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Influence of temporal variation and host condition on helminth abundance in the lizard *Tropidurus hispidus* from north-eastern Brazil

J.A. Araujo Filho[1]*, S.V. Brito[2], V.F. Lima[1], A.M.A. Pereira[1], D.O. Mesquita[3], R.L. Albuquerque[4] and W.O. Almeida[2]

[1]Programa de Pós-graduação em Bioprospecção Molecular, Universidade Regional do Cariri – URCA, R. Cel Antônio Luis, 1161, Pimenta, CEP 63100-000, Crato, CE, Brazil: [2]Departamento de Química Biológica, Universidade Regional do Cariri – URCA, R. Cel. Antônio Luiz, 1161, Pimenta, CEP 63105-000, Crato, CE, Brazil: [3]Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, PB 58051-900, Brazil: [4]Department of Biology, University of California, Riverside, 900 University Avenue, Riverside 90521, California, USA

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Abstract

Ecological characteristics and environmental variation influence both host species composition and parasite abundance. Abiotic factors such as rainfall and temperature can improve parasite development and increase its reproduction rate. The comparison of these assemblages between different environments may give us a more refined analysis of how environment affects the variation of helminth parasite abundance. The aim of the present study was to evaluate how temporal variation, host size, sex and reproduction affect helminth abundance in the *Tropidurus hispidus* lizard in Caatinga, Restinga and Atlantic Forest environments. Overall, larger-sized lizards showed higher helminth abundance. We found a monthly variation in the helminth species abundance in all studied areas. In the Caatinga area, monoxenic and heteroxenic parasites were related to the rainy season and to the reproductive period of lizards. In Restinga, monoxenic and heteroxenic helminth species were more abundant during the driest months. In the Atlantic Forest, the rainy and host reproductive season occurred continuously throughout the year, so parasite abundance was relatively constant. Nevertheless, heteroxenic species were more abundant in this area. The present results showed that the temporal variation, body size, sex, reproductive period and habitat type influence the abundance and composition of helminth species in *T. hispidus*.

Introduction

Parasites can influence hosts in many ways by affecting their behaviour (Levri, 1999), reducing the male host's capability of fighting for female access, reducing testicle and clutch size (Schall & Dearing, 1987) and consequently changing their reproductive success (Dunlap & Schall, 1995). Changes in male colouration can also be caused by some parasites and identified by females, reducing their mating success (Dunlap & Schall, 1995).

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*E-mail: araujofilhoaj@gmail.com

The abundance of parasites in vertebrates may vary depending on the sex of the host; usually males have a higher parasite load, either due to behaviour (disputes over females and territory) or to physiological differences caused by different hormones, such as the presence of testosterone, which inhibits the immune system, favouring infection (Hamilton & Zuk, 1982; Folstad & Karter, 1992; Dunlap & Schall, 1995; Zuk & McKean, 1996).

Climatic factors affect host (Hawkins *et al.*, 2003) and parasite (Minguez & Giambérini, 2012) species distribution and survival in nature. Spatial and temporal variation play an important role in helminth species abundance and composition (Hamann *et al.*, 2006; Brito *et al.*, 2014a). Climatic variations can alter behavioural activity patterns and even the immune system of hosts, causing seasonal differences in parasite infections (Møller *et al.*, 2003). Some ecological studies show that climate can affect parasite composition and abundance even in phylogenetically distant hosts (Altizer *et al.*, 2006; Carvalho & Luque, 2011). Abiotic conditions, such as rainfall and temperature, can increase helminth parasite abundance (Griffiths *et al.*, 1998; Gambhir *et al.*, 2012). Rainfall can also affect environmental moisture, indirectly impacting developmental stages of the parasite larvae (Narayanan *et al.*, 1961).

Additionally, phylogenetic relations, ecological adaptation and habitat use can also influence the composition and abundance of parasite species in different environments (Bush *et al.*, 1990; Janovy *et al.*, 1992; Brooks *et al.*, 2006; Brito *et al.*, 2014b). Comparison of different parasite populations can reveal mechanisms of local adaptations to the environment and immune response of the host (Poulin, 1997; Poulin & Valtonen, 2001). According to Brito *et al.* (2014a, b), spatial and temporal variation and habitat use are crucial predictors of lizard parasite abundance in the semi-arid region of the Brazilian north-east. However, comparative studies of host populations are more common among fish, bird and mammal populations (Poulin *et al.*, 2010), while lizard populations and their parasites in the Neotropical region are still to be analysed.

