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Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area

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Abstract

In the present study, we aimed to describe the composition of endoparasites associated with anurans from an altitudinal rainforest enclave in northeastern Brazil. Additionally, we tested if microhabitat use influences endoparasite abundance and richness, as well as the hypothesis that larger frogs tend to be more parasitized. We sampled 306 individuals from 25 anuran species that were necropsied and analysed using a stereomicroscope. The total endoparasite prevalence was 79.08%, with a parasitic community consisting of 46 taxa. Overall, we found the common pattern described for Neotropical amphibians, which is the predominance of generalist and direct-cycle parasites. Twenty new host records and two possible new parasite species were found, highlighting the importance of this type of inventory. We also observed that microhabitat use was associated with a significant difference in parasite richness between groups, in which arboreal and terrestrial species, and aquatic and arboreal species contributed to these differences. Moreover, larger frogs tended to be more parasitized regarding only an interspecific view. Our results suggest that parasite richness is directly related to infection cycle and how the host exploits its habitat.

Introduction

Parasites are diverse organisms that are an integral part of nature, representing most of the global biodiversity and one of the most common life strategies on the planet (Windsor, 1998; Poulin & Morand, 2004; Kuris, 2008). Parasitic organisms are also ecologically important (Marcogliese, 2004; Poulin & Morand, 2004) because they are closely related to environmental conditions, and thus, might be considered potential indicators of environmental quality (Catalano *et al.*, 2013). Despite the increase of parasitological studies, the science as a whole is still far from having complete knowledge about the parasite biodiversity and ecology on Earth (Poulin & Morand, 2004). Therefore, inventories are the basis for studies, and determining which and how many species is part of an ecosystem is essential for understanding the diversity and functioning of organisms (Segalla *et al.*, 2021). In addition, these organisms are involved in various processes of nature regulation and might influence host population conditions because they interfere in crucial processes such as competition, migration, dispersal and speciation (Vitt & Caldwell, 2009; Matias *et al.*, 2018). Thus, knowledge about parasite diversity and distribution is important to understand the role of parasite—host ecological relationships on ecosystem dynamics (Poulin & Krasnov, 2010; Campião *et al.*, 2015b).

The altitudinal enclaves of humid montane forests known as 'brejos-de-altitude' [highland swamps] are isolated areas in the morphoclimatic domain of the Caatingas, which are marked by a high degree of endemism of their herpetofauna (Borges-Nojosa & Caramaschi, 2003; Albuquerque *et al.*, 2012; Borges-Nojosa *et al.*, 2016). As they are considered exceptional environments, due to local climatic conditions, they form isolated systems considered as unique elements (Vanzolini, 1981; Borges-Nojosa & Caramaschi, 2003). Such areas are classified as of extreme biological importance (MMA, 2000; Sousa *et al.*, 2004), and responsible for the greatest richness of anurans in Ceará state, northeastern Brazil (Roberto & Loebmann, 2016). Despite the recent increase of parasitological studies dealing with anurans from these mountains (Silva-Neta *et al.*, 2020; Mascarenhas *et al.*, 2021; Machado *et al.*, 2022), their parasite diversity is still underestimated.

According to Aho (1990), anurans show low parasite richness that is variable and isolationist when compared to other vertebrate groups. However, some amphibian species may present

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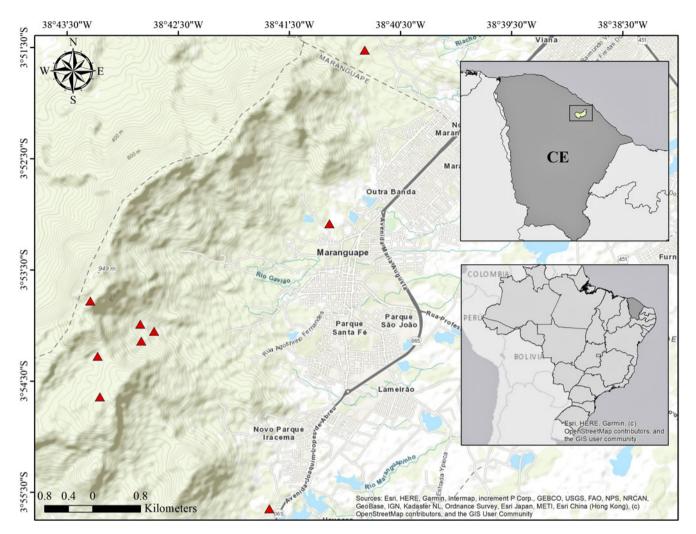


Fig. 1. Schematic map of the sampling points in Maranguape mountain, Ceará state, northeastern Brazil. Red triangles represent sampling points.

a higher richness of helminths (Hamann et al., 2006), being currently accepted that amphibians harbour rich and diverse helminth fauna (Campião et al., 2014; Oliveira et al., 2019; Mascarenhas et al., 2021; Machado et al., 2022). Recently published studies (e.g. Campião et al., 2015b; Lins et al., 2017; Oliveira et al., 2019; Silva-Neta et al., 2020; Mascarenhas et al., 2021) report processes that influence the structure of helminth communities in amphibians, including host size, genus, diet, site of infection, species and behaviour. In addition, features of host habitats are key factors in parasite colonization (Goater et al., 2005), drawing attention to the composition of parasite communities, which vary widely among host populations of the same species (Poulin et al., 2011; Bezerra et al., 2016).

In the present study: (i) we aimed to describe the composition of endoparasites associated with anurans from an altitudinal rainforest enclave in northeastern Brazil; (ii) to test if microhabitat use influences endoparasite abundance and richness; and (iii) to test the hypothesis that larger frogs tend to be more parasitized.

Material and methods

Study area

Sampling took place in the Maranguape mountain, Ceará state, northeastern Brazil (fig. 1), a crystalline residual massif with a

maximum altitude of 920 m, vegetation composed of humid forest covering the highest points, dry forest in the intermediate points gradually replacing the humid forest, and Caatinga in the lowlands (Borges-Nojosa & Caramaschi, 2003). The climatic regime is defined by two distinct seasons: dry season from June to December, and rainy season from January to May, with average annual precipitation of 1300 mm, and temperatures ranging from 26°C to 28°C (Ceará, 2002; IPECE, 2017).

