semitaeniatus. In addition to their taxonomic proximity, these species shared similar microhabitats and diets (Rodrigues, 2003; Gomes et al., 2015). Gimnodactylus geckoides was similar to tropidurids, and is a species with general foraging habits, which may contribute to the similarities between the endoparasites observed (Rodrigues, 2003). These species are commonly associated with rocky areas, and have general diets (Rodrigues, 2003; Gomes et al., 2015). The use of similar habitats and consumption of similar diets may contribute to similarities observed in the composition of endoparasite species (Hamann et al., 2006; Brito et al., 2014b).

There was significant variation observed regarding the dominance of endoparasites among host species, as well as within each host species. For the component community present in A. ocellifera, dominance was determined by the pharyngodonid, P. cesarpintoi. This endoparasite genus is widely dispersed in South America, and infects several families of lizards, notably infecting Teiidae (Ávila & Silva, 2010). In G. geckoides and B. heathi, the nematode P. alvarengai was the dominant species. Along with other pharyngodonids, P. alvarengai has a monoxenic cycle and

is commonly found in generalist lizards (Ávila *et al.*, 2012, Brito *et al.*, 2014a).

Within the host species *P. pollicaris*, the nematode *S. oxkutzcabiensis* was dominant. The nematode has been frequently associated with lizards (Gekkota) in several environments of South America (Ávila & Silva, 2010), including semiarid regions (Brito *et al.*, 2014a, b; Lima *et al.*, 2017). The generalist lizard *T. hispidus* had the greatest number of associated endoparasites in this study. The species is widely dispersed in Caatinga areas and its habitat use and diet is variable (Rodrigues, 2003). The heteroxenic nematode *P. lutzi* was the dominant species in the infracommunity of this host. *Physaloptera* sp. are often associated with carnivorous lizards (Bursey *et al.*, 2005; Ávila & Silva, 2010; Brito *et al.*, 2014a; Lima *et al.*, 2017). The component community of the tropidurid, *T. semitaeniatus*, is primarily composed of the nematode *S. oscari*, which infects a wide range of hosts from different families in South America (Ávila & Silva, 2010).

To the best of our knowledge, this is the first study to evaluate the influence of average abundance on endoparasitic variance in semiarid areas, and our results indicate that endoparasite infrapopulation variance are highly restricted by average abundance per host values. Further, the structure of the component community regarding the use of host species is random.

Environments that are subjected to large seasonal variations have high parasite aggregation values, because species can synchronize the release of infective forms according to season, which may contribute to increased levels of infection and aggregation (Sherrard-Smith *et al.*, 2015). In contrast, parasite populations that are highly interactive (e.g. occupy the same site of infection) tend to be more strongly regulated by average abundance (Bottomley *et al.*, 2005). These assumptions may be especially true for lizard hosts in semiarid regions, and their effects in other groups of hosts should be assessed.

Conflicts of interest. None.

Ethical standards. All authors gave their consent to participation in the study. The study was approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) with permission to collect the animals.

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