Tropidurus lizards are found in both open areas and forests throughout South America (Frost *et al.*, 2001). *Tropidurus hispidus* (Spix, 1825) is a diurnal, abundant, sit-and-wait forager (Rodrigues, 1987) with an opportunistic feeding behaviour (Vitt, 1995). Its habitat use varies between the dry and rainy season (Kolodiuk *et al.*, 2009), and its diet changes according to prey availability (Gomes *et al.*, 2015), which can increase the chances of infection by different parasite species (Griffiths *et al.*, 1998).

Here we evaluate the effect of host condition (body size, sex and reproduction), abiotic variables and seasonality on the helminth species abundance and composition in *T. hispidus* lizards from Caatinga, Restinga and Atlantic Forest environments in north-eastern Brazil.

Materials and methods

Collection and examination of lizards

An average of ten adult lizards per month were captured in the areas of Caatinga (07°29′S, 36°20′W), Atlantic Forest (07°08′S, 34°50′W) and Restinga (6°17′S, 35°02′W) in the municipalities of Cabaceiras and João Pessoa in the state of Paraíba and in Barra do Cunhaú, Canguaretama municipality, Rio Grande do Norte state, respectively. Field trips were carried out from November 2010 to February 2012, covering at least a 12-month period for each area in order to observe seasonal variation and the effect of the reproduction period on the parasite abundance. Caatinga is a semi-arid area with low rainfall (250–800 mm/year), mostly concentrated between November and April (Nimer, 1989). The temperature varies between 22 and 26°C (Nimer, 1989). In the Atlantic Forest region there is continuous rainfall almost throughout the year, with an annual average of 1859 mm (IBGE, 1985). The temperature varies between 23 and 26°C. In the Restinga area, rainfall is concentrated between March and September, with an annual average of 1625 mm, and the temperature varies between 21 and 33°C (IDEMA, 2000).

Lizards were collected manually and sacrificed immediately after capture with a lethal dose of Thiopental®. Then, lizard snout–vent length (SVL) was measured with a metal ruler (to 0.1 cm), lizards were fixed with 10% formalin and deposited in 70% alcohol at the Herpetological Collection of the Federal University of Paraíba (CHUFPB). The lizards were dissected in the laboratory and their gonads were analysed to determine sex and sexual maturity. Males with developed testicles and epididymis with convolutions, and females with vitellogenic follicles in the ovaries and/or eggs in the oviducts, were considered reproductively active. The size at maturity of each sex and population was defined by the smallest reproductively active lizard.

Subsequently, helminth parasites from the body cavity, lungs and gastrointestinal tract of each lizard were collected under a stereomicroscope magnifying glass, deposited in the Parasitological Collection of the Regional University of Cariri (URCA-P), assembled on slides with lactophenol and later analysed by light microscopy. Parasite prevalence, intensity and abundance were calculated according to the specifications of Bush *et al.* (1997).

Data analysis

The General Linear Model was used (GLM) from Statistica software version 8.0 (StatSoft Inc., Tulsa, Oklahoma, USA), considering the Poisson distribution, to investigate the effect of seasonal variation on the parasite abundance in *T. hispidus* from the three studied environments and between sexes. Only the most prevalent helminth species (>5%) from adult hosts were considered, to avoid the influence of ontogenetic factors. Helminth species were classified according to their life cycle (monoxenic and heteroxenic), and whether the abundance of parasites varied seasonally according to their life cycle was analysed.

Two linear regressions were performed with Statistica software version 8.0 to evaluate the influence of the monthly proportion of reproductively active individuals on parasite prevalence, and to evaluate the effect of the SVL of the lizards on the abundance of helminths.

A Canonical Correspondence Analysis (CCA) coupled with 9999 random permutations was used throughout the Monte Carlo test using Canoco 4.5 (Ter Braak, 1986), to verify whether biotic and abiotic factors influence the abundance of helminth species in the lizards. We

Table 1. The prevalence (%) and intensity (I) of infection of helminth species in *T. hispidus* from three locations in Caatinga, Restinga and Atlantic Forest; ranges given in brackets.

