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How epidemiological patterns shift across populations in an exotic lizard

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Research Paper

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Abstract

Several factors influence the dynamics and structure of parasite communities. Our goal was to investigate how the community composition, prevalence and abundance of parasites change across seven populations of the exotic lizard *Hemidactylus mabouia* in Northeast Brazil, and to describe ontogenetic and sex variations. We found differences in the composition of component communities and patterns of infection according to the host body size across the lizard populations. We did not find any variation between the sexes regarding epidemiological patterns, which can probably be explained by the similar diet and habitat use of male and female *H. mabouia*. An unusually high abundance and prevalence of trematodes infecting this host lizard was apparent when we compared other native lizard hosts, and we suggest that local environmental conditions might be advantageous to the development and life cycle of these parasites due to the abundance of all the intermediate and definitive hosts.

Introduction

Parasites are recognized as having important roles in ecological and evolutionary host dynamics (Gregory & Keymer, 1989; Poulin, 1997), and the investigation of factors influencing the dynamics and structures of parasite communities is central to host ecology research. For example, it is helpful to understand the spatial distribution of parasites for the study of host extinction, emerging diseases, biological invasions and climate changes (Morand & Krasnov, 2010). Because parasites are recognized as fundamental factors effecting the dynamics and structure of diversity within wild communities, assessing the composition and epidemiology of parasite communities is essential for conservation management (Fournié *et al.*, 2015), as well as understanding their influence on native fauna or invasive species.

Several factors influence the dynamics and structure of parasite communities. These factors can be associated with the environment (e.g. climatic seasonality and environmental heterogeneity) or with the host (e.g. size, sex, diet and behaviour) (Aho, 1990). Sex differences in infection patterns can be due to ecological (morphology and behaviour) or physiological (hormonal or immune) factors (Zuk & McKean, 1996), such as when males and females have differential exposure to pathogens because they have different foraging rates. Ontogenetic differences in infection levels and richness are expected because they can be related to differences in physiology, behaviour, habitat or diet between juveniles and adults (Poulin, 1997). In this sense, patterns of infection (e.g. abundance and prevalence) can be influenced by complex interactions between local abiotic and biotic proprieties (Pope *et al.*, 2005; Borer *et al.*, 2010; Moore & Borer, 2012).

Parasites that inhabit exotic species may originate from the exotic species' native habitat or from its current location through interaction with native hosts. Exotic species have, on average, a lower parasite richness and are less heavily parasitized than native populations, a result of the reduced probability of parasite introduction through exotic species, the absence of intermediate hosts and the host-specific limitations on native parasites adaptions to new hosts (Torchin *et al.*, 2003); and this reduction in natural parasites aids the successful invasion by the exotic species. In addition, invasive species can potentially influence native parasite dynamics by altering ecological interactions in two ways: by disease facilitation, when the exotic species increases the infection of native hosts by parasites, or by suppressive spill-over, when the parasite suppresses the ability of the exotic species to expand and, thus, becomes invasive (Chalkowski *et al.*, 2018).

Despite recent studies on the neotropical helminthic fauna of lizards (Ávila & Silva, 2013; Barreto-Lima *et al.*, 2011), our knowledge of the ecological aspects of host–parasite relationships remains scarce, as most of these studies simply listed the species and their hosts. *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Squamata, Gekkonidae) is a lizard species

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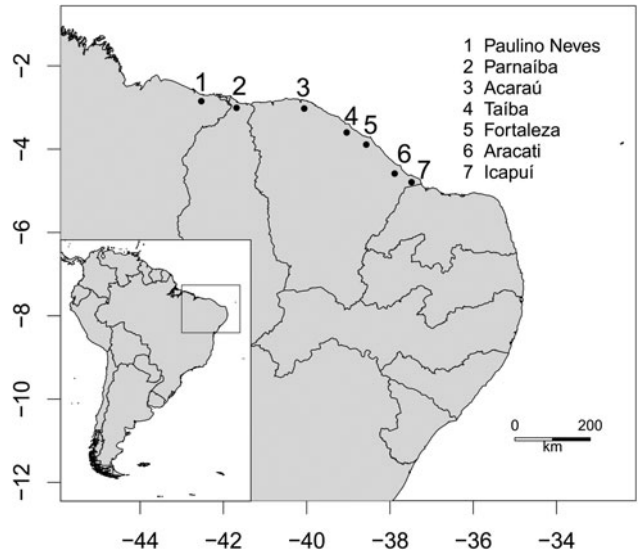


Fig. 1. Sampling map of *Hemidactylus mabouia* in Northeast Brazil.

