

Article

Helminth's assemblage of a small frog in the Brazilian semiarid: parasite-host-environment relationships

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ABSTRACT. Parasite infections may contingency different aspects of the hosts' lives, and are usually expected to directly or indirectly compromise host reproduction. However, although amphibians have historically been study models in parasite ecology, the effects of parasitism on amphibians' reproduction remain unknown. Thus, we investigated how the parasite load varies as a function of climatic seasonality (rainy and dry season) and intrinsic host characteristics (size and sex), as well as the relationship between parasite load and reproductive investment in males and females of a small frog (*Pseudopaludicola pocoto* Magalhães, Loebmann, Kokubum, Haddad & Garda, 2014) in the Brazilian semiarid region. The parasitological parameters of the studied population were not influenced by the season of the year or by the hosts' body size, but females of *P. pocoto* had a higher prevalence and intensity of infection than males. The number of oocytes and the volume of the testes were not related to the parasite load, revealing that the parasitism did not negatively impact the gonadal investment in *P. pocoto*. Our findings suggest that short-lived species, such as the tiny *Pseudopaludicola* species, have a high reproductive investment independent of their parasitic interactions. In addition, this should be true mainly in those species that live in seasonally dry environments, such as *P. pocoto*, in which reproduction is even more constrained by the shortened and unpredictable rainy period.

KEYWORDS. Amphibia, *Pseudopaludicola*, seasonality, reproductive allocation, Nematoda.

RESUMO. Assembleia de helmintos em uma pequena rã no semiárido brasileiro: relação parasito-hospedeiro-ambiente. Como infecções parasitárias podem contingenciar diversos aspectos da vida dos hospedeiros, de modo geral, espera-se que o parasitismo comprometa direta ou indiretamente a reprodução dos hospedeiros. Contudo, apesar dos anfíbios historicamente terem sido modelos de estudos em ecologia parasitária, os efeitos do parasitismo na reprodução de anfíbios permanecem incompreendidos. Neste trabalho investigamos como a carga parasitária varia em função da sazonalidade climática (período chuvoso e seco) e de características intrínsecas do hospedeiros (tamanho e sexo), bem como a relação entre a intensidade de infecção e o investimento reprodutivo em machos e fêmeas de uma pequena rã (*Pseudopaludicola pocoto* Magalhães, Loebmann, Kokubum, Haddad & Garda, 2014) no semiárido brasileiro. Os parâmetros parasitológicos da população estudada não foram influenciados pela estação do ano nem pelo tamanho corpóreo dos hospedeiros, mas as fêmeas de *P. pocoto* apresentaram maior prevalência e intensidade de infecção que os machos. A carga parasitária não foi relacionada com o número de ovócitos nem com o volume dos testículos, revelando que o parasitismo não impactou negativamente o investimento gonadal em *P. pocoto*. Nossos achados sugerem que espécies com baixa longevidade, como as diminutas espécies de *Pseudopaludicola*, apresentam um alto investimento reprodutivo independente de suas interações parasitárias. Complementarmente, isto deve ocorrer sobretudo naquelas espécies que vivem em ambientes sazonalmente secos, como *P. pocoto*, nos quais a reprodução é ainda mais contingenciada pela brevidade e imprevisibilidade do período chuvoso.

PALAVRAS-CHAVE. Amphibia, *Pseudopaludicola*, sazonalidade, esforço reprodutivo, Nematoda.

Macroparasites, such as helminths, can interact with their hosts in many different ways, which can cause severe damage, subtle injuries, or even not generate apparent disadvantages for the hosts (POULIN, 2007). These different consequences may be related to factors such as environmental conditions where interactions are established (MINCHELLA, 1985), as well as intrinsic host and parasite features (MINCHELLA, 1985; GALVANI, 2003; DYBDAHL & STORFER, 2003; POULIN, 2007).

Parasites that live in environments with high climatic seasonality might have contingencies in terms of survival,

transmissibility and reproduction (ALTIZER *et al.*, 2006; CHANDRA & GUPTA, 2007; POULIN, 2007). For example, in semiarid regions where rainfall is scarce, unpredictable and has high variability between years (AB'SABER, 2003), helminths can be affected by the high risk of desiccation of eggs and larvae, as well as the unavailability of active hosts most of the time (PERRY, 1999; MADELAIRE *et al.*, 2020). Thus, in these environments, rainy periods tend to be more favorable for the infection, development and reproduction of helminths (POULIN & MORAND, 2000; CHANDRA & GUPTA, 2007).