	Location					
	Caatinga		Restinga		Atlantic Forest	
Helminth species	%	I	%	I	%	I
Cestoda						
Linstowiidae						
Oochoristica sp.	–	–	0.66	1 (1)	19.8	2 (1–8)
Nematoda						
Heterakidae						
S. oscari	–	–	3.33	1.6 (1)	40.4	6.4 (1–42)
Molineidae						
O. subauricularis	–	–	0.66	11 (11)	–	–
Pharyngodonidae						
P. alvarengai	2.32	2 (1–3)	6.66	4.6 (1–6)	8.08	3.2 (1–11)
Parapharyngodon sp.	34.88	4.7 (1–48)	50.66	6.1 (1–81)	32.35	4.4 (1–14)
P. verrucosus	3.87	4.6 (2–12)	4.66	12.4 (3)	9.5	5.6 (1–18)
Physalopteridae						
P. lutzi	46.51	5.9 (1–29)	67.33	17.2 (1–184)	81.61	10.8 (1–67)
Onchocercidae						
Piratuba sp.	3.1	7.2 (1–24)	–	–	–	–
Pentastomida						
Raillietiellidae						
R. mottae	–	–	0.66	1 (4)	–	–

considered the following abiotic factors: annual temperature, seasonal temperature, annual temperature amplitude, annual rainfall, rainfall in the wet months, rainfall in the dry months and the area of collection of the specimens (obtained from WordClim; Hijmans *et al.*, 2005). The biotic data used in the analyses were: SVL, sex, abundance and richness of parasite species. All of these variables were correlated to the abundance of helminth species found in the three studied environments.

Results

Four hundred and eleven lizards were collected (Restinga: 72 males and 77 females; Caatinga: 67 males and 61 females; Atlantic Forest: 54 males and 80 females). One Cestoda, one Pentastomida and seven Nematoda species were found. The helminth species were mostly those with an indirect life cycle: *Oochoristica* sp. (Luhe, 1898), infecting the stomach and intestine; *Strongyluris oscari* (Travassos, 1923), in intestine; *Physaloptera lutzi* (Cristofaro *et al.*, 1976), in stomach, intestine and lungs; *Piratuba* sp. (Freitas & Lent, 1947), in the body cavity; and *Raillietiella mottae* (Almeida *et al.*, 2008), in the lungs. Only *Parapharyngodon* sp. (Chartteji, 1933), infecting the stomach, intestine and lungs, *P. alvarengai* (Freitas, 1957) and *P. verrucosus* (Freitas & Dobbin, 1959), in the intestine, and *Oswaldocruzia subauricularis* (Travassos, 1917), in stomach, were monoxenic (see Riley, 1986; Anderson, 2000; Bush *et al.*, 2001). This was the first record of *Piratuba* sp., *P. verrucosus* and *O. subauricularis* infecting *T. hispidus* lizards (table 1).

Helminth composition and levels of infection

No sexual dimorphism was observed in SVL (Wald = 4.7, df = 2, $P > 0.09$), and the linear regression analysis revealed that helminth abundance is positively correlated with body size (table 2).

Table 2. Linear regression analysis between snout/vent length (SVL) of male and female *T. hispidus* from Caatinga, Restinga and Atlantic Forest and total abundance of helminth species.

Location						
Caatinga		Restinga		Atlantic Forest		
Male	Female	Male	Female	Male	Female	Regression analysis
12.21	6.55	8.97	10.2	25.81	13.05	F
0.14	0.13	0.11	0.10	0.31	0.13	R^2
0.0008	0.013	0.003	0.001	0.0005	0.0005	P

Table 3. General linear model to show the changes in the abundance of selected helminth species and the prevalence of infection higher than 5% in *T. hispidus* from the three locations of Caatinga, Restinga and Atlantic Forest.

Helminth species	Wald statistic	P
Parapharyngodon alvarengai	19.85	0.0004
Parapharyngodon sp.	106.24	0.0001
P. verrucosus	26.64	0.0002
Physaloptera lutzi	616.4	0.0001
Strongyluris oscari	119.1	0.0001
Oochoristica sp.	7.5	0.005

Lizards from the Restinga environment showed higher helminth parasite abundance (W = 716.6, GLM = 2, $P < 0.001$) and richness; the helminth species showed differences in abundance between the areas (table 3). Both the sampling period and lizard sex were correlated with