Sampling

Anuran sampling occurred during the rainy season, from April to May 2019 (15 days of sampling) and from February to May 2020 (17 days of sampling), through visual and auditory searches (Bernarde, 2012). The sampling period started at dusk and extended until midnight (17:00–00:00 h), which is the time period when the majority of anuran species are most active in foraging and reproduction. For each individual, we determined the microhabitat use considering the site of capture (arboreal, aquatic or terrestrial).

The collected specimens were euthanized with a lethal injection of sodium thiopental (Thiopentax*), following the ethical procedures of the Federal Council of Veterinary Medicine - CFMV (2013). Afterwards, we measured the mass with a Pesola scale (precision 0.1 g) and the snout-vent length (SVL) using a Mitutoyo*



Fig. 2. Anurans found in Maranguape mountain, Ceará state, northeastern Brazil: (A) *Rhinella diptycha*; (B) *Rhinella granulosa*; (C) *Adelophryne maranguapensis*; (D) *Boana raniceps*; (E) *Corythomantis greeningi*; (F) *Dendropsophus minusculus*; (G) *Dendropsophus minutus*; (H) *Dendropsophus nanus*; (I) *Dendropsophus tapacurensis*; (J) *Scinax x-signatus*; (K) *Trachycephalus typhonius*; (L) *Adenomera juikitam*; (M) *Leptodactylus fuscus*; (N) *Leptodactylus macrosternum*; (O). *Leptodactylus mystaceus*; (P) *Leptodactylus pustulatus*; (Q) *Leptodactylus syphax*; (R) *Leptodactylus troglodytes*; (S) *Leptodactylus vastus*; (T) *Physalaemus cuvieri*; (U) *Elachistocleis piauiensis*; (V) *Proceratophrys cristiceps*; (W) *Proceratophrys renalis*; (X) *Pithecopus gonzagai*; and (Y) *Pristimantis relictus*.

digital caliper (precision 0.01 mm). Voucher specimens were fixed in 10% formalin according to Calleffo (2002) and deposited in the Herpetological Collection of the Federal University of Ceará (CHUFC – A 9762 to A 9953), Fortaleza, Brazil.

Parasitological procedures

We necropsied the anurans after performing a ventral incision and examined for the presence of endoparasites in the organs (gastrointestinal tract, lungs, liver and kidneys) and internal cavity using a stereomicroscope according to Amato *et al.* (1991). For species identification, we collected and prepared the endoparasites following specialized methodologies according to each taxonomic group (Yamaguti, 1971; Schmidt, 1986; Vicente *et al.*, 1991; Andrade, 2000). Temporary slides were analysed using a light microscope. Voucher specimens were deposited in the Parasitological Collection of the Universidade Federal do Ceará (CPUFC – 196 to 441), Fortaleza, Brazil.

 Table 1. The endoparasite community found in the anuran species from Maranguape mountain, Ceará state, northeastern Brazil.

Parasites	n	N.H	P (%)	M.I. + R	Ab. ± S.E.	S.I.
Acanthocephala						
Centrorhynchus sp.	168	14	16.67	0.69 (1–15)	0.55 ± 0.50	S. C. SI. I
Oligacanthorhynchus sp.	16	3	1.96	0.07 (1–10)	0.05 ± 1.47	C.
Annelida						
Dero (Allodero) lutzi	4	3	0.98	0.02 (1–2)	0.01 ± 0.33	UD.
Nematoda						
Aplectana crucifer	7	1	0.33	0.03 (7)	0.02	LI.
Aplectana membranosa	43	6	4.58	0.18 (1-9)	0.14 ± 0.69	SI. LI.
Aplectana meridionalis	45	1	1.96	0.19 (3-21)	0.15 ± 2.81	SI. LI.
Capillaria sp.	1	1	0.33	0.004 (1)	0.003	UD.
Cosmocerca brasiliense	10	1	0.33	0.04 (10)	0.03	SI. LI.
Cosmocerca parva	265	12	13.07	1.10 (1-74)	0.87 ± 2.08	S. SI. LI.
Cosmocerca podicipinus	46	1	1.63	0.19 (2–26)	0.15 ± 4.28	S. SI. LI.
Cosmocerca rara	85	4	1.96	0.35 (2-48)	0.28 ± 7.76	SI. LI.
Cosmocerca sp.	282	10	15.36	1.17 (1-41)	0.92 ± 1.32	S. SI. LI.
Cosmocercoides sp.	4	1	0.52	0.02 (4)	0.01	LI.
Falcaustra mascula	23	4	1.31	0.10 (1-11)	0.08 ± 2.49	SI. LI.
Ochoterenella convoluta	4	1	0.33	0.02 (4)	0.01	C.
Ochoterenella cf. vellardi	12	1	0.65	0.05 (2–10)	0.04 ± 4	C.
Ochoterenella sp.	4	3	0.65	0.02 (1-3)	0.01 ± 1	C. S.
Oswaldocruzia mazzai	980	15	27.12	4.05 (1–87)	3.20 ± 1.90	C. S. SI.
Oxyascaris caatingae	21	3	0.98	0.09 (1–18)	0.07 ± 5.50	SI. LI.
Parapharyngodon cf. duniae	15	1	0.65	0.06 (6–9)	0.05 ± 1.50	SI. LI.
Physaloptera sp.	247	19	19.61	1.02 (1–37)	0.81 ± 0.78	C. S. LV.
Physalopteroides venancioi	8	2	0.65	0.03 (2-6)	0.03 ± 2.0	C. S. SI.
Porrocaecum sp.	13	4	1.31	0.05 (1–8)	0.04 ± 1.60	C. S. LV.
Raillietnema spectans	1026	13	13.73	4.24 (1–253)	3.35 ± 7.79	SI. LI.
Rhabdias breviensis	276	11	11.44	1.14 (1-80)	0.90 ± 2.68	LG. LV.
Rhabdias cf. stenocephala	10	2	1.63	0.04 (1-4)	0.03 ± 0.54	LG.
Rhabdias pseudosphaerocephala	27	2	0.98	0.11 (9)	0.09	LG.
Rhabdias sp.	447	13	14.38	1.85 (1–105)	1.46 ± 2.90	LG.
Schrankiana schranki	905	4	1.96	3.74 (1–700)	2.96 ± 111.62	SI. LI.
Strongyloides sp.	14	6	2.61	0.06 (1–4)	0.05 ± 0.41	S. SI. LI.
Nematoda gen. sp.	7	2	0.65	0.03 (1-6)	0.02 ± 2.50	S. LI.
unidentified Ascarididae larvae	2	2	0.52	0.008 (1)	0.007	C.
unidentified Cosmocercidae larvae	1740	18	18.30	7.19 (1–247)	5.69 ± 7.36	S. SI. LI.
Platyhelminthes						
Cestoda						
Cylindrotaenia americana	6	2	0.98	0.02 (2)	0.02	SI.
Monogenea						
Polystoma cf. lopezromani	14	2	0.98	0.06 (1-8)	0.05 ± 2.02	UB.
Trematoda						
Catadiscus marinholutzi	1	1	0.33	0.004 (1)	0.003	LI.