Aspects inherent to hosts such as size, sex and vagility can substantially influence helminth infection rates (AHO, 1990; PRICE, 1990; HAMANN *et al.*, 2006; TOLEDO *et al.*, 2015, 2018). For example, hosts with larger body sizes tend to harbor a greater number of parasites (POULIN, 2007; CAMPIÃO *et al.*, 2015). The impairment or inhibition of reproduction in hosts is one of the ways the parasites maintain the host in good energetic conditions (HURD, 2001; HEINS *et al.*, 2004). Thus, it is plausible to expect that parasitism can compromise the reproductive investment of hosts (HURD, 2001). However, if on the one hand a reduction in fecundity can be an adverse effect of energy limitation provoked by infection. On the other hand, it can constitute a host defensive strategy, resulted of greater investment in survival at the expense of reproduction (HURD, 2001).

Amphibians has been historically good study models for parasitic ecology, as they harbor a high diversity of parasites (CAMPIÃO *et al.*, 2014) and many species are locally abundant and easy to sample (DUELLMAN & TRUEB, 1994). It is known that parasitic infections can affect anuran population dynamics (JOHNSON & MACKENZIE, 2009; VREDENBURG *et al.*, 2010), with parasitological parameters that can vary ontogenetically (CAMPIÃO *et al.*, 2009; TODELO *et al.*, 2015) and differ between the sexes (VAN SLUYS *et al.*, 2006). As reproduction in amphibians is an activity with high energy demand (WELLS, 2007), it is expected that parasitic infections may also compromise their reproductive efficiency. However, there is a relative lack of information on the general effects of parasitism on the reproductive investment of hosts (HURD, 2001; GALDINO *et al.*, 2014; KISS *et al.*, 2019), particularly for amphibians (PRÖHL *et al.*, 2013).

Parasitic interactions in amphibians have been more studied in wet tropical environments (SANTOS & AMATO, 2010; AGUIAR *et al.*, 2015; TOLEDO *et al.*, 2015, 2017, 2018) than in dry tropical environments (MORETTI *et al.*, 2017; SILVA *et al.*, 2018a; MADELAIRE *et al.*, 2020). The Caatinga corresponds to the largest area of Tropical Dry Forest in South America (DA SILVA *et al.*, 2017) and harbor one of the richest amphibian fauna among semiarid regions in the world (GARDA *et al.*, 2017). However, knowledge about parasitism in Caatinga anurans is basically constituted by punctual infection records (TELES *et al.*, 2014, 2017, 2018) and lists of helminth fauna for some host species (TELES *et al.*, 2015; ALCANTARA *et al.*, 2018; OLIVEIRA *et al.*, 2019). Since these semiarid environments have a marked seasonality in relation to water availability, which is a limiting factor both for amphibians (CARVALHO *et al.*, 2010; MADELAIRE & GOMES, 2016) and for helminths (PERRY, 1999; MADELAIRE *et al.*, 2020), it reinforces the need to provide information on host-parasite interactions between helminths and anurans in the Caatinga domain.

In the Brazilian semiarid region, most frogs concentrate their reproductive activities in the short rainy period of the year (ARZABE *et al.*, 2005; JARED *et al.*, 2019). This is also the case of the tiny frog *Pseudopaludicola pocoto* Magalhães, Loebmann, Kokubum, Haddad & Garda, 2014, a species described in the last decade, which despite being

common and widely distributed in the Brazilian semiarid region (PEREIRA *et al.*, 2015; LANTYER-SILVA *et al.*, 2016), has little ecological information available (SILVA *et al.*, 2018a, b). The community of helminths that parasitize *P. pocoto* is known for only one location in the Caatinga (SILVA *et al.*, 2018a) and the relationships between its parasite load and its reproductive investment are completely unknown. In this study, we evaluated the ecological interactions between *P. pocoto* and its associated helminth fauna, specifically investigating: 1) how marked rainfall seasonality affects the parasitological parameters; 2) in what extension host body size and sex influence the parasite load and; 3) what are the relationships between the parasite load with the reproductive investment of females and males hosts.

