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HELMINTHOLOGY - REVIEW

Rich but random: parasite communities of snouted treefrog, *Scinax fuscovarius* (Anura: Hylidae), in Bodoquena Mountains, western Brazil

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Abstract

Hosts represent discrete habitats that contain finite parasite communities, and individual hosts can be used as replicates in parasitism studies, such as investigations of the processes that mediate the formation of parasite communities. However, within a single host population, there may be singularities among individuals that affect parasite contact rates. Accordingly, the goals of the present study were to document the parasites associated with the small treefrog *Scinax fuscovarius*, to verify possible variation and co-occurrences in parasite infracommunities, and to assess the effects of host characteristics (size and sex) on infracommunity structure. Treefrog specimens ($n = 75$) were collected from the Bodoquena Mountains in Mato Grosso do Sul, Brazil. After collection, the specimens were transported to the laboratory, and examined for parasitic. The parasites found were removed, fixed, and identified. Patterns in parasite infracommunity organization were analyzed using the checkerboard score index, which was calculated using a presence-absence matrix. The matrix was randomized under the null hypothesis that the infracommunities independently represent the component community. Forty-two (56%) of the individuals harbored at least one parasite, and a total of 500 metazoan parasites were recovered, with a particularly rich composite community of 18 taxa, including 13 nematodes, two trematodes, one cestode, one oligochaete, and one mite larvae. The parasite species were randomly distributed among the infracommunities, with no evidence of co-occurrence, segregation, or aggregation. However, both body size and sex influenced infection, with larger hosts harboring more parasites and parasites were more abundant in male specimens and more species rich in female specimens. These results suggest that the parasite infracommunities of *S. fuscovarius* are shaped by both random factors and individual host characteristics.

Keywords Amphibians · Co-occurrences · Hosts · Infracommunities

Introduction

Parasites live in structured communities that are influenced by the environments provided by their hosts (Poulin 1997), and such structured communities facilitate the investigation of variation in parasite assemblage patterns at different scales (Krasnov et al. 2010, 2006; D'Bastiani et al. 2020). Infracommunities may represent the most tangible scale of parasite organization, since they reflect the assembling of parasite species among individual hosts within a host population (i.e., component community; Bush et al. 1997); individual hosts can be considered study replicates for host populations (Kuris et al. 1980; Poulin 2011).

It has long remained unclear, in parasite ecology, whether parasite infracommunities are structured and, thus, reflect an underlying predictable process (Holmes and Price 1986). Such structured infracommunities would differ from random expectations and would provide insight into interactions

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among parasite species within a community (Huston 1994; Poulin 1996c). For example, higher-than-expected infracommunity richness could indicate that a parasite species facilitates the entry of other species (Poulin 2007b; Clark et al. 2016), and lower-than-expected infracommunity richness could indicate competition or competitive exclusion (Gotelli and Rohde 2002). Regardless of the richness of a component community, individual infracommunities are unlikely to include all available parasites, owing to infracommunity support capacity (Poulin 2007b). Thus, a certain randomness in infracommunity assemblages, which are composed of subsets of the regional pool of parasite species, is to be expected and does not necessarily indicate the absence of structure patterns or interactions (Gotelli and Rohde 2002). Determining which parasite species can co-occur will provide insight into parasite distribution patterns and interactions.

The effect of host characteristics on the heterogeneity of infracommunities remains poorly understood. In general, larger hosts possess greater surface area through which infectious parasite stages can enter (Hamann and González 2010; Hamann et al. 2014; Hamann and González 2015) and consume more prey, which could serve as intermediate hosts for indirectly transmitted parasites (Poulin 2007a; Benesh et al. 2021). Larger hosts also provide complex habitats for parasite establishment and exploitation (Poulin 1997), and together, these factors can promote greater parasite co-occurrences and richness in larger hosts (Poulin 1996c). However, some studies have reported that host body size has little effect on parameters (e.g., abundance, richness) of parasitic communities (Hamann et al. 2006; Toledo et al. 2013; Sena et al. 2018). Therefore, it would be valuable to conduct further studies on the effects of host body size on infracommunity parameters, such as abundance, intensity, and prevalence. Host sex can also influence infracommunity assemblages and parameters, especially during reproductive stages, owing to changes in hormonal conditions that can alter host physiology and behavior (Tinsley 1989; Poulin 1996c). Thus, parasite communities may indicate whether the individual characteristics of their hosts limit or facilitate parasite infection (Morand et al. 1999).