Table 1. (Continued.)

Parasites	n	N.H	P (%)	M.I. + R	Ab. ± S.E.	S.I.
Catadiscus propinquus	76	3	2.61	0.31 (2-22)	0.25 ± 2.67	SI. LI.
Choledocystus simulans	37	1	0.98	0.15 (1–35)	0.12 ± 11.33	SI.
Choledocystus vitellinophilum	1	1	0.33	0.004 (1)	0.003	SI.
Gorgoderina parvicava	3	1	0.33	0.01 (3)	0.01	UB.
Lophosicyadiplostomum sp.	17	3	0.98	0.07 (3-7)	0.06 ± 1.33	K.
Mesocoelium monas	3	1	0.65	0.01 (1-2)	0.01 ± 0.50	SI.
Neohaematoloechus neivai	56	1	1.31	0.23 (3–21)	0.18 ± 4.18	G. SI.
Rauschiella linguatula	13	2	1.96	0.05 (1-4)	0.04 ± 0.60	S. SI.
Rudolphitrema sp.	5	1	0.33	0.02 (5)	0.02	SI.
unidentified Metacercaria larvae	53	4	1.96	0.22 (5–18)	0.17 ± 2.05	K.
Total	7042	242	79.08	29.09 (1–700)	23.01 ± 1.58	

n, number of parasites; N.H., number of infected hosts; P%, prevalence; M.I., mean intensity; R, range; Ab., abundance; S.E., standard error; S.I., site of infection; C, cavity; S, stomach; SI, small intestine; LI, large intestine; LV, liver; LG, lung; G, gallbladder; PA, pancreas; K, kidney; UB, urinary bladder; and UD, urinary duct.

We measured the following parasitological parameters according to Bush *et al.* (1997): prevalence (percentage of parasitized amphibians in each host species); mean intensity of infection (mean number of parasites in parasitized amphibians); and mean parasite abundance.

Statistical analyses

We used the non-parametric Kruskal-Wallis test (Shapiro-Wilk < 0.05) to investigate whether parasite richness and abundance vary in response to microhabitat used by anuran species (aquatic, arboreal and terrestrial), followed by Dunn's *post-hoc* test to investigate which groups contributed most to the differences (*P*-values adjusted with the Benjamini-Hochberg method). Regarding both interspecific and intraspecific views, we tested the influence of anuran body size (SVL and mass) on the abundance and richness of parasites with a linear mixed model, using host sex as a random effect. For this test, we used only anuran species with more than five individuals parasitized. Analyses and graphs were performed using the packages ggplot2 (Wickham, 2016), nlme (Pinheiro & Bates, 2000), vegan (Oksanen *et al.*, 2016) and FSA (Ogle *et al.*, 2022) from R software (R core team, 2021).

Results

We sampled 306 individuals from 25 anuran species (fig. 2), of which 242 individuals (75 females, 161 males and six juveniles) were parasitized with at least one parasite taxon. We found 7042 helminth specimens, with an overall prevalence of 79.08%, mean infection intensity of 29.09 and total abundance of 23.01 ± 1.58. The endoparasite community consisted of 46 taxa. The most abundant taxa were *Raillietnema spectans*, *Oswaldocruzia mazzai* and *Schrankiana schranki*. The highest prevalence values were observed for *Oswaldocruzia mazzai*, *Physaloptera* sp. and *Centrorhynchus* sp. Endoparasite richness ranged from two to 17 parasites taxa per host, *Oswaldocruzia mazzai* and *Physaloptera* sp. being the most prevalent parasites (table 1).

The most parasitized anurans were *Trachycephalus typhonius* (n = 17), *Pristimantis relictus* (n = 17) and *Physalaemus cuvieri* (n = 15). *Adelophryne maranguapensis* was not parasitized, while

Leptodactylus troglodytes (n = 2), Rhinella granulosa (n = 3) and Adenomera juikitam (n = 3) had few associated parasite taxa. In addition, we found 20 new host records and two possible new parasite species (table 2).

We observed that microhabitat use was associated with a significant difference in parasite richness between groups (H = 13.35, P = 0.0012), in which Dunn's *post-hoc* test evidenced that arboreal and terrestrial species (P = 0.001) and aquatic and arboreal species (P = 0.023) contributed significantly to these differences (fig. 3). By contrast, parasite abundance did not vary significantly between groups (H = 5.2821, P > 0.05).

We also observed that larger frogs (SVL) tend to be more parasitized considering the parasite abundance (T = 2.148, P = 0.0328) and richness (T = 4.576, P = 0.0001), regardless of sex (intercept = 0.0041 and 0.1291, respectively) (fig. 4). Mass had no significant influence on both abovementioned parasitological descriptors (P > 0.05). In an intraspecific view, parasite load (richness and abundance) seemed not to be influenced by the size of each anuran species (table 3).

Discussion

Communities of endoparasites associated with anurans generally show high richness and diversity (Campião et al., 2014); in the present study, we found 46 parasite taxa, corroborating this pattern. Following the same infection pattern found in other Neotropical anurans (Lins et al., 2017; Oliveira et al., 2019; Silva-Neta et al., 2020; Mascarenhas et al., 2021), as well as in other vertebrate groups, such as reptiles (Brito et al., 2014; Carvalho et al., 2018), mammals (Santos et al., 2015; Biolchi et al., 2021) and birds (Santos et al., 2015), nematodes was the helminth group with the highest representation (65.2%) of the collected specimens. Nematodes are abundant in the number of species, generalists, and well distributed in the environment. Species with direct life cycle reach their hosts by oral ingestion or active penetration of infectious larvae through the skin, not requiring an intermediate host for their development (Anderson, 2000), which facilitates the dispersion and high incidence of infection of this parasite group. Although parasitological studies dealing with anuran communities in northeastern Brazil have recently increased, there are still important gaps in our

 Table 2. List of endoparasites found in the anuran species from Maranguape mountain, Ceará state, northeastern Brazil and literature review for previous records.