MATERIAL AND METHODS

Fieldwork was carried out in Assú municipality (5°34'38"S, 36°54'30"W), a semiarid area located in the western region of the state of Rio Grande do Norte, Brazil. This macroregion is classified according to Köppen-Geiger as presenting a Warm Semiarid Climate (BSh), which may present a variation in annual precipitation from 400 to 1000 mm depending on the location, and annual average temperatures ranging between 22°C and 35°C (DA SILVA *et al.*, 2017; INMET, 2018). The Brazilian semiarid region is characterized by high temperatures and seasonal rains, with short rainy periods of three to four months, with unpredictable rainfall, and the dry season lasting from 7 to 10 months (DA SILVA *et al.*, 2017). Assú municipality has historically an average annual precipitation of 587.4 mm, with a concentration of rainfall between February and May, whilst September use to be the driest month in the region (MEDEIROS *et al.*, 2005).

We sampled specimens of *Pseudopaludicola pocoto* through active searches along breeding sites (SCOTT JR & WOODWARD, 1994). The samplings took place in three temporary ponds, in the rainy months (March and May 2017, February, April and May 2018) and in the dry months (September and October 2017). We collect 94 individuals of *Pseudopaludicola pocoto*, 41 females and 53 males, including 23 collected in rainy and 71 in dry season. Individuals were manually captured and collected under licenses from *Instituto Chico Mendes de Conservação da Biodiversidade* (n°. 58431-1 and n°. 35650-1). The sampled individuals were transferred to the *Laboratório de Ecologia e Comportamento Animal* – LECA of the Universidade Federal Rural do Semi-Árido – UFERSA, in the municipality of Mossoró, Rio Grande do Norte state, where their body size was measured in terms of snout-vent length (SVL) with a caliper (resolution 0.01 mm). After that, the individuals were euthanized following the recommended ethical precepts (RESOLUÇÃO DO CONSELHO FEDERAL DE BIOLOGIA – CFBIO n°. 301/2012) and had their internal organs (gonads, lungs, stomach, small and large intestines) removed for parasite inspection. For proper fixation of the helminths, the organs were fixed in 70% alcohol at 60°C, and preserved in 70% alcohol for further screening, counting and identification. After necropsy, the

individuals of *P. pocoto* were fixed in 10% formalin, preserved in 70% alcohol and deposited in the *Coleção Herpetológica do Semiárido* – CHSA at UFERSA (CHSA.A 642, 665, 681, 683-687, 700-708, 710-715, 726-732, 744-750, 755-766, 786-811, 813-816, 990, 1041-1047 and 1055-1061).

For taxonomic identification, the parasites were clarified in Lactofenol, subjected to compression between the slide and cover slip, and analyzed using an optical microscope. We identified the parasite specimens at the lowest possible taxonomic level according to BACHER & VAUCHER (1985), VICENTE *et al.* (1991) and, MORDEGLIA & DIGIANI (1998). Twenty-seven helminths could not be identified because they had diagnose structures were damaged, but were included in general parasitological metrics. We calculate the total prevalence rate (%); the mean intensity of infection and mean abundance following BUSH *et al.* (1997). These values were calculated separately by infection site, host sex and climatic season. All the helminths recorded belong to Rhabditida (SCHOCH *et al.*, 2020), feeding through valves in the esophageal bulb (ANDERSON, 2000). Thus, in view of the similar mechanisms of these parasites interact with the hosts, we consider the total number of helminths per host as the proxy to parasite load.

The reproductive investment of females was measured in terms of the total number of post-vitellogenic (mature) oocytes, those oocytes collored with a dark brown animal pole and a milky vegetative pole (PEROTTI, 1997; MELCHORS *et al.*, 2004). For males, we consider the mean testes volume of each individual as a proxy for reproductive investment (EMERSON, 1997). The testis volume (in mm³) was calculated using the prolate spheroid formula: $V = 4/3\pi (L/2) (W/2)^2$, where “V” is the testis volume, “L” is the testis length and “W” is the testis width (ANJOS & ROCHA, 2008). We measured the width and length of each testis using a digital caliper (resolution 0.01 mm). Twenty-eight specimens of *P. pocoto* were excluded from this analysis as they did not have mature oocytes or the testes were degraded.