native to and widely distributed throughout Africa (Carranza & Arnold, 2006), but it is an exotic invader that has become well established in anthropic environments of America (Baldo *et al.*, 2008; Rocha *et al.*, 2011). Aspects of its ecology have been thoroughly described (Vitt, 1995; Rocha & Anjos, 2007; Anjos & Rocha, 2008), as have its parasites (Anjos *et al.*, 2005; Ávila & Silva, 2013; Harris *et al.*, 2015). Rocha *et al.* (2011) raised concerns about *H. mabouia* as an invasive species in Brazil, since it is sometimes found in natural environments and could possibly compete with native gekkonids species. However, we generally consider each urban aggregation of *H. mabouia* as a separate population, as they do not have a continuous distribution among cities and natural environments. Additionally, because this lizard species has a wide distribution, its relative abundance and several ecological aspects are well understood, and it is considered a good model organism for ecological studies. In this way, understanding host–parasite interactions and epidemiological patterns across the different *H. mabouia* populations can help with studies of interactions with native species to reveal the stability of this species in Brazil.

In this study, our goal was to investigate spatial variations in the composition and epidemiological levels of infection by helminth parasites in seven populations of *H. mabouia* in Northeast Brazil, and to describe the ontogenetic and sex variations within these epidemiological patterns.

Materials and methods

We collected lizards from seven urban sites on the north-eastern coast of Brazil (fig. 1) during the wet season, between March and June 2013. The linear distances between the collection sites varied from 48 to 619 km. This study area is a biogeographically complex region, with vegetal species from several Brazilian biomes, including Caatinga (xerophytic vegetation), Cerrado (savanna-like vegetation), Atlantic and Amazon rainforests and vegetation from a 'resting' ecosystem, typical of the Brazilian coast (Ab'Sáber, 2001; Moro *et al.*, 2015). Annual rainfall ranges from 986 to 1222 mm/year, and average temperatures range from 26 to 27.5°C across all collection sites (Santos-Filho, 2009; Oliveira & Frota, 2011; Castro *et al.*, 2012). We collected lizards manually or with a rubber band (an elastic strip manually fired at a target), between 18:00 and 05:00 h. Individuals were anesthetized with ketamine and euthanized with potassium chloride (AVMA, 2013). The lizards were fixed in 10% formaldehyde, preserved in 70% alcohol and deposited in the 'Coleção de Herpetologia da Universidade Federal do Ceará'.

To obtain parasites, we dissected the lizards and inspected their organs (stomach, intestines, lungs, liver, gall bladder and body cavity) for endoparasites. We removed the parasites and preserved them in 70% ethanol. We then identified the helminths and pentastomids and deposited them in 'Coleção Helmintológica do Departamento de Parasitologia do Instituto de Biociências of Unesp, Campus de Botucatu'. We measured the snout-vent length (SVL) of the lizards using digital callipers (0.01 mm of precision) and evaluated the sex by inspecting the gonads. We used the parasite ecology terms from Bush *et al.* (1997).

We used generalized linear models (GLMs) to test differences in prevalence (using binomial distribution) and intensity of infection (using Poisson distribution) related to size (SVL), sex and sites, using the most frequent parasite species found at all sampling sites. In these analyses, we only used the host individuals if we could assess the sex. We used GLM (using negative binomial distribution) to test if parasite richness correlated with host size (SVL). To test the differences in the composition of component communities between sites and differences in the composition of males and females, we performed a permutational multivariate analysis of variance (PERMANOVA) test (with 1000 permutations). We analysed the variables using a significance level of $P < 0.05$. Analyses were conducted in R program (R Development Core Team, 2018) using MASS and Vegan packages.

Results

We collected 227 specimens of *H. mabouia* from the seven sites across the north-eastern coast of Brazil, in which we found one pentastomid and nine helminth species, including one Acanthocephala, two trematodes, three cestodes and three nematodes (table 1). Despite recognizing two species of digenetic trematodes, we could not quantify all specimens due to methodological issues, and they were referred to as Digenea. The nematode *Parapharyngodon alvarengai* was the most prevalent helminth, present in 32.15% of individuals, and Digenea was the most abundant taxa, with a mean intensity of 9.3 trematodes per host, representing 63.9% of all helminth specimens collected (table 1). *Parapharyngodon alvarengai* was the only helminth species found at all the sampling sites, so we used this species to test the host–parasite epidemiological relationships for sex, size and geographic variations.