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
Bufonidae				
Rhinella diptycha	unidentified Cosmocercidae larvae	13.3	16.7	-
(n = 15; P% = 86.7)	Cosmocerca sp.	26.7	3.5	new record
	Ochoterenella sp.	6.7	0.2	Aguiar et al., 2021
	Oswaldocruzia mazzai	53.3	8.9	Aguiar et al., 2021
	Physaloptera sp.	13.3	0.4	Amorim et al., 2019
	Raillietnema spectans	6.7	0.9	Amorim et al., 2019
	Rhabdias pseudosphaerocephala	20	1.8	Aguiar et al., 2021
	Rhabdias sp.	60	4.8	Amorim et al., 2019; Aguiar et al., 2021
	Schrankiana schranki	6.7	0.1	new record
	Centrorhynchus sp.	13.3	0.6	new record
	Oligacanthorhynchus sp.	6.7	0.1	new record
	Mesocoelium monas	13.3	0.2	new record
Rhinella granulosa	Oswaldocruzia mazzai	66.7	3.2	Silva-Neta et al., 2020
(n = 6; P% = 83.3)	Physaloptera sp.	66.7	5.7	Campião et al., 2014; Teles et al., 2018
	Raillietnema spectans	83.3	14.8	Teles et al., 2018; Silva-Neta et al., 2020
Strabomantidae				
Pristimantis relictus	unidentified Cosmocercidae larvae	15.6	7.2	-
(n = 45; P% = 88.9)	Aplectana membranosa	13.3	0.5	new record
	Aplectana meridionalis	13.3	1	new record
	Capillaria sp.	2.2	0.02	new record
	Cosmocerca parva	8.9	0.1	new record
	Cosmocerca rara	2.2	1.1	new record
	Cosmocerca sp.	33.3	1.4	new record
	Ochoterenella cf. vellardi	4.4	0.3	new record
	Oswaldocruzia mazzai	2.2	0.02	new record
	Physaloptera sp.	13.3	0.2	new record
	Raillietnema spectans	20	6.1	new record
	Rhabdias breviensis	15.6	0.2	new record
	Rhabdias sp.	13.3	0.7	new record
	Strongyloides sp.	2.2	0.02	new record
	Nematoda gen. sp. (females)	2.2	0.02	a
	Choledocystus simulans	6.7	0.8	new record
	Gorgoderina parvicava	2.2	0.1	new record
Eleutherodactylidae				
Adelophryne maranguapensis	-	-	-	not parasitized
Hylidae				
Boana raniceps	unidentified Cosmocercidae larvae	60	30.67	-
(n = 15; P% = 93.3)	Aplectana membranosa	6.7	0.53	Aguiar et al., 2021; Sani et al., 2021
	Cosmocerca parva	13.3	5.67	González & Hamann, 2011, 2015; Machado et al., 2022

Table 2. (Continued.)

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
	Cosmocerca rara	6.67	1.73	new record
	Oswaldocruzia mazzai	46.67	17.2	Campião et al., 2015a; Machado et al., 2022
	Oxyascaris caatingae	6.67	0.07	new record
	Physaloptera sp.	13.33	1.27	Campião et al., 2016a; Graça et al., 2017; Sani et al., 2021
	Physalopteroides venancioi	6.67	0.4	Campião et al., 2016b
	Rhabdias breviensis	33.33	9.67	new record
	Rhabdias sp.	40	8.73	Graça et al., 2017; Sani et al., 2021; Machado et al., 2022
	Strongyloides sp.	6.67	0.27	new record
	Centrorhynchus sp.	20	0.8	new record
	Choledocystus vitellinophilum	6.67	0.07	Travassos et al., 1969; Aguiar et al., 2021
Corythomantis greeningi	unidentified Cosmocercidae larvae	20	11	-
(n = 5; P% = 100)	Cosmocerca sp.	20	2.2	new record
	Oswaldocruzia mazzai	60	1.2	new record
	Rhabdias sp.	20	2.6	new record
	Dero (Allodero) lutzi	20	0.2	Morais et al., 2017
	Polystoma cf. lopezromani	20	0.2	new record
Dendropsophus minusculus	unidentified Cosmocercidae larvae	13.3	0.8	-
(n = 15; P% = 40)	Cosmocerca parva	6.7	0.8	new record
	Physaloptera sp.	6.7	3.4	new record
	Rhabdias breviensis	13.3	0.8	new record
	Centrorhynchus sp.	6.7	0.4	new record
	Cylindrotaenia americana	6.7	0.4	new record
	unidentified Metacercaria larvae	6.7	2.2	-
Dendropsophus minutus	unidentified Cosmocercidae larvae	6.3	2.5	-
(n = 16; P% = 75)	Cosmocerca parva	31.3	2.9	new record
	Cosmocerca sp.	12.5	0.1	Martins-Sobrinho et al., 2017
	Ochoterenella sp.	6.3	0.06	new record
	Oswaldocruzia mazzai	6.3	0.06	new record
	Physaloptera sp.	6.3	0.06	new record
	Raillietnema spectans	6.3	0.06	new record
	Rhabdias breviensis	6.3	0.4	new record
	Rhabdias pseudosphaerocephala	6.3	0.1	new record
	Rhabdias sp.	6.3	0.06	new record
	Centrorhynchus sp.	6.3	0.9	new record
	Lophosicyadiplostomum sp.	6.3	0.4	Aguiar et al., 2021
	unidentified Metacercaria larvae	6.3	0.3	-
Dendropsophus nanus	unidentified Cosmocercidae larvae	7.7	0.06	-
(n = 13; P% = 38.5)	Centrorhynchus sp.	23.1	0.8	Campião et al., 2014

Table 2. (Continued.)