In amphibian populations, biotic characteristics that can be good conditioning factors in the co-occurrences of parasites in their infracommunities (Kehr et al. 2000; Brooks et al. 2006Hamann and González 2010). For instance, the low dispersion of individuals within host populations can promote parasite sharing (Esch et al. 1988). Indeed, amphibians generally remain close to their reproductive sites, and individual hosts are likely to experience similar food availability and similar opportunities for acquiring local parasites (Holmes and Price 1986; Esch et al. 1988; Wells 2007). Particularities of individual hosts can also affect rates of contact with parasites, with certain characteristics making hosts more or less susceptible to parasites or pathogens (Poulin 2007b).

The hylid treefrog *Scinax fuscovarius* (Lutz, 1925) is distributed in the midwest, northeast, and southeast regions of Brazil, as well as in northern Argentina, Paraguay, and Bolivia (Frost 2018). The species is arboreal; is found in open areas of the Brazilian savanna (i.e., Cerrado); and, during its reproductive period, mainly occurs around permanent and semi-permanent bodies of water (Melo et al. 2007; Fig. 1a). The parasite fauna of *S. fuscovarius* in an Atlantic Forest region of southern Brazil was recently described (Santos et al. 2016).

Because the parasite communities of *S. fuscovarius* in the Bodoquena Mountains (midwest Brazil) have yet to be described, the first goal of the present study was to establish a checklist of parasite species in the region. Variation of parasite infracommunities and the responses of such communities to host attributes (e.g., body size and sex) were also evaluated in order to answer the following questions: (i) Does variation occur in *S. fuscovarius* parasite infracommunities, and if so, is it random?; (ii) Does aggregation or segregation occur among *S. fuscovarius* parasite species?; and (iii) Is variation, if any, among *S. fuscovarius* parasite infracommunities associated with hosts traits? It was expected that the distribution of parasite infracommunities in *S. fuscovarius* would differ from a random distribution and that variation would be influenced by host characteristics, such as body size, physiology, and habitat.

Materials and methods

Host and parasite collection

Treefrog (*S. fuscovarius*) specimens ($n = 75$) were collected at night by active searching in the Bodoquena Mountain region, at Fazenda Estancia Mimosa, in the municipality of Bonito, Mato Grosso do Sul State (20° 58′ 49″ S, 56° 30′ 32″ W; *datum*: WGS84), on the border of the Nabileque region of the Pantanal (Fig. 1b) in October and November of 2015. After collection, the specimens were transported to the laboratory, where they were euthanized by applying 5% lidocaine ointment to their abdomens, sexed, and measured (snout-vent length, SVL) using a digital caliper (0.1-mm accuracy).

The nematodes and cestode cyst were fixed using 5% heated formalin, preserved in 70% ethyl alcohol, clarified using glycerin, and mounted on slides. The trematodes were compressed between slides and coverslips, stained using Delafield's hematoxylin, and clarified using Faia creosote. Oligochaetes and mite larvae were mounted on slides with Amann's lactophenol and Hoyer's medium, respectively (Amato et al. 1991; Eiras et al. 2000).

