

Temporal variation in diet and helminth abundance in the spiny-tailed lizard, *Strobilurus torquatus* Wiegmann, 1834 (Squamata: Tropiduridae) from the Brazilian Atlantic Forest

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Abstract. Spatial and temporal variations can influence the abundance and biology of parasite species and even the transmission process, as well as the diet, reproduction and distribution of hosts. We studied the influence of seasonality on the diet and endoparasites of the lizard *Strobilurus torquatus*. The lizards were collected during a period of one year, in the Engenho Gargaú Private Reserve of Natural Heritage, located in the municipality of Santa Rita, in the state of Paraíba, Northeast Brazil. Thirty-three lizards were analysed, of which 30 were parasitised (overall prevalence of 90%) with the helminths *Physaloptera lutzi* (prevalence of 69.6%), *Spauligodon lobo* (51.5%), *Strongyluris oscar* (15.1%) and *Haplometroides odhneri* (3.0%). Our analysis showed that endoparasite abundance was influenced by host body size. Host sex also influenced endoparasite abundance, where males were parasitised more than females. When comparing the two seasons (dry and rainy), we observed that the greatest endoparasites abundance occurred during the rainy season. Regarding the lizards' diet, we observed a high niche overlap (overlap index of 0.999), which indicates that males and females of *S. torquatus* consumed practically the same prey during the analysed period. The life cycle of the endoparasites found in *S. torquatus* was linked to seasonal variation, and the behavioural and physiological differences between sexes may have influenced the variations in endoparasite abundance.

Keywords. Brazil, endoparasites, Nematode, seasonality, Trematoda.

INTRODUCTION

Lizards are known to act as hosts to several parasites, such as nematodes (e.g., Brito et al., 2014a, b; Araújo-Filho et al., 2016; Teixeira et al., 2017), cestodes (e.g., Brito et al., 2014a, b; Araújo-Filho et al., 2016), trematodes (e.g., Teixeira et al., 2018; Amorim and Ávila, 2019; Araújo-Filho et al., 2020; Teixeira et al., 2021) and pentastomids (Almeida et al., 2008; Brito et al., 2014a, b; Araújo-

Filho et al., 2016). These animals are excellent models for studying how ecological and evolutionary relationships determine the distribution and parasite abundance, since they inhabit different environments, utilize various foraging strategies and present different trophic interactions, body sizes, and reproductive strategies (Aho, 1990).

Several factors can affect the survival and distribution of parasites in host populations (Laferty and Kuris, 2005), such as variations in environmental conditions

(i.e., temperature, humidity, and precipitation), changes in the availability of intermediate hosts, and physiological changes in final hosts (Noble, 1966; Lafferty and Kuris, 2005; Vasconcellos et al., 2010; Brito et al., 2014b; Araújo-Filho et al., 2016), which are commonly seen in environments with well-defined seasonal regimes (Da Silva et al., 2019; Amorim and Ávila, 2019).

Seasonal changes can influence parasite abundance, richness and composition in several ways (Miranda and Andrade, 2003; Fontes et al., 2003; Lafferty and Kuris, 2005). For example, an increase in temperature favours some parasite species, which may accelerate their reproduction rates, resulting in an increase in population sizes (Lafferty and Kuris, 2005). Temperature is also very important for host species that are ectothermic and require external heat sources for internal temperature regulation. Another climatic factor that can affect parasite species is precipitation, which may favour parasites that lay their eggs in the environment, as well as those that have an aquatic life stage (Lafferty and Kuris, 2005).

In recent years, many studies have sought to analyse the influence of seasonal variations on lizard populations and their endoparasites (Ribeiro and Freire, 2011; Gambhir et al., 2012; Brito et al., 2014a, b; Araújo-Filho et al., 2016; Oliveira et al., 2017; Amorim and Ávila, 2019). These studies demonstrated that seasonal variations can influence behaviour, reproduction, diet (Miranda and Andrade, 2003; Ribeiro and Freire, 2011) and endoparasite infection rates in lizards (Fontes et al., 2003; Salkeld et al., 2008; Gambhir et al., 2012; Brito et al., 2014a, b; Araújo-Filho et al., 2016; Amorim and Ávila, 2019). Additionally, historical factors (Brito et al., 2014a, b), coupled with ecological traits, can also influence the compositions of host parasite communities.