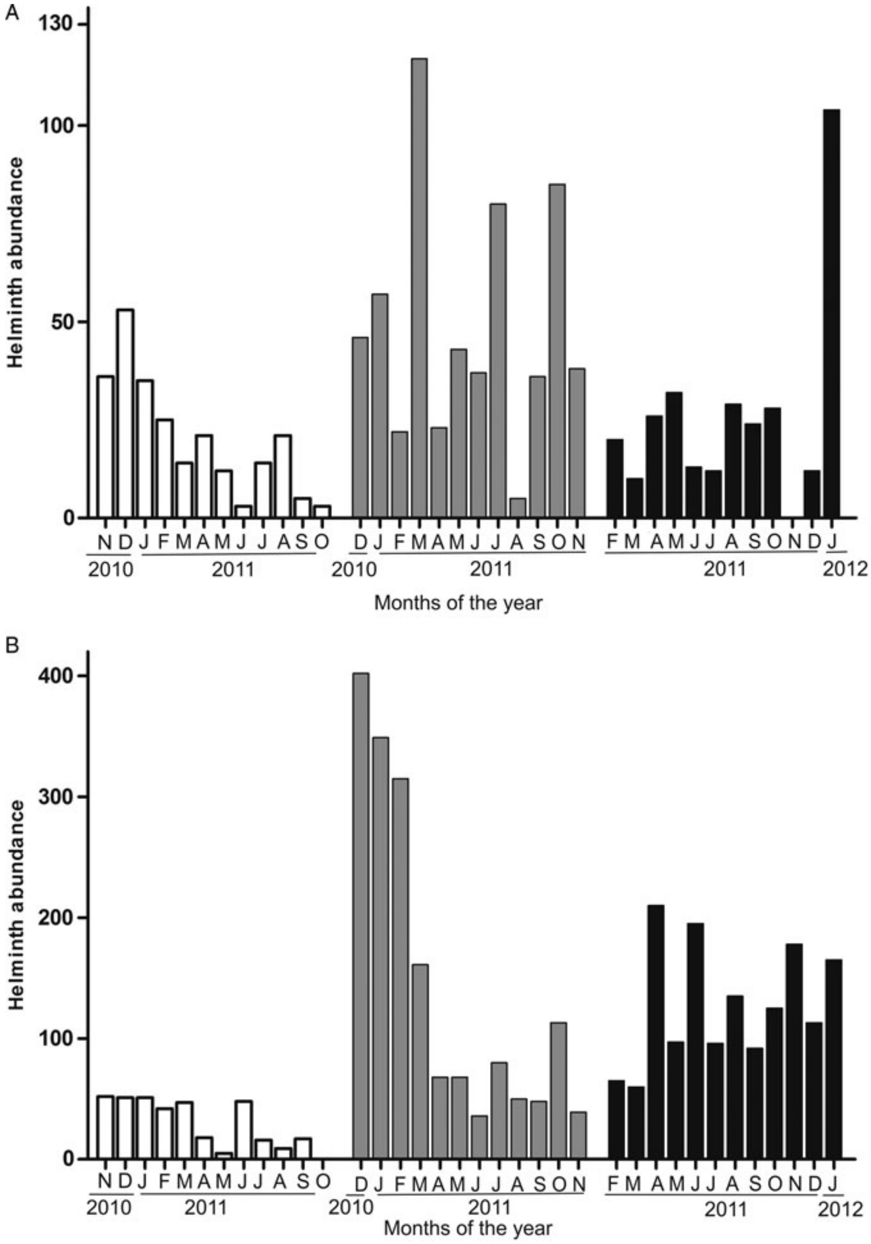

Fig. 1. Total monthly abundance of individuals of (A) monoxenous and (B) heteroxenous helminth species from the three locations Caatinga (white bars), Restinga (grey bars) and Atlantic Forest (black bars) from November 2010 to January 2012.

parasite abundance in the Restinga (month: $W = 519.32$; sex: $W = 9.42$; month/sex: $W = 285.34$, $GLM = 11$, $P < 0.001$) and Atlantic Forest areas (month: $W = 118.57$; sex: $W = 12.18$; month/sex: $W = 231.62$, $GLM = 11$, $P < 0.001$). Only *T. hispidus* from Caatinga did not show significant differences of infection by helminths between sexes (month: $W = 154.57$; sex: $W = 0.678$, $P > 0.4$; month/sex: $W = 90.27$, $GLM = 11$, $P < 0.001$). We also observed higher levels of infection for both males and females during the reproductive and rainy months (fig. 1). The proportion of individuals found in the reproductive period influenced the prevalence of parasites in the Caatinga ($F = 18.67$, $R^2 = 77.9$, $P < 0.02$) but not in the Restinga ($F = 0.3514$, $R^2 = -14.9$, $P > 0.05$) and Atlantic Forest ($F = 6.05$, $R^2 = 50.2$, $P > 0.06$) areas.