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
	Cylindrotaenia americana	15.4	0.3	Hamann & Kehr, 1998
	Lophosicyadiplostomum sp.	7.7	0.4	Queiroz et al., 2020
Dendropsophus tapacurensis	unidentified Cosmocercidae larvae	5.9	0.06	-
(n = 17; P% = 23.5)	Physaloptera sp.	17.6	0.4	new record
	Rhabdias breviensis	5.9	0.06	new record
Scinax x-signatus	unidentified Cosmocercidae larvae	17.4	2	-
(n = 23; P% = 69.6)	Aplectana membranosa	4.3	0.04	new record
	Cosmocerca parva	8.7	0.5	new record
	Cosmocerca rara	4.3	0.2	new record
	Cosmocercoides sp.	4.3	0.2	a
	Physaloptera sp.	21.7	1.9	new record
	Rhabdias breviensis	26.1	2.9	new record
	Rhabdias sp.	13	3.2	new record
	Strongyloides sp.	4.3	0.04	new record
	Centrorhynchus sp.	8.7	1.2	Martins-Sobrinho et al., 2017
	Oligacanthorhynchus sp.	4.3	0.04	new record
	Dero (Allodero) lutzi	4.3	0.04	Morais et al., 2017
	Lophosicyadiplostomum sp.	4.3	0.1	new record
	unidentified Metacercaria larvae	4.3	0.3	-
Trachycephalus typhonius	unidentified Ascarididae larvae	5.6	0.1	-
(n = 18; P% = 100)	unidentified Cosmocercidae larvae	50	13.5	-
	Aplectana crucifer	5.6	0.4	new record
	Cosmocerca parva	5.6	0.2	new record
	Cosmocerca sp.	27.8	3.3	Campião et al., 2014
	Oswaldocruzia mazzai	55.6	10.4	new record
	Parapharyngodon cf. duniae	11.1	0.8	Bursey & Brooks, 2004
	Physaloptera sp.	5.6	0.1	Campião et al., 2016a; Graça et al., 2017
	Raillietnema spectans	22.2	1.1	new record
	Rhabdias breviensis	5.6	0.1	new record
	Rhabdias sp.	5.6	0.1	Graça et al., 2017
	Schrankiana schranki	5.6	0.1	new record
	Strongyloides sp.	11.1	0.3	new record
	Nematoda gen. sp. (female)	5.6	0.3	a
	Centrorhynchus sp.	38.9	0.7	Aguiar et al., 2021
	Dero (Allodero) lutzi	5.6	0.1	Graça et al., 2017
	Polystoma cf. lopezromani	11.1	0.7	Campião et al., 2014; Graça et al., 2017
Leptodactylidae				
Adenomera juikitam	Cosmocerca sp.	25	0.5	new record
(n = 8; P% = 25)	Oswaldocruzia mazzai	12.5	0.13	new record

Table 2. (Continued.)

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
Leptodactylus fuscus	Cosmocerca parva	25	0.3	Morais, 2013; Campião et al., 2014
(n = 4; P% = 100)	Physaloptera sp.	50	2	Morais, 2013
	Raillietnema spectans	50	29.5	Silva-Neta et al., 2020
	Rhabdias sp.	50	1.3	Cañizales, 2021
	Schrankiana schranki	75	50.5	Morais, 2013
	Centrorhynchus sp.	50	1.3	Sani <i>et al.</i> , 2021
	Catadiscus propinquus	25	0.5	Aguiar et al., 2021
Leptodactylus macrosternum	unidentified Cosmocercidae larvae	14.3	0.2	-
(n = 14; P% = 100)	Cosmocerca parva	25 0.3 Morais, 2013; Campião et al., 2014	González & Hamann, 2011; Campião et al., 2014	
	Cosmocerca sp.	14.3	0.7	new record
	Falcaustra mascula	7.1	0.07	Morais, 2013; Graça et al., 2017
	Oswaldocruzia mazzai	35.7	5.1	Silva-Neta et al., 2020
	Physaloptera sp.	42.9	2.2	Campião et al., 2016a; Queiroz et al., 2020; Vieira et al., 2021
	Physalopteroides venancioi	7.1	0.1	Morais, 2013; Campião et al., 2016a
	Rhabdias breviensis	21.4	0.5	new record
	Rhabdias sp.	35.7	0.9	González & Hamann, 2011; Graça et al., 2017; Queiroz et al., 2020; Vieira et al., 2021
	Centrorhynchus sp.	21.4	0.3	Campião et al., 2014
	Porrocaecum sp.	7.1	0.6	González & Hamann, 2015
	Catadiscus propinquus	7.1	0.1	Queiroz et al., 2020
	Rauschiella linguatula	14.3	0.4	Graça et al., 2017; Aguiar et al., 2021
Leptodactylus mystaceus	Cosmocerca sp.	66.7	0.7	new record
(n = 3; P% = 100)	Oswaldocruzia mazzai	66.7	1.7	Campião et al., 2015a
	Physaloptera sp.	33.3	0.07	Queiroz et al., 2020
	Raillietnema spectans	33.3	2.7	Silva-Neta et al., 2020
Leptodactylus pustulatus	unidentified Cosmocercidae larvae	9.1	0.3	-
(n = 11; P% = 90.9)	Cosmocerca sp.	9.1	0.4	new record
	Oxyascaris caatingae	9.1	0.2	new record
	Physaloptera sp.	9.1	0.5	Morais, 2013
	Rhabdias cf. stenocephala	36.4	0.5	new record
	Rhabdias sp.	9.1	0.2	new record
	Centrorhynchus sp.	18.2	0.5	new record
	Catadiscus propinquus	54.5	6.5	new record
	Rauschiella linguatula	36.4	0.7	new record
Leptodactylus syphax	Falcaustra mascula	50	4.5	Morais, 2013
(n = 2; P% = 100)	Ochoterenella convoluta	50	2	new record
	Oswaldocruzia mazzai	100	3.5	new record
	Raillietnema spectans	100	96	new record
	Rhabdias cf. stenocephala	50	2	new record
	Porrocaecum sp.	50	1	new record
Leptodactylus troglodytes	unidentified Cosmocercidae larvae	100	1	-
-				(Continu

Table 2. (Continued.)