The component communities from each population of the host *H. mabouia* were slightly different in composition (PERMANOVA: $F = 1.78$; $R^2 = 0.09$; $P = 0.008$). The intensity of infection in *P. alvarengai* varied across sites, but the prevalence was similar (table 2 and fig. 2). In these analyses, we excluded the host individuals if we were not able to identify the sex, which was usually the case in very young specimens. Host size positively correlated with the prevalence and intensity of infection in *P. alvarengai* and with endoparasite richness (table 2 and fig. 3). Sex did not influence the composition of the parasite component communities (PERMANOVA: $F = 0.911$; $R^2 = 0.008$;

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Table 1. Parasite species of the lizard host *Hemidactylus mabouia*.

Species	Site	*P* (%) (range)	MII ± SD (range)	IS
NEMATODA				
Parapharyngodon alvarengai (Freitas, 1956)	All	32.15 (23.3–41)	2.43 ± 2.15 (1–11)	SI, LI
Physaloptera retusa (Rud, 1819)	1, 3, 4, 5, 7	6.16 (5–21.8)	3.21 ± 4.21 (1–10)	S, SI, LI
Skrjabinodon sp. (Inglis, 1968)	5	1.32 (7.6)	11.33 ± 1.19 (1–30)	LI
TREMATODA				
Digenea: *Platynosomum* sp. (Looss, 1907) and *Paradistomum* sp. (Kossack, 1910)	All	31.71 (15.6–46.6)	9.4 ± 11.78 (1–59)	GB, SI, BC
CESTODA				
Oochoristica sp. (Lühe, 1898)	1, 2, 3, 4, 5, 7	6.16 (3.2–11.7)	1.28 ± 2.75 (1–5)	SI
Plerocercoid larvae	3, 5, 6, 7	2.2 (2.5–6.4)	6.4 ± 8.53 (1–21)	BC, LI
Proteocephalidae (La Rue, 1911)	3	0.88 (6.4)	1 ± 0 (1)	SI
ACANTHOCEPHALA				
Centrorhynchidae (larvae) (Van Cleave, 1916)	1, 2	1.76 (3.3–10)	3.75 ± 1.7 (2–6)	BC
PENTASTOMIDA				
Raillietiella frenatus (Ali *et al*., 1981)	1, 3, 5	3.96 (2.5–20)	3.33 ± 3.5 (1–11)	LU

Collection sites: (1) Paulino Neves ($n = 30$); (2) Parnaíba ($n = 30$); (3) Acaraú ($n = 31$); (4) Taíba, São Gonçalo ($n = 34$); (5) Fortaleza ($n = 39$); (6) Aracati ($n = 31$); (7) Icapuí ($n = 32$). *P*, prevalence (for all sampled specimens from all sites) and the range among populations; MII, mean intensity of infection; SD, standard deviation; IS, infection sites; S, stomach; SI, small intestine; LI, large intestine; BC, body cavity; LU, lung; LI, liver; GB, gall bladder.

Table 2. GLM analysis results, which we used as predictors of the prevalence and intensity of infection of the most abundant and frequent parasite species found in the host, *Hemidactylus mabouia*, across all populations (*Parapharyngodon alvarengai*) and, as response variables, the size (SVL, snout-vent length), sex and collection site of the host.

Predictor and variables	df	*P*-value	Distribution family
Prevalence of *P. alvarengai*			Binomial
SVL	162	**<0.001**	
Sites	156	0.768	
Sex	155	0.468	
Intensity of *P. alvarengai*			Poisson
SVL	162	**<0.001**	
Sites	156	**0.003**	
Sex	155	0.109	
Parasite richness			Negative binomial
SVL	223	**<0.001**	
Sites	217	0.591	

The last GLM result shows parasite richness as predictor variable and SVL as response.

$P = 0.45$), the prevalence or intensity of infection in *P. alvarengai* (table 2).

Discussion

Lizards are hosts for several helminth species in Neotropical areas (Ávila & Silva, 2013), and the host populations investigated in this study had endoparasite component communities of three to seven species. All the parasites can also be found in native host lizards (Ávila & Silva, 2013), except for *Raillietiella frenatus*, which probably came with this exotic host from its native habitat (Anjos *et al*., 2008). We found variations in the richness and composition of the component parasite communities, which may be associated with the level of anthropic impact between the sampled sites because, although the host *H. mabouia* may be a characteristic anthropic species, this parasitic fauna is common to other regional lizard species (Ávila & Silva, 2013). As a result, an area with a low diversity of lizard fauna, such as large urban environments, will probably be accompanied by a poor diversity of parasite fauna, affecting the richness of component communities of all remaining host species.