To investigate the factors affecting the parasite load, we performed a model selection by simplification of a full generalized linear model (GLM), considering a Poisson error distribution of the response variable (parasite load; i.e. the total number of parasites per host, including zeros) and all interactions between explanatory variables: snout-vent length (in mm), sampling period (rainy and dry season), and sex (female or male). To evaluate the possible negative effects of parasite load on reproductive investment, we first searched for influence of host body size (SVL) on the response variables (log transformed number of oocytes and raw testis volume) using Simple Linear Regressions (SLR). When a significant relationship was found (only in males, see results), we extracted the residuals from the regression model for further analysis. So, we made one sided Spearman's Correlations (SC) between parasite load (the total number of parasites per host, including zeros) and gonads' parameters (log transformed number of oocytes for females, and residuals from testis volume~SVL regression model for males). Prior to analysis, we evaluated the datasets regarding premises of

homoscedasticity and error distributions. Whenever possible, we transformed the response variable for the use of parametric tests. All statistical analyses were conducted in R environment v.3.6.1 (R CORE TEAM 2019), considering a significance level $\alpha = 0.05$, and using the package “beeswarm” v.0.2.3 (EKLUND, 2016) for graphical purposes. Descriptive characterization of variables was provided as mean \pm one standard error.

RESULTS

We found a total of 91 helminths in *Pseudopaludicola pocoto*, and the mean intensity of infection (MII) was 1.78 ± 0.18 parasites per host. We recorded at least one helminth for 51 hosts, representing 54% of total prevalence.

The host population was infected by three nematodes species: *Cosmocerca parva* Travassos, 1925 (13 males and 6 females) (Cosmocercidae), *Physaloptera* sp. (8 larvae) (Physalopteridae), and *Oxyascaris* sp. (37 females) (Oxyascarididae) (Tab. I). In most of the infected hosts (86%), we found only one species of helminth, with no host harboring all three species simultaneously. The highest prevalence of helminths was in the digestive tract, mainly in small intestine (38%), followed by large intestine (14%) and stomach (12%). The small intestine was parasitized by *Oxyascaris* sp. (64%), *C. parva* (27%) and *Physaloptera* sp. (9%), the stomach by *C. parva* (67%) and *Physaloptera* sp. (33%), and the large intestine only by *Oxyascaris* sp. Only one individual of *Physaloptera* sp. was found in body cavity, and no lungs or gonads were infected. Regarding mean intensity of infection by site, large intestine was more infected (MII = 1.69; n = 13) than small intestine (MII = 1.53; n = 36) and stomach (MII = 1.09; n = 11) (Tab. I).

Concerning the infection patterns along the time, 56% of hosts were infected in rainy season with a mean intensity of infection of 1.38 ± 0.22 , while in the dry season the prevalence was 53% with mean intensity of infection of 1.92 ± 0.16 . In relation to intersexual differences, 61% of females (SVL 13.19 ± 0.14 mm) and 49% of males (SVL 11.81 ± 0.21 mm) were infected, with a mean intensity of infection of 2.04 ± 0.26 for females and 1.53 ± 0.10 for males. The overall parasite load was not influenced by body size nor sampling period, and the minimal adequate model had only host sex as the unique significant parameter (GLM - Z = -2.37; p = 0.02; Fig. 1).

Tab. I. Helminth assemblage associated with *Pseudopaludicola pocoto* (Anura, Leptodactylidae) (n = 51 frogs) from the municipality of Assú, Rio Grande do Norte State, Brazil. HN = total number of hosts per parasite species; PN = total number of nematode parasites; TPR = total prevalence rate (%); MII = mean intensity of infection, MA = mean abundance and IS = infection site (St = stomach; SI = small intestine; LI = large intestine; Cav = body cavity).