Biotic and abiotic conditions and life cycle

Biotic and abiotic factors significantly influenced helminth species abundance (first canonic axis; trace = 0.078; F ratio = 14.888; $P = 0.0001$). Similarly, canonical axes were

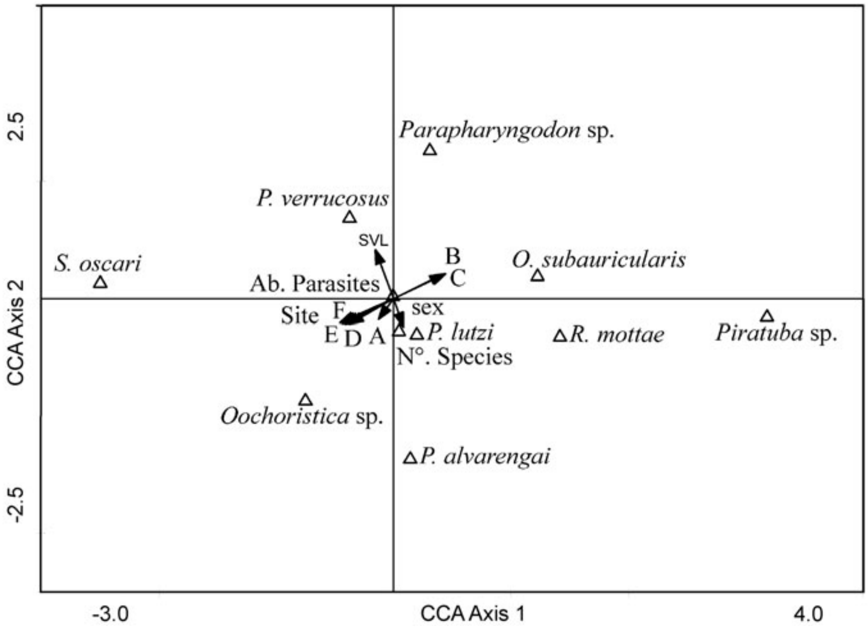

Fig. 2. Graphical representation of the Canonical Correspondence Analysis (CCA), to show abiotic and biotic characteristics (arrows) and helminth species (triangles) including general abundance and species richness in *Tropidurus hispidus*. Ab. Parasites, overall helminth abundance; SVL, snout–vent length; A, annual temperature; B, seasonal temperature; C, annual temperature amplitude; D, annual rainfall; E, rainfall in the wet months; and F, rainfall in the driest months.

significant (fig. 2) (trace = 0.150; *F* ratio = 7.490; $P = 0.0001$).

Oochoristica sp. abundance was related to the studied area (site), annual temperature (A), annual rainfall (D), rainfall in the wet months (E) and rainfall in the driest months (F). *Oswaldocruzia subauricularis* abundance was related to seasonal temperature (B) and annual temperature amplitude (C), while SVL was related to overall helminth abundance (Ab. Parasites) and *P. verrucosus* abundance. Species richness (N°. Species) and abundance of *P. lutzi* were related to lizard sex.

In Caatinga, helminth abundance peaked during rainy months (November to April) and monoxenic and heteroxenic species exhibited significant differences in their monthly abundance (fig. 1). This indicates that temporal variation and reproduction period affected the fluctuation of parasite species. The abundance of helminth species decreased in the driest months of the year. In Restinga, parasite abundance varied between species. Monoxenic and heteroxenic helminths were more abundant in the driest months (October to May) (fig. 1). In the Atlantic Forest, the abundance of helminth species with a prevalence greater than 5% was higher between April and November and, overall, heteroxenic species were more abundant than monoxenic species (fig. 1).

Discussion

The body size of the host is clearly one of the main influences in parasite populations (Poulin, 2004; Kamiya *et al.*, 2014). Other studies with *Tropidurus* lizards found a positive relationship between body size and the intensity of parasite infection (Anjos *et al.*, 2012; Pereira *et al.*, 2012). Corroborating the island biogeography theory (see MacArthur & Wilson, 1967), the body of the host acts as an island to the parasite species. Bigger hosts can provide greater habitat variability and, consequently, promote greater parasite abundance and diversity (Kamiya *et al.*, 2014). Additionally, Poulin & Nascimento (2007) found an isometric relationship between host biomass and parasite biomass, which indicates that larger-sized hosts can support more parasites, thereby corroborating our linear regression results showing that the largest lizards (both males and females) had greater parasite abundance in all the areas analysed.