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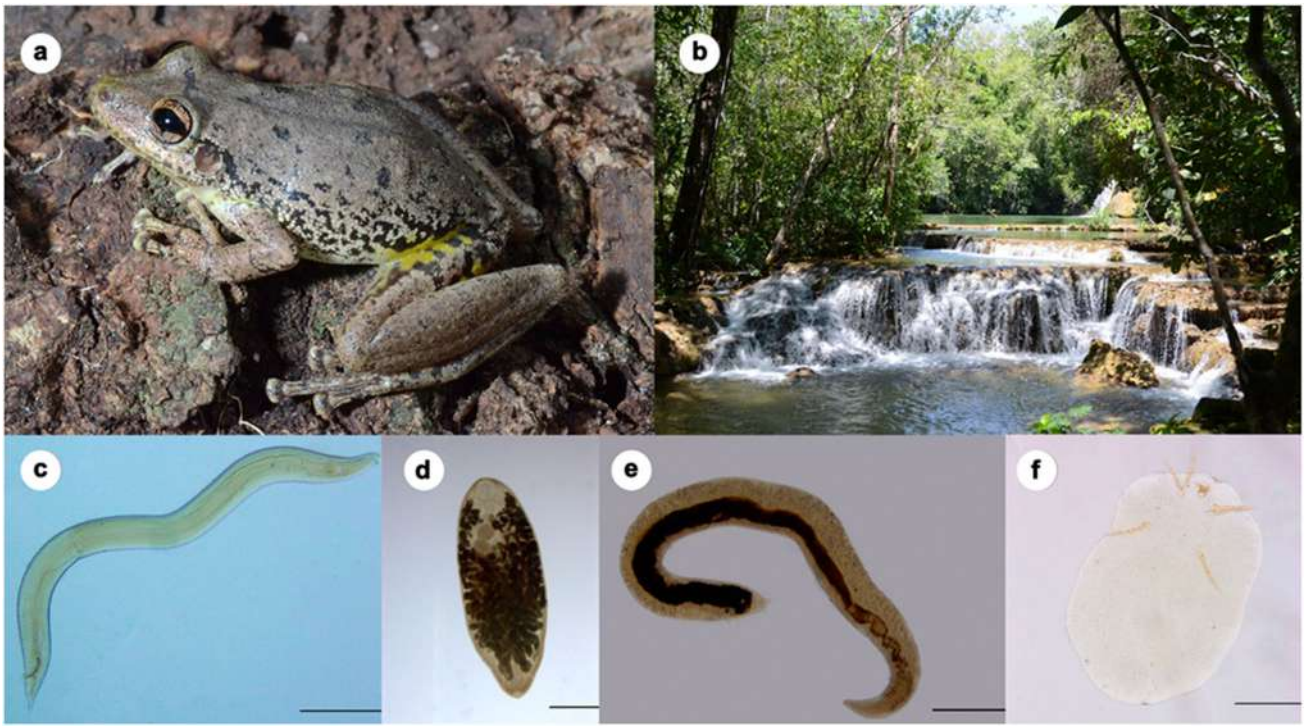

Fig. 1 A summary with our study system, showing **a** specimen of *Scinax fuscovarius* (Lutz, 1925), study site **b** in the Bodoquena Mountain region, and some of the parasites reported: **c** male of *Aplectana lopesi*; **d** *Mesocoelium monas*; **e** *Rhabdias* sp.; **f** *Eutrombicula* sp

After removing the parasites, the frogs were fixed and preserved using 4% formaldehyde and 70% alcohol, respectively, and were deposited in the Mato Grosso do Sul Federal University Zoological Reference Collection (ZUFMS; AMP 04,110–04,184). Parasite vouchers were also fixed in 70% alcohol and deposited in the same collection (ZUFMS; NEM 00,029–00,043, PLA 00,006–00,008, ANN 00,001, CHE 00,165).

Data analysis

Mean parasite abundance, intensity, and prevalence were calculated according to Bush et al. (1997), and parasite richness was estimated using a species accumulation curve with a first-order Jackknife estimator (Jackknife 1). Patterns in parasite infracommunity organization were analyzed using the checkerboard score (C-score) index, which was calculated using a presence-absence matrix. The matrix was randomized under the null hypothesis that the infracommunities (parasite species present in individual hosts) independently represent the component community (Bush et al. 1997). Thus, the C-score index represents the mean number of possible parasite species pairs that do not co-occur (Stone and Roberts 1990). The FF algorithm (fixed rows and columns), in which each row represents a parasite taxa and each column represents a host specimen, was used to maintain observed values (Gotelli 2000) so that the algorithm did not restrict the number of parasite taxa that a host could harbor and so that all individual hosts were equally likely to host individual parasite species (Krasnov et al. 2010). Five thousand randomizations were performed using a presence-absence matrix with the software EcoSim 7.72 (Gotelli and Entsminger 2009). The significance of the C-score values were analyzed from the biological data (observed value) and the mean value of the simulated matrices (value expected