Nematoda	HN	PN	TPR(%)	MA	IS	
<i>Cosmocerca parva</i>	16	19	17.02	1.19	0.20	St, SI
<i>Oxyascaris</i> sp.	23	37	24.47	1.61	0.39	SI, LI
<i>Physaloptera</i> sp.	7	8	7.45	1.14	0.08	St, SI, Cav

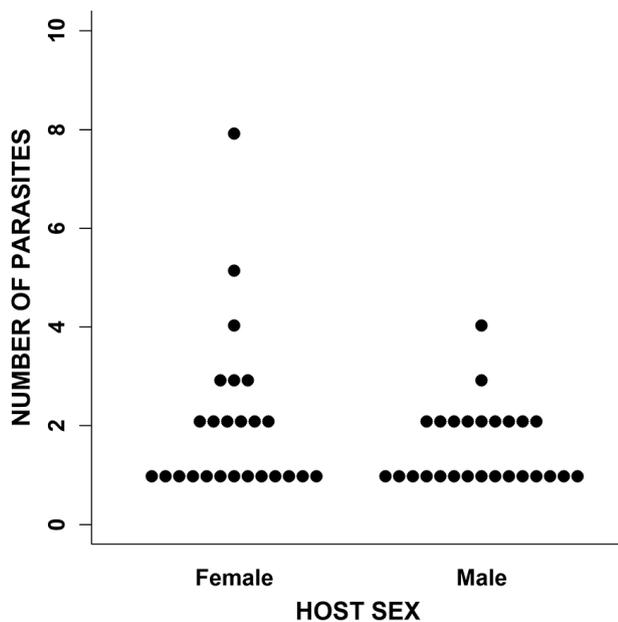


Fig. 1. Parasite load (total number of helminths per host) between females (N= 41) and males (N= 53) of *Pseudopaludicola pocoto* (Anura) from Assú municipality, Rio Grande do Norte state, northeastern Brazil.

Regarding influence of parasite load on reproductive investment, we considered 32 females and 34 males for which number of oocytes and testes volume were respectively quantified. The number of oocytes was not influenced by body size (SLR - $R^2 = 0.01$; $p = 0.60$), and the parasite load was not negatively correlated with the number of oocytes (SC - $r = 0.03$; $p = 0.57$). The mean testes volume was positively affected by body size (SLR - $R^2 = 0.11$; $p = 0.05$), but the parasite load was not negatively correlated the testis volume after removed the effects of body size (SC - $r = -0.15$; $p = 0.20$).

DISCUSSION

Nematode parasites are most commonly found in frogs of the Leptodactylidae (CAMPIÃO *et al.*, 2014), with eight species previously known to parasitize *Pseudopaludicola pocoto* (SILVA *et al.*, 2018a). We recorded three species of Nematoda parasitizing *P. pocoto* in Assú municipality, Rio Grande do Norte state. *Cosmocerca parva* is widely distributed in South American anurans (CAMPIÃO *et al.*, 2014) and has previously been reported to parasitize other Caatinga amphibians (OLIVEIRA *et al.*, 2019), including *P. pocoto* (SILVA *et al.*, 2018a). *Oxyascaris* sp. and *Physaloptera* sp. recorded by us in *P. pocoto* could not be identified at the species level, as there were only females of *Oxyascaris* sp. (diagnostic characters in males - (BACHER & VAUCHER, 1985) and larvae of *Physaloptera* sp. (anurans are intermediate hosts - BOQUIMPANI-FREITAS *et al.*, 2001). The total prevalence observed in Assú population was similar to that found for another population of *P. pocoto* located 400 km away (50% in SILVA *et al.*, 2018a and 54% in the present study). However, we observed a higher mean intensity of infection in the study area ($MII = 1.8 \pm 1.3$ parasites/

host) than that previously recorded for another population ($MII = 1.0 \pm 0.5$ parasite/host) (SILVA *et al.*, 2018a). As other species of *Oxyascaris* and *Physaloptera* have also been reported to parasitize *P. pocoto* (SILVA *et al.*, 2018a), our results suggest that the helminth fauna composition in *P. pocoto* may not vary substantially between populations.