Tropiduridae is one of the most diverse lizard families in the Neotropical region (Torres-Carvajal, 2004; Rodrigues et al., 2013; Lima-Silva et al., 2021), comprising 138 species that are distributed across eight genera. One of these genera, *Strobilurus* Wiegmann 1834, is composed of only one species, *Strobilurus torquatus* Wiegmann, 1834 (Uetz et al., 2021), the spiny-tailed lizard, for which there is little available information on its ecology (Rodrigues et al., 1989), distribution (Rodrigues et al., 2013) and associated endoparasite fauna (Teixeira et al., 2020; Lima-Silva et al., 2021).

Strobilurus torquatus (Fig. 1) is diurnal, arboreal and insectivorous (Rodrigues et al., 1989). Males are usually larger-bodied than females, and have longer tibias, which may be related to their territorial behaviour (Rodrigues et al., 1989; Frost et al., 2001; Rodrigues et al., 2013; Lima-Silva et al., 2021). This species is distributed along the coastal Atlantic Forest, extending from the state of Rio de Janeiro



Fig. 1. Specimen of the rare lizard *Strobilurus torquatus* from the Atlantic Forest, north-eastern Brazil. (Photo: Silva, W.P)

in the extreme south, through the state of Pernambuco in the north, to the isolated enclaves of tropical forest within the Caatinga in the state of Ceará, in west. (Salles-Silveira et al., 2010; Rodrigues et al., 2013; Lima-Silva et al., 2021). Despite its wide distribution range, *S. torquatus* is considered a rare species due to its low local abundance, resulting in a lack of basic information about its biology, ecology and parasitic fauna (Lima-Silva et al., 2021). Therefore, this study aims to verify the influence of seasonality on the diet and endoparasites of *Strobilurus torquatus*.

MATERIAL AND METHODS

Study area and collections

The lizards were collected in the Engenho Gargaú Private Reserve of Natural Heritage (hereafter PRNHEG; 06°59'52"S, 34°57'30"W), located in the municipality of Santa Rita, in the state of Paraíba, Northeast Brazil (Fig. 2). PRNHEG covers an area of 1,058.62 ha, preserving one of the most significant remaining fragments of the Atlantic Forest in north-eastern Brazil (ICMBio, 1994). The climate is tropical, with an average temperature of 25.7° C. The collections took place over 8 days for each sampled month, where sampling during the months of lower rainfall occurred between September 2016 and January 2017 (average of 34 mm for these months) and sampling during the months of greater rainfall occurred from March 2017 to July 2017 (average of 135 mm for these months) (Climate-Data, 2017).

The primary sampling method was manual collection during active-search surveys. All campaigns were carried out with a team of researchers made up of three members, and searches were conducted between 09:00 am and

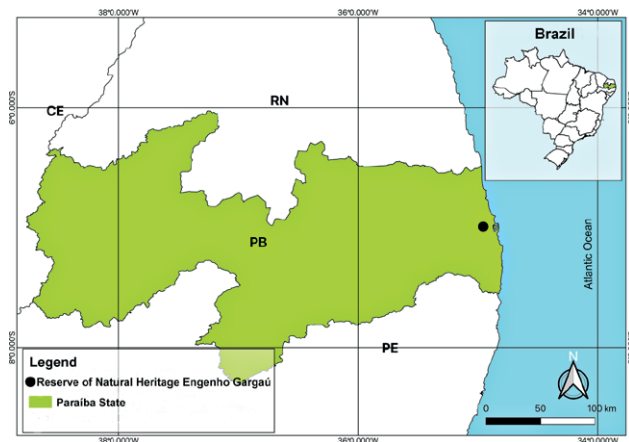


Fig. 2. Study area, remnant Atlantic Forest fragments, located in the municipality of Santa Rita, in the state of Paraiba - PB. Modified from Teixeira et al. (2021).