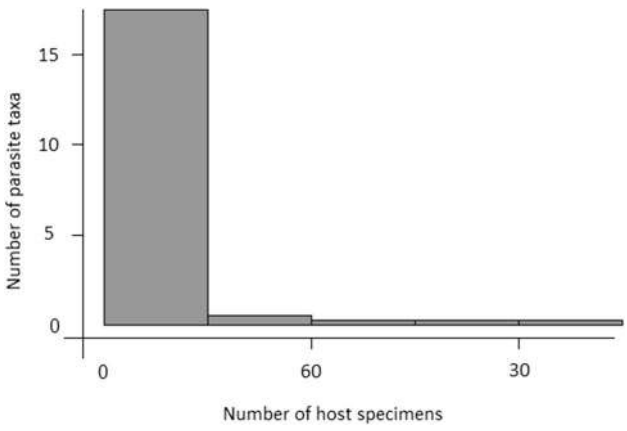

Fig. 2 Distribution of parasites *Scinax fuscovarius* infracommunities, where the first bar shows that few hosts harbor many parasites but most hosts harbor few parasites

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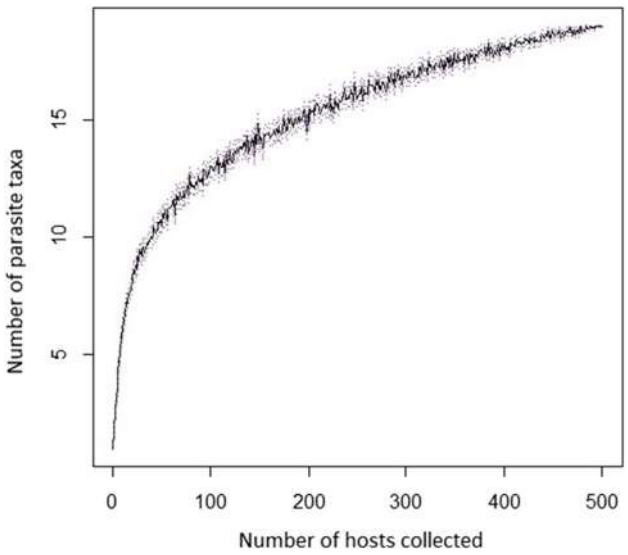

Fig. 3 Accumulation curve of species based on the taxa of metazoan parasites found in the hosts of *Scinax fuscovarius*

at random). Mean C-scores that exceed those of simulated (random) datasets indicate species segregation, whereas those that fail to exceed the mean scores of simulated datasets indicate species aggregation (Gotelli and Rohde 2002). Segregation can indicate the reduction of a species' niche to the detriment of the presence of other species, thereby eliminating competitors, which is a non-interactive factor (Holmes 1973), whereas aggregation is the result of different parasite distributions in hosts, with few parasites occurring in many hosts and few hosts with many parasites (Shaw and Dobson 1995).

The Kruskal–Wallis (*H*) and Dunn's post hoc tests were used to evaluate differences in the body size (SVL) of male, female, and juvenile hosts, and the effect of SVL on infection parameters (parasite abundance and richness) was evaluated in R version 3.1.1 (R Core Team 2016) using the zero-inflated Poisson (ZIP) model, i.e., the "zeroinfl" function of the "pscl" package (Jackman 2015), which calculates model parameters by independently separating count data and zero excesses (Oksanen et al. 2013). Since the studied population had a 1:1 sex ratio, the male, female, and juvenile specimens were represented as 1, − 1, and 0, respectively, in order to prevent correlation problems with host age and sex (Bolker 2007).

Results

Forty-two (56%) of the 75 specimens harbored at least one parasite, with most hosts harboring many parasites and a smaller number harboring only a few parasites (Fig. 2), and a total of 500 metazoan parasites were recovered, thereby

Table 1 Infection parameters of the parasites associated with the treefrog *Scinax fuscovarius* in the Bodoquena Mountain region, Mato Grosso do Sul, Brazil. Prevalence (P%), mean abundance (M.A.), mean intensity (M.I.), standard error (S.E.)