Host sex (and the differences associated with it, such as hormonal and behavioural differences) is closely related to parasite number, population dynamics and infections caused by them (Hamilton & Zuk, 1982; Schall & Dearing, 1987; Folstad & Karter, 1992; Dunlap & Schall, 1995; Salvador *et al.*, 1996; Roulin *et al.*, 2001; Martínez-Padilha *et al.*, 2007; Galdino *et al.*, 2014). Male lizards in the Restinga and Atlantic Forest areas might show higher levels of helminth abundance caused by some of these factors, such as high testosterone concentrations and the stress caused by fighting for territory (Schall & Dearing, 1987; Salvador *et al.*, 1996). Males of *T. hispidus* are known for their territorial behaviour, but some differences in helminth species abundance between males and females can also be related to diet, sexual dimorphism and differences in habitat use by each sex (Aho, 1990; Fontes *et al.*, 2003; Pereira *et al.*, 2012).

The comparison between the proportion of reproductive individuals per month and helminth prevalence was statistically significant in Caatinga. Regardless of specific species, the reproductive condition can increase the level of stress through the intensification of social contact, fights for territory and/or a greater resource allocation to reproduction. These factors could enhance the propensity for becoming infected (Schall & Dearing, 1987; Carvalho & Luque, 2011). Physiological mechanisms originating from hormonal differences can be considered as being responsible for the different levels of infection found during the reproduction period of males and females (Zuk & McKean, 1996).

Monoxenic species can be especially susceptible to moisture and environmental temperature variation, because the infection is caused directly by ingesting eggs (orally) or by larvae (through the skin) (Anderson, 2000). This could explain the relationship between the rainiest months and the greater abundance of monoxenic helminth parasites. In Restinga, the greater abundance of monoxenic and heteroxenic parasite species in the dry season can be related to seasonal changes in diet. Because some insects used as intermediate hosts exhibit seasonal variation in their abundance, the composition and establishment of heteroxenic helminth species can also be affected (Vasconcellos *et al.*, 2010). We did not observe either temporal variation or differences in the reproduction period in the Atlantic Forest, so the variation found in the helminth populations here may be a consequence of other factors, such as habitat use and/or type of prey ingested (Roca *et al.*, 2005; Hamann *et al.*, 2006, 2014; Brito *et al.*, 2014b). Also, the ontogeny and diet of the host determined the helminth assemblage in *T. torquatus* in the Atlantic Forest (Pereira *et al.*, 2013), and the type of soil and fauna (eggs, predators or parasite larvae) can also affect the reproduction and survival of parasites (Harwood, 1936; Thieltges *et al.*, 2008), showing effects on their abundance in the definitive host(s) (Harwood, 1936).

The helminth species infection model of *T. hispidus* in the three studied areas is composed of generalist species, whose abundance is related to the host body size and reproduction, and to the rainy period. It was impossible to isolate a unique condition as being responsible for the variation in the helminth abundance. Thus, both the environment and some host aspects are influential factors in the organization of the helminth community components in *T. hispidus* from the studied areas. We emphasize the importance of how the study of the same species across different environments can reveal geographic and seasonal differences in the acquisition and abundance of helminth species.

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Conflict 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 with permission to collect the animals.

References

Aho, J.M. (1990) Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. pp 157–196 *in* Esch, G.W., Bush, A.O. & Aho, J.M. (*Eds*) *Parasite communities: Patterns and processes*. London, Chapman & Hall.

Almeida, W.O., Freire, E.M.X. & Lopes, S.G. (2008) A new species of Pentastomida infecting *Tropidurus hispidus* (Squamata: Tropiduridae) from Caatinga in Northeastern Brazil. *Brazilian Journal of Biology* **68**, 631–637.

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M. & Rohani, P. (2006) Seasonality and the dynamics of infectious diseases. *Ecology Letters* **9**, 467–484.

Anderson, R.C. (2000) *Nematode parasites of vertebrates: Their development and transmission*. Wallingford, Oxon, CABI.

Anjos, L.A., Ávila, R.W., Ribeiro, S.C., Almeida, W.O. & Silva, R.J. (2012) Gastrointestinal nematodes of the lizard *Tropidurus hispidus* (Squamata: Tropiduridae) from a semi-arid region of Northeastern Brazil. *Journal of Helminthology* **4**, 1–7.

Brito, S.V., Ferreira, F.S., Ribeiro, S.C., Anjos, L.A., Almeida, W.O., Mesquita, D.O. & Vasconcellos, A. (2014a) Spatial–temporal variation of parasites in *Cnemidophorus ocellifer* (Teiidae) and *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Tropiduridae) from Caatinga areas in northeastern Brazil. *Parasitology Research* **3**, 1163–1169.

Brito, S.V., Corso, G., Almeida, A.M., Ferreira, F.S., Almeida, W.O., Anjos, L.A., Mesquita, D.O. & Vasconcellos, A. (2014b) Phylogeny and microhabitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of northeast Brazil. *Parasitology Research* **11**, 3963–3972.