05:00 pm (after this period, a severe decrease in sunlight within the forest hindered lizard visualization), totalling 192 hrs of sample effort by campaign.

We complemented active-search sampling with pitfall traps. A total of 25 sets of traps were installed. Each set consisted of four buckets (volume of 20 litres) arranged in a “Y” shape, totalling 100 buckets distributed throughout the study area (see Oliveira et al., 2017).

The lizards were fixed in 10% formaldehyde, preserved in 70% alcohol, and deposited in the Herpetological Collection of the Universidade Federal da Paraiba (UFPB) sequential voucher number CHUFPB-29020 to CHUFPB-29058.

Parasitological identification

In the laboratory, the lizards were sacrificed following the current ethical guidelines, using doses of Lidocaine 2%. Subsequently, the snout-vent lengths (SVL) of the samples were recorded using a Mitutoyo digital caliper 150mm, accurate to 0.001mm. Finally, the body mass of each specimen was measured using a precision scale (accuracy: +/- 0.3%). During the necropsies, gonad inspections and animal sexing were performed. Afterwards, their lungs and gastrointestinal tracts were analysed in search of endoparasites.

All endoparasites found were collected, counted, and later mounted on temporary slides for identification. To identify the nematodes, the specimens were bleached with Lactophenol. In the case of trematodes, the specimens were stained with Carmin, before being mounted on slides with Eugenol solution. Taxonomic identification was achieved using the following relevant keys and

descriptions: Ramallo et al. (2002), Anderson et al. (2009), Pereira et al., (2017) and Alves et al., (2022) for nematode identification and Silva et al. (2007) for trematode identification. The endoparasites were deposited in the Paulo Young Invertebrate Collection (UFPB) - CHUFPB (UFPB-NEM: 03, 05, 06; UFPB-DIG: 03, 04, 05).

Data analysis

Mean intensity (MII) and prevalence (P%) of infection were calculated following Bush et al. (1997), who described the former as “the total number of parasites of a given species divided by the number of hosts infected with that species of parasite” and the latter as “the number of hosts infected with a species of parasite divided by the number of examined hosts”.

We used generalised linear mixed models (GLMM) to verify if endoparasite abundance was influenced by the physical characteristics of the hosts (Mass and SVL) and by environment seasonality (dry and rainy seasons). Linear models allow for the exploration of one variable (the dependent variable) as a function of another (the independent variable), in addition to having special terms for inserting random effects (Bates et al., 2014).

In the first model, using a Poisson distribution, we verified whether host body mass influenced endoparasite abundance. Endoparasite abundance corresponded to the response variable, while body mass corresponded to the independent variable, and host sex was allocated as a random effect. In the second model, also using a Poisson distribution, we verified whether host SVL influenced endoparasite abundance. Endoparasite abundance corresponded to the response variable and SVL corresponded to the independent variable, while host sex was allocated as a random effect, to prevent the sexual dimorphism of the species from influencing the results. For the third model, we attempted to verify whether endoparasite abundance was influenced by seasonality, using the Poisson distribution and the log function. For this, we performed an interaction between parasite abundance, host sex and seasonality. All analyses were performed using R Software and the lme4 package (Bates et al., 2014; R Core Team, 2018).

We analysed all the stomach contents of the collected lizards and the prey found were identified to the lowest possible taxonomic level. Subsequently, we calculated niche width which was only based on the number of prey items. This index was calculated through the inverse of Simpson’s diversity index (Simpson, 1949), which is calculated by the following equation:

$$B = \frac{1}{\sum_{i=1}^n P_i^2}$$

where i is the prey category, P is the proportion of prey category i and n is the number of categories. Niche width was based on the number of prey items from pooled stomachs.