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
	Raillietnema spectans	100	17	new record
Leptodactylus vastus	unidentified Cosmocercidae larvae	22.2	0.4	-
(n = 9; P% = 100)	Falcaustra mascula	11.1	1.2	new record
	Ochoterenella sp.	11.1	0.1	new record
	Oswaldocruzia mazzai	55.6	1.6	Silva-Neta et al., 2020
	Oxyascaris caatingae	11.1	2	new record
	Physaloptera sp.	55.6	3.3	new record
	Raillietnema spectans	11.1	28.1	Silva-Neta et al., 2020
	Rhabdias breviensis	44.4	1.9	new record
	Rhabdias sp.	33.3	4	new record
	Schrankiana schranki	11.1	77.8	Campião et al., 2014
	Centrorhynchus sp.	33.3	2.9	new record
	Oligacanthorhynchus sp.	44.4	1.6	new record
	Neohaematoloechus neivai	44.4	6.2	new record
	Porrocaecum sp.	11.1	0.2	new record
Physalaemus cuvieri	unidentified Cosmocercidae larvae	17.2	6.7	-
(n = 29; P% = 96.6)	Aplectana membranosa	3.4	0.1	new record
	Cosmocerca parva	27.6	1	Santos & Amato, 2013
	Cosmocerca podicipinus	10.3	0.2	new record
	Cosmocerca rara	24.1	2.5	new record
	Cosmocerca sp.	20.7	0.5	Aguiar et al., 2015
	Oswaldocruzia mazzai	27.6	0.4	Oliveira et al., 2019
	Physaloptera sp.	17.2	0.6	Toledo <i>et al.</i> , 2017; Sani <i>et al.</i> , 2021;
	Raillietnema spectans	17.2	2.3	Oliveira et al., 2019; Silva-Neta et al., 2020
	Rhabdias breviensis	3.4	0.03	new record
	Rhabdias sp.	17.2	1.6	Graça et al., 2017; Toledo et al., 2017; Aguiar et al., 2021
	Strongyloides sp.	10.3	0.2	new record
	Centrorhynchus sp.	3.4	0.03	new record
	Porrocaecum sp.	3.4	0.2	new record
	Rudolphitrema sp.	20.7	0.3	new record
Microhylidae				
Elachistocleis piauiensis	Cosmocerca parva	50	9.5	new record
(n = 4; P% = 75)	Physaloptera sp.	25	0.3	new record
	Raillietnema spectans	25	1	new record
Odontophrinidae				
Proceratophrys cristiceps	unidentified Cosmocercidae larvae	50	0.04	-
(n = 2; P% = 100)	Aplectana membranosa	50	0.04	Teles et al., 2017; Silva et al., 2019
	Falcaustra mascula	50	0.04	Silva et al., 2019
	Physaloptera sp.	50	1	Teles <i>et al.</i> , 2017; Silva <i>et al.</i> , 2019
Proceratophrys renalis	unidentified Ascarididae larvae	7.1	0.1	-
(n = 14; P% = 92.9)		21.4	3.1	-

Table 2. (Continued.)

Hosts (n = 306)	Parasite species	P (%)	A.M.	Reference
<u> </u>	unidentified Cosmocercidae larvae			
	Aplectana membranosa	14.3	0.4	new record
	Cosmocerca parva	42.9	1.4	new record
	Oswaldocruzia mazzai	85.7	13.8	new record
	Physaloptera sp.	21.4	0.7	new record
	Raillietnema spectans	28.6	1.5	new record
	Centrorhynchus sp.	21.4	0.6	new record
Phyllomedusidae				
Pithecopus gonzagai	unidentified Cosmocercidae larvae	21.4	1.5	-
(n = 14; P% = 92.9)	Cosmocerca parva	7.1	0.07	Martins-Sobrinho et al., 2017
	Cosmocerca brasiliense	7.1	0.7	new record
	Oswaldocruzia mazzai	7.1	0.5	new record
	Physaloptera sp.	14.3	0.3	new record
	Rhabdias breviensis	14.3	0.7	new record
	Strongyloides sp.	14.3	0.1	new record
	Centrorhynchus sp.	42.9	1.1	Martins-Sobrinho et al., 2017
	Catadiscus marinholutzi	7.1	0.07	new record
	unidentified Metacercaria larvae	21.4	2.1	-

n, number of hosts; P%, prevalence; and A.M., abundance.

knowledge about them. For example, of the 25 host species sampled herein, six have not been surveyed for parasites yet. In addition, we present 20 new host records (see table 2), reinforcing the importance of parasite checklists.

Due to the increase in parasitological studies (Mascarenhas et al., 2021), it is quite common to find records of parasites not

previously reported for host species (Aguiar *et al.*, 2014; Silva *et al.*, 2019). In the last decade, several studies on parasitism in Neotropical amphibians have been conducted (Madelaire *et al.*, 2012; Aguiar *et al.*, 2015; Chero *et al.*, 2016; Amorim *et al.*, 2019; Silva-Neta *et al.*, 2020; Sani *et al.*, 2021; Machado *et al.*, 2022), with the nematode parasites *Falcaustra mascula*,

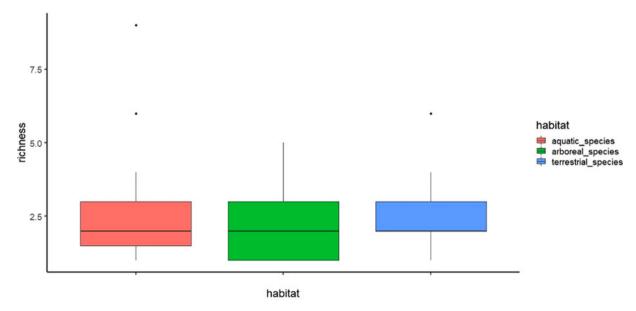


Fig. 3. Boxplot representing the parasite richness between the groups of microhabitats used by the anurans.

apossible new species.

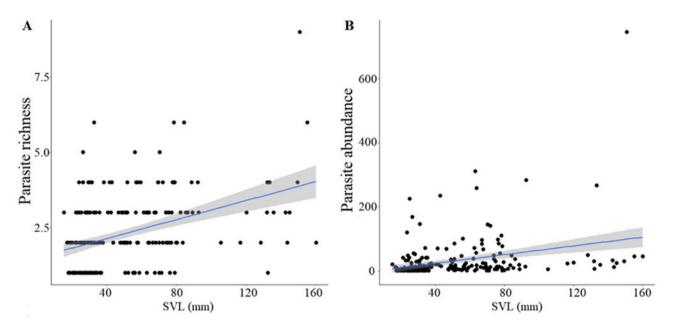


Fig. 4. Relationship of parasite richness (A) and abundance (B) with the host's body size (anuran interspecific view) from Maranguape mountain, Ceará state, northeastern Brazil

Ochoterenella sp., Oswaldocruzia mazzai, Oxyascaris oxyascaris, Physaloptera sp., Raillietnema spectans and Rhabdias sp. being the most commonly reported species. In our study, we found the same scenario, despite the low prevalence for some of the aforementioned species. This result is possibly due to the wide distribution of these parasites and their generalist habitats regarding host selection (Campião et al., 2014, 2015b; Oliveira et al., 2019). In addition, the lack of taxonomic studies can be a limiting factor for an accurate identification of some parasite species distributed in the studied region. However, the description of new species has been increasing as parasitological studies progress (Felix-Nascimento et al., 2020).