Metazoan parasites	P%	M.A. ± S.E	M.I. ± S.E	Site of infection
Nematoda				
Aplectana sp. (larval)[§]	2.60	1.20 ± 1.10	48 ± 1.30	Small intestine
Aplectana lopesi (adult)	12	0.20 ± 0.10	1.80 ± 0.10	Small intestine and large intestine
Ascarididae gen. sp. (adult)[§]	2.60	0.02 ± 0.02	1.0 ± 0.02	Small intestine and large intestine
Cosmocerca brasiliense (adult)	1.30	0.01 ± 0.01	1.0 ± 0.02	Small intestine
Cosmocerca parva (adult)	5.30	0.06 ± 0.03	1.2 ± 0.04	Small intestine and large intestine
Cosmocercidae gen. sp. (adult)	2.60	0.02 ± 0.02	1.0 ± 0.02	Small intestine and large intestine
Cosmocercoidea fam. gen. sp.[§] (larval)	5.30	0.20 ± 0.10	4.50 ± 0.20	Small intestine and large intestine
Oxyascaris caudacutus (adult)	15	0.40 ± 0.10	2.50 ± 0.10	Small intestine and large intestine
Philometridae gen. sp. (adult)[§]	4	0.04 ± 0.04	3 ± 0.06	Small intestine
Rhabdias sp. (adult)	1.30	0.01 ± 0.01	1.0 ± 0.02	Lung
Rhabdias cf. *elegans* (adult)[§]	16	0.90 ± 0.50	5.90 ± 0.50	Lung
Rhabdias cf. *fuelleborni* (adult)[§]	2.60	0.10 ± 0.09	5.0 ± 0.11	Lung
Spirurida fam. gen. sp. (larval)[§]	1.30	0.01 ± 0.01	1.0 ± 0.02	Small intestine
Trematoda				
Mesocoelium monas (adult)[§]	1.30	0.30 ± 0.30	22 ± 0.40	Small intestine
Neascus sp. (larval)[§]	1.30	0.60 ± 0.60	48 ± 0.90	Muscle
Cestoda				
Proteocephalidea fam. gen. sp. (cyst)[§]	1.30	0.02 ± 0.03	2.0 ± 0.04	Muscle
Annelida				
Dero (*Allodero*) *lutzi* (adult)	2.60	1.60 ± 1.60	60 ± 1.70	Bladder and kidneys
Arthropoda				
Eutrombicula sp. (larval)[§]	8	0.70 ± 0.50	9 ± 0.50	Subcutaneous

[§]New host records

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representing a particularly rich component community of 18 taxa (13 nematodes, two trematodes, one cestode, one oligochaete, one mite larvae). Species richness estimation showed a deviation of 2 ± 2 (Jackknife 1 = 26,893; Fig. 3). Most (65.2%) of the parasites were helminths, including 13 nematode taxa (44.8%), two trematodes (17.2%), and one cestode (0.4%), also oligochaete *Dero* (*Allodero*) *lutzi* (24%) and parasitic larvae of the mite *Eutrombicula* sp. (10.8%) were also observed (Table 1).

The C-score of the biological dataset (8.80392) and the mean C-score of the simulated dataset (8.78693) were statistically similar ($p = 0.59$), thereby indicating a random pattern in infracommunity composition and confirming the null hypothesis of random structuring (Fig. 4). This finding also indicates a lack of segregation or aggregation among the metazoan parasites of *S. fuscovarius*.

However, parasite abundance and richness were affected by host body size and sex, with males ($n = 38$; range = 31.06–46.93 mm) being significantly larger than juveniles ($n = 6$; range = 28.57–35.2 mm; $H = 14.43$, $P = 0.0007$) but not females ($n = 31$; range = 19.19–47.33 mm). Parasites were more abundant in male specimens (Fig. 5a; Table 2) and more species rich in female specimens (Fig. 5b).