A few studies have been published on the biogeography of parasitism in wildlife, and these indicate that variation in parasite abundance across space is determined mainly by local-scale biotic and abiotic attributes (Blasco-Costa *et al*., 2015; Fournié *et al*., 2015). Both the prevalence and intensity of infection in *H. mabouia* increase with body size, but we found the correlation with intensity can change between populations, indicating that local environmental conditions or intrinsic properties of the host population and community influence the parasite composition and epidemiological patterns of infection (Borer *et al*., 2010; Seabloom *et al*., 2010). In fact, local host diversity can reduce the risk of infection and disease, and consecutively drive the host community structure (Halliday *et al*., 2018), as well as reduce the abundance of some parasites (Civitello *et al*., 2015). In this way, differences in parasite abundance and richness between host populations investigated in this study might reflect the local host diversity, which can vary depending on the size of the city and the degree of separation between green areas and, therefore, other lizard species. Small cities, like Paulino Neves, can have a high parasite richness because the contact between *H. mabouia* with native lizards is more frequent, as there are green areas close to the anthropic buildings where the exotic host *H. mabouia* live. On the other hand, big cities like

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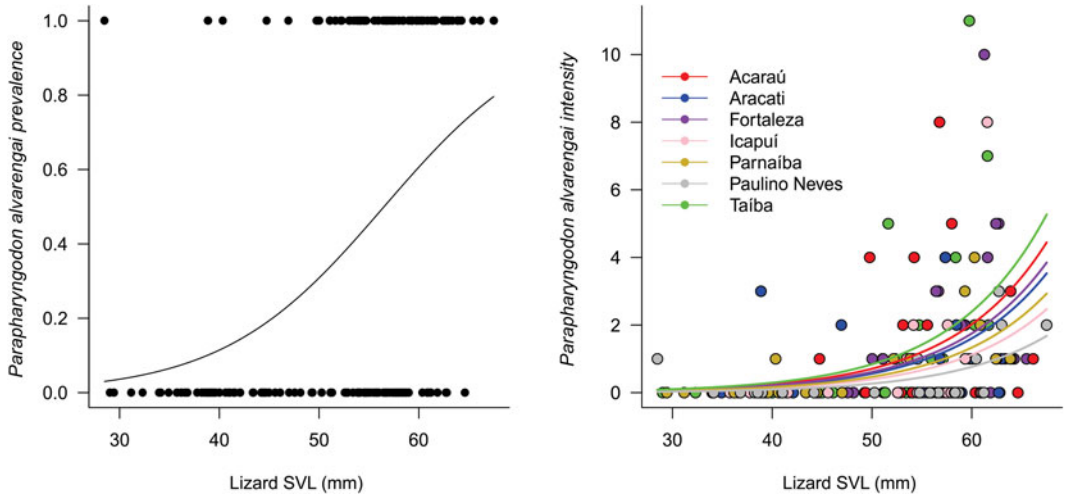


Fig. 2. Prevalence and intensity of infection of the most common parasite found in the host, *Hemidactylus mabouia*, and their relation to host size (SVL, snout vent length) in the seven sampled sites. Prevalence was similar between sites; however, the intensity relationships differed, representing the relationships of parasite intensity with the different host sizes at the sites.

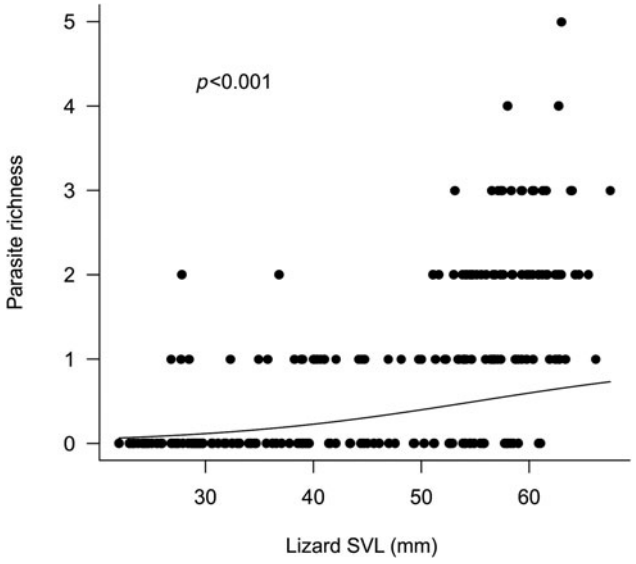


Fig. 3. Relation between the number of endoparasite species (richness) and host size (SVL, snout-vent length) in the lizard, *Hemidactylus mabouia*, showing an increase of richness with size.