Oswaldocruzia mazzai showed the highest prevalence (27.12%) and was present in 60% of the parasitized host species in the anuran community in our study. This result may be related to the direct life cycle of this parasite and the simple mode of transmission (Anderson, 2000). The genus Physaloptera had the second highest prevalence (19.61%). Parasites of this group are commonly found in all anuran parasite studies and have also been observed in several classes of terrestrial vertebrates (Ogassawara et al., 1986; Tung et al., 2009; Cabral et al., 2018). In amphibians, they are usually found in the larval stage, suggesting that these vertebrates are used as paratenic hosts. We also collected four individuals of Cosmocercoides sp. (one male and three females) in the large intestine of one specimen of Scinax x-signatus. The species was assigned to the genus Cosmocercoides due to the presence of a large number of rosette-like caudal papillae surrounded by punctuations. This is the first record of Cosmocercoides sp. for altitudinal rainforest enclave areas within the large Caatinga phytophysiognomy, nevertheless, further studies are necessary to define the species. Additionally, we also provide the first record of infection in Brazil of the species Parapharyngodon cf. duniae.

We also found nematode larvae parasitizing the small intestine and/or large intestine of several host species. Larvae of this type are commonly found in amphibian and reptile species (Ávila & Silva, 2010; Campião *et al.*, 2014), and this larval stage may be

associated with the monoxenous cycle of the parasite (Anderson, 2000), besides representing a recent infection and/or reproduction of the adult parasites in the host.

Platyhelminthes was the second most diverse phylum found in the present study, with 13 different taxa belonging to three classes (Cestoda, Monogenea and Trematoda). The most diverse class of Platyhelminthes was Trematoda with 11 taxa recorded. The aquatic habitat facilitates trematodes' infection, which usually have snails as intermediate hosts (Madelaire et al., 2012). These parasites also use amphibians as intermediate hosts (Guillén-Hernández et al., 2000), found more often in aquatic and semiaquatic frogs such as leptodactylids (Campião et al., 2014; Oliveira et al., 2019). Catadiscus propinquus was the most abundant trematode and represents a new host record for Leptodactylus pustulatus. Indeed, some species are new host records; however, all trematodes had low prevalence considering the species pool (see table 2). Cestodes were represented by Cylindrotaenia americana, a cestode commonly found in Brazil, including in altitudinal rainforests' enclaves (Oliveira et al., 2019; Silva-Neta et al., 2020). Herein, we provide the first record of this cestode in the treefrogs Dendropsophus minusculus and Dendropsophus nanus. Regarding monogenean parasites, we found 14 individuals of Polystoma cf. lopezromani parasitizing Corythomantis greeningi and Trachycephalus typhonius. Polystoma is the most diverse genus known in Polystomatidae (Sinnappah et al., 2001), having a direct life cycle, which can be completed in the gills of tadpoles or urinary duct of adult anurans (Bentz et al., 2006).

Acanthocephalans are extensively reported for reptiles (Matias et al., 2018; Araújo et al., 2020) and amphibians (Oliveira et al., 2019; Silva-Neta et al., 2020) as cystacanths. They are parasites with indirect life cycle, in which arthropods act as intermediate hosts, and fish, mammals or waterfowl as final hosts (Baker, 2007). The presence of these cystacanths in amphibian hosts indicates that these species are used as paratenic hosts, possibly infected through the diet. In the present study, we found two genera represented by *Centrorhynchus* and *Oligacanthorhynchus*. *Centrorhynchus* sp. is the most common

Table 3. Relationship between parasite richness and abundance with anuran body size (snout-vent length (SVL) and mass), regarding an interspecific view, obtained through linear mixed models.

	Para	asite richness			Parasite abundance			
Таха	St. D. ± S.E.	Т	Р	RE	Т	Р	RE	
Bufonidae								
Rhinella diptycha				0.000131			0.00604	
mass	141.86 ± 39.34	-0.566	0.586		-0.584	0.575		
SVL	31.09 ± 8.62	0.183	0.859		0.322	0.755		
Hylidae								
Boana raniceps				1.721969			43.6378	
mass	6.62 ± 1.76	0.0891	0.930		-0.262	0.798		
SVL	7.80 ± 2.08	0.880	0.399		-0.067	0.947		
Dendropsophus minutus				2.577e-05			0.00364	
mass	0.17 ± 0.05	-0.116	0.910		0.099	0.923		
SVL	3.13 ± 0.94	1.562	0.162		-0.294	0.776		
Scinax x-signatus				7.145e-05			0.00087	
mass	0.49 ± 0.12	0.453	0.658		-1.731	0.108		
SVL	2.60 ± 0.65	-0.537	0.600		1.964	0.073		
Trachycephalus typhonius				2.401e-05			0.00168	
mass	6.69 ± 1.57	-0.734	0.474		-1.429	0.174		
SVL	10.02 ± 2.36	0.498	0.625		1.305	0.212		
Leptodactylidae								
Leptodactylus macrosternum				2.686e-05			0.00090	
mass	25.08 ± 6.70	0.727	0.485		0.971	0.356		
SVL	15.34 ± 4.10	0.966	0.359		-1.110	0.295		
Leptodactylus pustulatus				0.4825533			13.08361	
mass	5.19 ± 1.64	-0.664	0.530		-0.743	0.485		
SVL	9.22 ± 2.91	0.754	0.479		1.190	0.278		
Leptodactylus vastus				6.832e-05			0.02836	
mass	104.23 ± 34.74	1.473	0.200		1.257	0.264		
SVL	37.15 ± 12.38	-0.352	0.738		-0.777	0.472		
Physalaemus cuvieri				2.987e-05			13.82402	
mass	0.42 ± 0.07	0.634	0.531		-0.263	0.794		
SVL	1.87 ± 0.35	-0.242	0.810		-0.427	0.672		
Odontophrynidae								
Proceratophrys renalis				3.469e-05			9.79580	
mass	3.47 ± 0.96	1.138	0.284		1.184	0.266		
SVL	3.33 ± 0.92	-0.475	0.645		-2.072	0.068		
Phyllomedusidae								
Pithecopus gonzagai				3.101e-05			0.00053	
mass	0.33 ± 0.09	1.249	0.243		0.790	0.449		
SVL	2.29 ± 0.63	-0.118	0.908		-0.093	0.927		
Strabomantidae								
Pristimantis relictus				4.676e-05			0.00264	

Table 3. (Continued.)