Discussion

The present study documented 11 new metazoan parasites for *S. fuscovarius* and provided insight into the distribution of five parasite taxa that had been previously recorded in *S. fuscovarius* from other locations (Table 3). The study also indicates that the distribution of parasite species among *S. fuscovarius* individuals is random, lacking aggregation and disaggregation, and that infection parameters are influenced by host body size and sex.

Previous studies of *S. fuscovarius* in regions of the Atlantic Forest (e.g., Santos et al. 2016; Graça et al. 2017) have reported lower parasite diversity but similar distribution patterns (e.g., parasite taxa with low prevalence), as well as some of the same parasite species, such as *Cosmorcerca brasiliense*, *C. parva*, Cosmocercidade gen. sp., *Dero* (*Allodero*) *lutzi*, and *Rhabdias* sp. (Table 3). As in the present study, previous studies have also reported that generalist parasites, such as nematodes, are the majority found. And when compared to reports of other amphibians in the study region (Campião et al. 2016a, b), the present study identified high parasite richness in the component community but

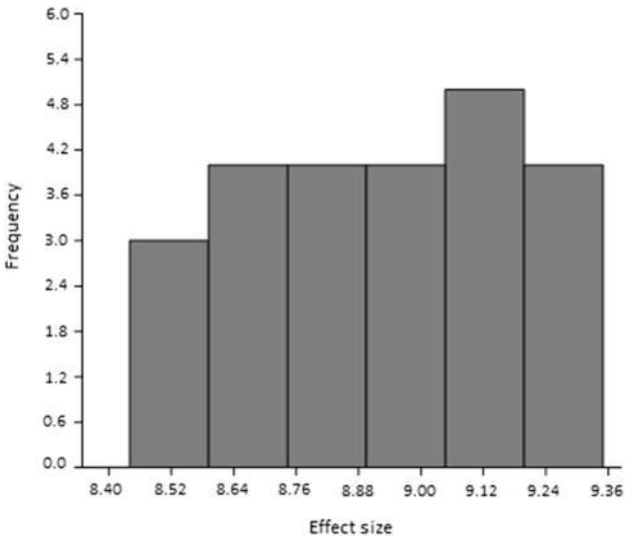

Fig. 4 Histogram of C-score FF algorithm (fixed rows and columns) to compare the results of the matrices; the effect size measures the number of standard deviations that the observed is above or below the average index of the simulated communities

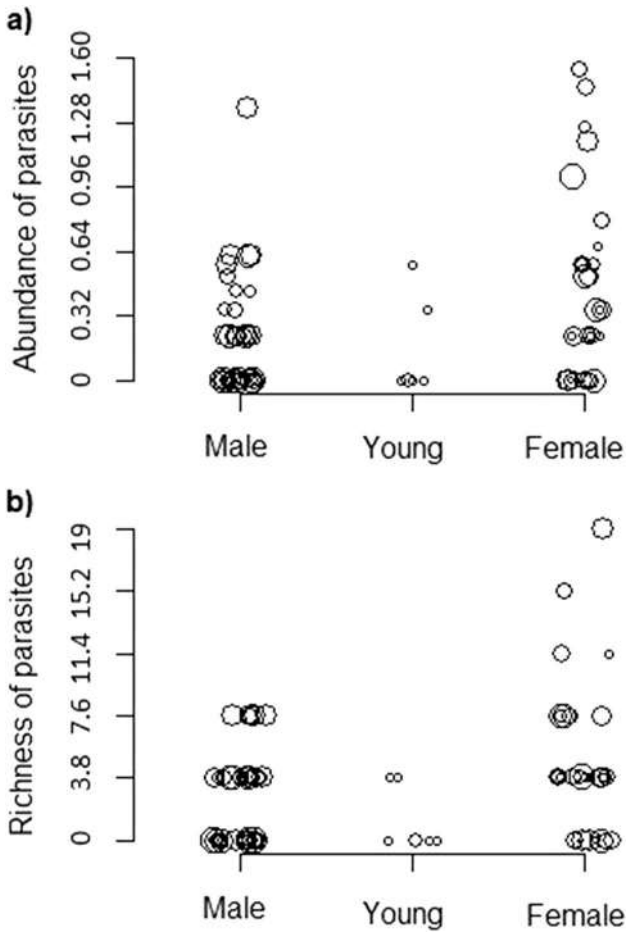

Fig. 5 Relationship between parasite descriptors with the body size (snout-vent length) of male, female, and young of *Scinax fuscovarius* collected in the Bodoquena Mountain region, Mato Grosso do Sul, Brazil. The size of the circles represents the body size of the hosts. **a** SLV of male, female, and young, with parasite abundance. **b** SLV of male, female, and young, with the richness of parasites