Brooks, D.R., León-Règagnon, V., McLennan, D.A. & Zelmer, D. (2006) Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology* **87**, 76–85.

Bush, A.O., Aho, J.M. & Kennedy, C.R. (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* **4**, 1–20.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostaki, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.

Bush, A.O., Fernández, J.C., Esch, G.W. & Seed, J.R. (2001) *Parasitism: The diversity and ecology of animal parasites*. 1st edn. 531 pp. Cambridge, Cambridge University Press.

Carvalho, A.R. & Luque, J.L. (2011) Seasonal variation in metazoan parasites of *Trichiurus lepturus* (Perciformes: Trichiuridae) of Rio de Janeiro, Brazil. *Brazilian Journal of Biology* **71**, 771–782.

Dunlap, K.D. & Schall, J.J. (1995) Hormonal alteration and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. *Physiological Zoology* **68**, 608–621.

Folstad, I. & Karter, A.J. (1992) Parasites, bright males, and immunocompetence handicap. *The American Naturalist* **139**, 603–622.

Fontes, A.F.F., Vicente, J.J., Kiefer, M.C. & Sluys, M.V. (2003) Parasitism by helminths in *Eurolophosaurus nanuzae* (Lacertilia: Tropiduridae) in an area of rocky outcrops in Minas Gerais state, Southeastern Brazil. *Journal of Herpetology* **37**, 736–741.

Frost, D.R., Rodrigues, M.T., Grant, T. & Titus, T.A. (2001) Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Molecular Phylogenetics and Evolution* **21**, 352–371.

Galdino, C.A.B., Ávila, R.W., Bezerra, C.H., Passos, D. C., Melo, G.C. & Zanchi-Silva, D. (2014) Helminths infection patterns in a lizard (*Tropidurus hispidus*) population from a semiarid Neotropical area: associations between female reproductive allocation and parasite loads. *Journal of Parasitology* **100**, 864–867.

Gambhir, R.K., Oinam, S. & Lakshmipyari, W. (2012) Seasonal dynamics of *Thelandros maplestonei* infection in the wall lizard, *Hemidactylus flaviviridis* in Imphal Valley, Manipur, India. *Journal of Parasitology Disease* **37**, 192–195.

Gomes, F.F.A., Caldas, F.L.S., Santos, R.A., Silva, B.D., Santana, D.O., Rocha, S.M., Ferreira, A.S. & Faria, R. G. (2015) Patterns of space, time and trophic resource use by *Tropidurus hispidus* and *T. semitaeniatus* in an area of Caatinga, Northeastern Brazil. *Herpetological Journal* **25**, 27–39.

Griffiths, A.D., Jones, H.I. & Christia, K.A. (1998) Effect of season on oral and gastric nematodes in the frillneck lizard from Australia. *Journal of Wildlife Diseases* **34**, 381–385.

Hamann, M.I., Kehr, A.I. & González, C.E. (2006) Species affinity and infracommunity ordination of helminths of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in two contrasting environments from northeastern Argentina. *Journal of Parasitology* **92**, 1171–1179.

Hamann, M.I., Kehr, A.I. & González, C.E. (2014) Helminth community structure in the Argentinean bufonid *Melanophryniscus klappenbachi*: importance of habitat use and season. *Parasitology Research* **113**, 3639–3649.

Hamilton, W.D. & Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Harwood, P.D. (1936) The effect of soil types on the helminths parasitic in the ground lizard, *Leiolopisma laterale* (Say). *Ecology* **17**, 694–698.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–3117.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

IBGE (Instituto Brasileiro de Geografia e Estatística). (1985) *Atlas Nacional do Brasil: Região Nordeste*. Rio de Janeiro, IBGE.

IDEMA (Instituto de Desenvolvimento Sustentável e Meio Ambiente). (2000) Rio Grande do Norte. Available at http://www.idema.rn.gov.br (accessed 2 February 2015).

Janovy, J., Clopton, R.E. & Percival, T.J. (1992) The roles of ecological and evolutionary influences in providing structure to parasite species assemblages. *Journal of Parasitology* **78**, 630–640.

Kamiya, T., O'Dwyer, K., Nakagawa, S. & Poulin, R. (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Review* **89**, 123–134.

Kolodiuk, M.F., Ribeiro, L.B. & Freire, E.M.X. (2009) The effects of seasonality on the foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata: Tropiduridae) living in sympatry in the Caatinga of northeastern Brazil. *Zoologia* **26**, 581–585.