	Par 	Parasite richness			Parasite ab	undance	
Taxa	St. D. ± S.E.	Т	Р	RE	Т	Р	RE
mass	0.48 ± 0.07	0.919	0.363		-0.196	0.864	
SVL	3.81 ± 0.60	-0.012	0.990		0.171	0.845	

St. D. ± S.E., standard deviation and standard error.

Significant values and percentage of variation in response that is explained by the fixed effects (mass and SVL) are represented by P and T values. Random effects were obtained through the intercept values (RE).

genus reported in Brazil for anuran hosts (Fabio, 1982; Smales, 2007). *Oligacanthorhynchus* sp. are heteroxenous parasites and usually have mammals as final hosts (Richardson *et al.*, 2014). In South America, they are reported infecting *Odontophrynus americanus* (Silva *et al.*, 2018) and *Pleurodema diplolister* (Silva-Neta *et al.*, 2020). This study is the first record of *Oligacanthorhynchus* sp. for the anurans *Leptodactylus vastus*, *Rhinella diptycha* and *Scinax x-signatus*.

Regarding the phylum Annelida, we found four individuals of *Dero (Allodero) lutzi* in the urinary duct of *Corythomantis greeningi, Scinax x-signatus* and *Trachycephalus typhonius*. The genus *Dero* is known to use frogs for transport and as hosts (Oda *et al.*, 2015). This behaviour is stimulated by chemicals released by the amphibians, which are used by the parasite for dispersal (Lopez *et al.*, 2005). *Dero (Allodero) lutzi* has been found parasitizing different amphibians, mainly arboreal species (Oda *et al.*, 2015), likely because these parasites are free-living inhabitants of bromeliad ponds and tree holes (Lopez *et al.*, 1999).

The characteristics and the way the host explores its habitat can influence the composition and structure of the helminth fauna, and explain the richness and diversity of the parasites associated with it (Poulin & Morand, 2004; Chandra & Gupta, 2007; Euclydes et al., 2021). Thus, anuran amphibians have a diverse parasite fauna due to their natural history (Prudhoe & Bray, 1982), which are generally associated with two types of environments, aquatic and terrestrial (Chandra & Gupta, 2007). Species of arboreal amphibians tend to have low parasite richness, due to a possible reduction in the encounter with infective parasitic larvae. On the other hand, host anurans with terrestrial or semi-aquatic habitats tend to have greater contact with the terrestrial environment when searching for water bodies, increasing the odds of contact with a greater number of parasites (Pizzatto et al., 2013; Euclydes et al., 2021).

However, we observed that the arboreal habitat had great parasite richness. The higher number of individuals classified as arboreal (n = 163) in the present study may be an explanation for the significant relationship of arboreal habitat with parasite richness. Most species classified as arboreal were found during the reproductive period, in which anurans seek out puddles and mate for reproduction, passing through terrestrial and aquatic environments. This provides a greater likelihood of direct contact with infectious larvae, which allows a greater variety of parasites to become established in these animals (Chandra & Gupta, 2007).

According to Todd (2007), endoparasitic helminths of amphibians require an aquatic environment for the development and transmission of their infective stages, as this promotes increased parasite transmission. However, we observed that the use of terrestrial and arboreal microhabitat contributed significantly to the abundance of parasites, showing that most helminth parasites of amphibians do not require an aquatic environment in the process of transmission and infection. Our data also indicated no

relationship between host sex and parasite richness, but this result may have been influenced by the difference in the number of individuals of each sex analysed (Madeira & Sogayar, 1993). Moreover, most anuran hosts do not present differentiation in habitat use according to sex, being both subject to the same chances of infection by infective larvae available in the environment. It is also noteworthy that biotic factors such as the immune system and host age also affect parasitism, as they influence the life of both parasite and host (Pietrock & Marcogliese, 2004).

Overall, at an interspecific view, we observed that larger frogs tend to be more parasitized. Indeed, larger hosts can support a higher parasite load and even higher species richness because they offer greater microhabitat diversity favouring the development and reproduction of parasites (George-Nascimento *et al.*, 2004; Campião *et al.*, 2015b). However, this hypothesis was not supported in the present study at intraspecific views. This pattern was also found in other parasitological studies dealing with amphibians (e.g. Oliveira *et al.*, 2019; Mascarenhas *et al.*, 2021; Machado *et al.*, 2022). It seems that this hypothesis might be more evidenced concerning a species pool with anuran species of different sizes (e.g. Silva-Neta *et al.*, 2020). Therefore, for congeneric species, we believe that other aspects such as microhabitat use, physiology, behaviour and seasonality, might have a greater influence on parasite load than the anuran size.

We conclude that the endoparasite composition of anurans from Maranguape mountain follow the common pattern described for Neotropical amphibians, showing high species richness and prevalence. We also recorded the first parasitological data for six anuran species and 20 new host records, which corroborates the hypothesis that amphibians are good models for parasite studies due to their way of life, behaviour and feeding. Furthermore, we stress the importance of parasite inventories for host species in understudied regions. We also emphasize that endoparasite composition has a significant relationship with the type of habitat used by the host due to the life cycle and mode of transmission of the parasites. As for the relationship between richness and host size, we indicate here that the size factor is predictive only if it has a large variation from the average host size.

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Conflicts of interest. None.

Ethical standards. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals. Collection permit Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (#72384-1 and #73215-1) and Ethic Committee on Animal Use of the Federal University of Ceará (CEUA-UFC) (#CEUA 6314010321).

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