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Table 2 The zero-inflated Poisson (ZIP) model of the relation between parasite abundance, species richness, and the body size (snout-vent-length) and sex of individuals of the treefrog *Scinax fuscovarius* Bodoquena Mountain region, Mato Grosso do Sul, Brazil

	Coefficient	Estimate	S.E	*Z*	*P*
Abundance of parasites	Intercept	0.078560	0.344189	−0.228	0.819
	Body size	0.056557	0.0008588	6.586	**>0.001**
	Sex	0.672743	0.055247	12.177	**>0.001**
Richness of parasites	Intercept	−1.74881	0.87159	−2.006	0.04481
	Body size	0.04125	0.02220	1.858	0.06312
	Sex	0.36524	0.13385	2.729	**0.00636**
	Residual	79.265			

Results in boldface are significant (P = significance value considering ⩽0.05)

Table 3 Records of metazoan parasites in *Scinax fuscovarius*

Identification of the parasite		Country	State	References
Helminth parasites				
Nematoda	*Aplectana* sp.	Brazil	Mato Grosso do Sul	Current study
	Aplectana lopesi	Brazil	Rio de Janeiro	Silva (1954)
		Brazil	Mato Grosso do Sul	Current study
		Brazil	Rio de Janeiro	Vicente et al. (1991)
	Ascarididae gen. sp.	Brazil	Mato Grosso do Sul	Current study
	Cosmocercoidea fam. gen. sp.	Brazil	Mato Grosso do Sul	Current study
	Cosmocercidae gen. sp.			
	Cosmocerca brasiliense	Brazil	Mato Grosso do Sul	Current study
		Peru	Not reported	Bursey et al. (2001)
		Brazil	Santa Catarina	Santos and Amato (2013)
		Brazil	Santa Catarina	Santos et al. (2016)
	Cosmocerca freitasi	Brazil	Rio de Janeiro	Silva (1954)
		Brazil	Rio de Janeiro	Vicente et al. (1991)
	Cosmocerca parva	Paraguay	Not reported	Masi Pallares and Maciel (1974)
		Locality not reported	Not reported	Baker and Vaucher (1984)
		Brazil	Santa Catarina	Santos and Amato (2013)
		Brazil	Santa Catarina	Santos et al. (2016)
		Brazil	Mato Grosso do Sul	Current study
	Oxyascaris caudacutus	Locality not reported	Not reported	Baker and Vaucher (1985)
		Brazil	Mato Grosso do Sul	Current study
	Philometridae gen. sp.	Brazil	Mato Grosso do Sul	Current study
	Physaloptera sp.	Brazil	Santa Catarina	Santos et al. (2016)
	Raillietnema sp.	Brazil	Paraná	Graça et al. (2017)
	Rhabdias sp.	Brazil	Paraná	Graça et al. (2017)
		Brazil	Mato Grosso do Sul	Current study
	Rhabdias (cf.) *elegans*	Brazil	Mato Grosso do Sul	Current study
	Rhabdias (cf.) *fuelleborni*	Brazil	Mato Grosso do Sul	Current study
	Schrankiana formosula	Brazil	Paraná	Graça et al. (2017)
	Spirurida fam. gen. sp.	Brazil	Mato Grosso do Sul	Current study
	Proteocephalidae gen. sp.	Brazil	Mato Grosso do Sul	Current study
Trematoda	*Mesocoelium monas*	Brazil	Mato Grosso do Sul	Current study
	Neascus sp.	Brazil	Mato Grosso do Sul	Current study
Cestoda	*Spirometra* sp.	Brazil	São Paulo	Oda et al. (2016)
Acanthocephala	*Pseudoacanthocephalus* sp.	Brazil	Santa Catarina	Santos et al. (2016)
Arthropod parasites				
Insecta	*Eutrombicula* sp.	Brazil	Mato Grosso do Sul	Current study
	Sarcophagidae	Brazil	Minas Gerais	Souza-Pinto et al. (2015)
Hirudinea	Not identified	Brazil	Paraná	Gambale et al. (2014)
Oligochaeta	*Dero* (*Allodero*) *lutzi*	Brazil	Paraná	Oda et al. (2015)
		Brazil	Paraná	Graça et al. (2017)
		Brazil	Mato Grosso do Sul	Current study