Levri, E.P. (1999) Parasite-induced change in host behavior of a freshwater snail: parasitic manipulation or byproduct of infection? *Behavioral Ecology* **10**, 234–241.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. 201 pp. Princeton, New Jersey, Princeton University Press.

Martínez-Padilha, J., Mougeot, F., Rodríguez-Pérez, L. & Bortolotti, G.R. (2007) Nematode parasites reduce carotenoid-based signaling in male red grouse. *Biological Letters* **3**, 161–164.

Minguez, L. & Giambérini, L. (2012) Seasonal dynamics of zebra mussel parasite populations. *Aquatic Biology* **15**, 145–151.

Møller, A.P., Erritzøe, J. & Saino, N. (2003) Seasonal changes in immune response and parasite impact on hosts. *The American Naturalist* **161**, 657–671.

Narayanan, E.S., Rao, S.B.R. & Thontadaraya, T.S. (1961) Effect of temperature and humidity on the rate of development of the immature stages of *Apanteles angaleti*

Muesebeck (Braconidae: Hymenoptera). *Proceedings of the National Academy of Sciences, India* **28**, 150–163.

Nimer, E. (1989) *Climatologia do Brasil*. 421 pp. Rio de Janeiro, Instituto Brasileiro de Geografia e Estatística.

Pereira, F.B., Sousa, B.M. & Lima, S.S. (2012) Helminth community structure of *Tropidurus torquatus* (Squamata: Tropidurus) in a rocky outcrop area of Minas Gerais state, Southeastern Brazil. *Journal of Parasitology* **98**, 6–10.

Pereira, F.B., Gomides, S.C., Sousa, B.M., Lima, S.S. & Luque, J.L. (2013) The relationship between nematode infection and ontogeny and diet of the lizard *Tropidurus torquatus* (Squamata: Tropiduridae) from the Atlantic Rainforest in Southeastern Brazil. *Journal of Helminthology* **87**, 364–370.

Poulin, R. (1997) Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics* **28**, 341–358.

Poulin, R. (2004) Macroecological patterns of species richness in parasite assemblages. *Basic and Applied Ecology* **5**, 423–434.

Poulin, R. & Nascimento, M.G. (2007) The scaling of total parasite biomass with host body mass. *International Journal for Parasitology* **37**, 359–364.

Poulin, R. & Valtonen, E.T. (2001) Nested assemblages resulting from host size variation: the case of endoparasite communities in fish hosts. *International Journal for Parasitology* **31**, 1194–1204.

Poulin, R., Guilhaumon, F., Randhawa, H.S., Luque, J.L. & Mouillot, D. (2010) Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* **1**, 1–8.

Riley, J. (1986) The biology of pentastomids. *Advances in Parasitology* **25**, 45–128.

Roca, V., Carretero, M.A., Llorene, G.A., Montori, A. & Martin, J.E. (2005) Helminth communities of two lizard populations (Lacertidae) from Canary Islands (Spain): host diet–parasite relationships. *Amphibia–Reptilia* **26**, 535–542.

Rodrigues, M.T. (1987) Sistemática, ecologia e Zoogeografia dos *Tropidurus* do grupo *Torquatus* ao sul do Rio Amazonas (Sauria: Iguanidae). *Arquivos de Zoologia* **3**, 105–230.

Roulin, A., Riols, C., Dijkstra, C. & Ducrest, A.L. (2001) Female plumage spottiness signals parasite resistance in the barn owl (*Tyto alba*). *Behavioral Ecology* **12**, 103–110.

Salvador, A., Veiga, J.P., Martin, J., Lopez, P., Abelenda, M. & Marisa, P. (1996) The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behavioral Ecology* **7**, 145–150.

Schall, J.J. & Dearing, M.D. (1987) Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidetalis*. *Oecologia* **73**, 389–392.

Ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–1179.

Thieltges, D.W., Jensen, K.T. & Poulin, R. (2008) The role of biotic factors in the transmission of freeliving endohelminth stages. *Parasitology* **135**, 407–426.

Vasconcellos, A., Andreazze, R., Almeida, A.M., Araujo, H.F.P., Oliveira, E. & Oliveira, U. (2010) Seasonality of insects in the semi-arid Caatinga of Northeastern Brazil. *Revista Brasileira de Entomologia* **54**, 471–476.

Vitt, L.J. (1995) The ecology of tropical lizards in the Caatinga of Northeast Brazil. *Oklahoma Museum of Natural History* **1**, 1–29.

Zuk, M. & McKean, K.A. (1996) Sex differences in parasite infection: patterns and processes. *International Journal for Parasitology* **26**, 1009–1024.