Aracati may have many anthropic buildings very distant from natural environments, hampering the transmission of parasites between the exotic and native lizards. Despite it being the largest city, Fortaleza can be considered an exception because the lizards were captured in an area very close to residual native forest, which enables interactions with native fauna and harbours a richness of parasite species.

We found similar compositions and epidemiological levels of infection in male and female lizards. Sex differences in epidemiological levels are expected, due to the physiological, behavioural or life history differences between males and females, which may affect immune responses and the probabilities of being infected throughout life (Vogel & Bundy, 1987; Zuk & McKean, 1996). For example, many parasite species with indirect life cycles are transmitted to their hosts through feeding; therefore, we can expect variations in the parasite species and levels of infection in host species with trophic sexual dimorphism. In our study, most of the parasite species infect their host via their food; however, there are no differences between females and males regarding diet or habitat (unpublished data), which explains why males and females had similar parasite communities and levels of infection.

We found that lizard body size positively correlated with endoparasite richness. This is in line with results from other populations of *H. mabouia* (Anjos *et al.*, 2005) and for other animal species (Aho, 1990; Barreto-Lima *et al.*, 2011), in which larger individuals had a higher probability of being infected, more parasite species and a greater abundance of parasites. Differences in body size can reflect ontogenetic differences in physiology, behaviour, habitat or diet, affecting the ways the hosts come in contact with the parasites, and a larger host has a higher chance of becoming parasitized in its lifetime (Poulin, 1997). Moreover, the Island Biogeography Theory (MacArthur & Wilson, 1967) proposed that larger islands shelter more richness than smaller ones and, if we think of the hosts as islands for the parasites (Kuris *et al.*, 1980), a larger host provides more space and can support more parasite species.

An unusual outcome of our investigation was the frequent and abundant presence of the trematodes *Platynosomum* sp. and *Paradistomum* sp. (Digenea group). This group of parasites was not found in other studied populations of *H. mabouia* in Brazil (Anjos *et al.*, 2005; Ávila *et al.*, 2012; Sousa *et al.*, 2014), despite Pinto *et al.* (2014) describing this lizard as part of the life cycle of *Platynosomum illiciens*, for which domestic cats are the main definitive hosts. These felids are common predators of *H. mabouia* and can carry high levels of infection in anthropic environments. Braga *et al.* (2016) found a 42.5% prevalence and intensity of 1–219 for the trematode in these felids in Fortaleza city, one of the sampling sites in the present study. However, there is no recorded data of digenetic trematodes in sympatric lizards of *H. mabouia* or in other populations of this species in north-eastern regions of Brazil (Anjos *et al.*, 2005; Ávila *et al.*, 2012; Bezerra *et al.*, 2015; Galdino *et al.*, 2014; Sousa *et al.*, 2014). Some Brazilian lizard species that harbour these trematode species contain a prevalence of between 7% and 28%, and intensities range from 1 to 25 (Vrcibradic *et al.*, 2002; Ávila & Silva, 2013),

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which is lower than what we observed in our study. The high prevalence and intensity in our data can be explained by conditions of temperature and humidity favourable to both intermediated hosts (molluscs and crustaceans) and metacercaria trematodes (Chai, 2014), as well as by the high number of abandoned domestic cats in urban sites, resulting in high levels of infection of both cats and *H. mabouia*. For these hosts, the high rate of infection can result in a disease-like thickening of the bile duct, mixed inflammatory infiltrate and ductal proliferation (Braga *et al.*, 2016), which was observed in our study, indicating an unbalanced host–parasite relationship – possibly due to the short time available for evolution with these parasites (Tizard, 2004).

Invasive species can be susceptible to native parasites, which can affect their establishment or expansion range. Barnett *et al.* (2018) found a native parasite that may reduce the survival of individuals of the congeneric host *Hemidactylus frenatus* in an Asian house gecko that had been accidentally introduced to many tropical and subtropical areas. In some places, such as Northern Australia, *H. frenatus* are spreading from urban areas into bushland (Hoskin, 2011). This is very similar to what was observed in Brazil for *H. mabouia*, which has a high abundance in urban areas but was also sometimes found invading natural environments (Rocha *et al.*, 2011). Further studies may help to elucidate if the high levels of infections by native parasites can interfere in the complete establishment of this exotic species in some areas of Brazil.

In the current study, we found that one species was more prevalent and abundant in all populations evaluated, but the levels of infection varied according to host size among sites. We did not find any variation in epidemiological patterns associated with sex, which is likely to be due to the similarity in diet and habitat use between male and female *H. mabouia*. Lastly, we found an unusually high abundance and prevalence of trematodes infecting *H. mabouia* and have included some hypotheses that may explain this anomaly.

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Conflicts of interest. None.

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