The prevalence and mean intensity of infection in *P. pocoto* did not differ between the rainy and dry seasons. In semiarid regions, it is expected that the activity of most frogs is restricted to the short rainy period of the year, when reproduction is concentrated (ABE, 1995; GARDA *et al.*, 2017). We expected that the number of parasites per host would be greater during the reproductive period (FILHO *et al.*, 2016; OLIVEIRA *et al.*, 2017), when the majority of anurans are active and, consequently, they would be more exposed to infection by parasites (POULIN & MORAND, 2000). However, as observed in another population (SILVA *et al.*, 2018a), we also recorded some *P. pocoto* individuals active in the first months of dry period next to remaining water bodies. In this sense, it is known that anuran species that have a prolonged period of activity tend to have prevalence and infection rates more distributed over time (MADELAIRE *et al.*, 2020). Thus, although the reproductive activity of *Pseudopaludicola* species are considered explosive, it is possible that *P. pocoto* behaves in an opportunistic way, taking advantage of fortuitous favorable conditions between years according to rainfall distribution. If this is true, this strategy could explain the low variation observed in the parasitological parameters of *P. pocoto* between the rainy and dry periods.

The body size of *P. pocoto* was not related to the parasite load. However, it is known that the body size of the host is in general positively related to the richness and abundance of parasites, both because large species have a greater capacity for ingesting prey, and because they have a larger surface area and body volume for colonization by helminths (CAMPIÃO *et al.*, 2015; TOLEDO *et al.*, 2018). Our results suggest that the low variation in body size of *P. pocoto* individuals is not enough to enable a significantly higher number of parasites in larger hosts. It is noteworthy that the widely known pattern of sexual dimorphism for anurans, in which females are larger than males (DUELLMAN & TRUEB, 1994), is not observed in *P. pocoto* (SILVA *et al.*, 2018b), contributing to explain the lack of relationship between body size and parasite load. In fact, *Pseudopaludicola* species are recognized by their small body size, a characteristic that can restrict the parasite load independent of intraspecific variation in body size (DURÉ *et al.*, 2004).

Sex significantly influenced the parasite load in *P. pocoto*, with the number of parasitized females 10% higher than those of males and with females harboring 30% more parasites than males. Although in general amphibians have low vagility compared to other vertebrates (WELLS, 2007), females occasionally travel longer distances than males (WELLS, 2007; WANG *et al.*, 2019). This displacement may be related to greater foraging/feeding intensity to offset

the greater energy demands for oocyte production (PRICE, 1990; MUTHS, 2003). Thus, it is possible that females of *P. pocoto* are doubly more susceptible to infection by helminths, both because of the possible greater vagility in search of prey (cutaneous infection route – POULIN, 2007), and because they feed on a greater diversity of prey (infection oral route – POULIN, 2007; LEIVAS *et al.*, 2018). Since the only study on the foraging ecology of *P. pocoto* did not assess the intersexual differences in diet (see SILVA *et al.*, 2018a), we recommend future studies on this topic to test the aforementioned predictions.

Hosts with a higher parasite load may present reproductive contingencies (MINCHELLA, 1985; HURD, 2001; BOWER *et al.*, 2018), but the reproductive investment of *P. pocoto* was not affected by the parasite load. It is known that anuran species with small body size tend to live shorter than larger ones (DUELLMAN & TRUEB, 1994; STARK & MEIRI, 2018). Consequently, despite the trade-off between growing and reproducing, short-lived species are expected to have a relatively higher reproductive investment (SCHARF *et al.*, 2015). Thus, it is possible that the species of *Pseudopaludicola*, among the smallest representatives of the Leptodactylidae (GIARETTA & KOKOBUM, 2003; ANDRADE *et al.*, 2016, 2020; PANSONATO *et al.*, 2016), have a low longevity and may present a high reproductive investment independent of their parasitic interactions (SILVA *et al.*, 2018a,b).

Although parasitic infections are often related to the damage of hosts (AGNEW *et al.*, 2000; GALDINO *et al.*, 2014; MORETTI *et al.*, 2017), this pattern did not occur in a *P. pocoto* population from Caatinga. As an environment with a short and unpredictable rainy season, the semiarid is known to exert an even greater contingency for the reproduction of amphibians, and may frame specific ecological and behavioral strategies (MADELAIRE & GOMES, 2016). For example, it has been suggested in last years that amphibians from semiarid regions have a relatively more intense immune response, contributing so that parasitic diseases do not cause substantial damage to reproduction (MADELAIRE *et al.*, 2017). In conclusion, keeping in mind that the patterns of the host's life history and their relationships with the environment can act as mediators of physiological responses to parasitism (MINCHELLA, 1985), our findings contribute to the understanding of the consequences of parasitic interactions in amphibians, revealing the nature of parasitism by nematodes in a small frog from a semiarid environment.

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