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low prevalence, which may have contributed to the low co-occurrence of parasite taxa in the infracommunities.

Variation in individual host susceptibility can result in either common or infrequent parasitic associations, such as those observed between *S. fuscovarius* and the mite larvae and oligochaetes (Morais et al. 2017; Mendoza-Roldan et al. 2020). Even though parasitic mites and oligochaetes are less prevalent in anurans than other parasite taxa, reports of these parasites in other *Scinax* species have been reported with some frequency (Oda et al. 2015; Graça et al. 2017; Morais et al. 2017; Jacinavicius et al. 2018; Mendoza-Roldan et al. 2020). In addition, the occurrence of the mite and oligochaete may be related to environmental factors, such as high humidity, which is one of the main characteristics of the Bodoquena Mountain region (Fig. 1b) and which has been previously reported to favor these parasite taxa (Oda et al. 2015; Mendoza-Roldan et al. 2020). In general, several factors can contribute to the probability of host infection by local composite communities and, thus, affect parasite infracommunities (Janovy et al. 1995; Poulin 2007b). The co-occurrence of all local parasite taxa in individual hosts becomes unlikely, exceptionally when in high prevalences (Poulin 1996; Tello et al. 2008).

The results of the present study support previous reports that host body size can affect parasite infection (Kamiya et al. 2014; Campião et al. 2015a), since the greatest parasite abundance was observed in males. However, the richest parasite infracommunities were recovered from female specimens, as previously reported for male *S. nasicus* in Argentina (Hamann and González 2010), which indicates that sex is also an important factor in the acquisition of parasites in anurans. During reproductive periods, anuran hosts can become more vulnerable to infection as a result of the high energy costs of breeding (Zuk 1990; Poulin 1996c). For example, male anurans, which spend their time searching for females, may stop feeding during this period, and females allocate more energy to egg production, which can reduce resistance to infection (Solé and Pelz 2007; Dare and Forbes 2009; Johnson and Hoverman 2014; Venesky et al. 2020). In the present study, such factors may account for the abundance of parasites observed in both sexes, since the specimens were collected during the species' reproductive period. However, the greater richness of parasites in female specimens is surprising, since most studies suggest that hormone-related immune modulation results in males being more affected by parasites (Poulin 1996a, c; Schalk and Forbes 1997; Klein 2004; Madelaire et al. 2018).

The parasite infracommunities in the present study were considered random samples of the component community, and even though neither aggregation nor segregation were observed, both host body size and sex were significantly related to infection parameters. The randomly assembled parasite infracommunities observed in the collected specimens may have been influenced by the ecological characteristics of individual hosts, and even though host body size and sex were associated with infracommunity structure, the factors did not explain the distribution of parasites in the hosts. Therefore, the composition of parasite infracommunities in the *S. fuscovarius* population studied was determined by random chance, but individual host characteristics were related to infracommunity structure, as indicated by their effects on quantitative infection parameters.

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Author contribution Designed the experiments: ICOS, KMC, and LERT. Conducted the experiments: ICOS. Analyzed the data: ICOS, ACAR, and KMC. Wrote the manuscript: ICOS, PS, KMC, and DJS.

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Declarations

Ethics approval All procedures were performed in accordance with guidelines on animal care and with the ethics guidelines of the institution where the study was conducted. Approval was granted by the National Council for Animal Experiment Control (CEUA; number 838/2017) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio; number 50586–1).

Conflict of interest The authors declare no competing interests.

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