We calculated niche overlap using the number of prey items from pooled stomachs to verify whether there was a difference in prey consumed by males and females and between seasons. Niche overlap was calculated using Pianka's index (Pianka, 1986), expressed by the following equation:

$$\phi_{jk} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are the consumption rates of prey category i , and j and k represent the sexes and seasons compared. This index ranges from zero (no overlap) to one (total overlap).

Descriptively, we individually calculated the Volume (V) of consumed prey, using the width and length of each prey item. From the volume, we were able to calculate the importance index value for each prey category.

The volume (V) of individual prey was calculated using the following formula:

$$V = \frac{4}{3} \pi \left(\frac{w}{2}\right)^2 \left(\frac{l}{2}\right)$$

where w is prey width and l is prey length.

To determine the importance of each prey category in the diet, we calculated the importance index based on pooled stomachs, using the following formula:

$$I = \frac{F\% + N\% + V\%}{3}$$

where $F\%$ is the percentage of occurrence, $N\%$ is the numerical percentage and $V\%$ is the volumetric percentage of the prey.

RESULTS

We analysed 33 lizards, of which 19 were males (mean SVL = 65.67 ± 14.06 mm), 12 were females (mean SVL = 58.53 ± 10.20 mm) and two were juveniles (removed from the statistical analysis of sex and seasonality interaction). We collected 23 lizards during the dry season, and ten during the rainy season. Because this lizard species is arboreal, only two individuals were captured by pitfall traps, both during the dry season. The difference in sample sizes was probably due to the fact

that this species is more reclusive during rainy days, and the fact that the sampling effort was strictly the same may have caused a decrease in the likelihood of lizards being found in the environment during the rainy season.

Of the specimens examined, 30 were parasitised, resulting in an overall prevalence of 90%. Four endoparasite species were found, three of which were nematodes (*Physaloptera lutzii* Cristofaro, Guimarães and Rodrigues, 1976; *Spauligodon loboii* Ramallo, Bursey and Goldberg, 2002 and *Strongyluris oscari* Travassos, 1923) and one was a digenean trematode (*Haplometroides odhneri* Ruiz and Perez, 1959) (Table 1).

The models indicated that endoparasite abundance was positively influenced by host body mass (R^2m : 0.95; R^2c : 0.95; Z-value: -7.485; $P < 0.001$) and SVL (R^2m : 0.95; R^2c : 0.95; Z-value: 11.521; $P < 0.001$). Regarding host sex, males were more parasitised than females (Z-value: 6.260; $P < 0.001$). When comparing the two seasons (dry and rainy), we observed that the greatest endoparasite abundance occurred during the rainy season (Z-value: -2.422; $P < 0.05$). Furthermore, our analysis of the interaction between sex and season indicated that during the rainy season male lizards exhibited greater endoparasite abundance (Z-value: -5.019; $P < 0.001$) (Figure 3).

Regarding diet, we did not observe differences between the proportions of prey consumed by males and females. Both sexes mainly preyed on ants, which represented 95% of the entire dietary composition of *S. torquatus*. During the rainy season, Formicidae represented 98% of the species' food composition, with an importance index of 86.92. Similar to the results observed for the rainy season, in the dry season, Formicidae corresponded to 96% of the food items consumed by *S. torquatus* with an importance index of 64.61 (Table 2).

Based on the number of prey items in the pooled stomachs, niche width was similar between sexes and seasons (Table 2). Finally, we observed a high niche overlap between sexes and seasons, with an overlap index of 0.999 in both analysed pairs, thus showing that the individuals consumed basically the same prey regardless of sex and period of the year.

DISCUSSION

The endoparasite species identified in *S. torquatus* are frequently found to parasitize other lizard species (Bursey et al., 2005; Ávila et al., 2012; Brito et al., 2014b; Lima et al., 2017; Araújo-Filho et al., 2020), with the exception of the parasite *Haplometroides odhneri*, parasites of the genus *Haplometroides* Odhner, 1910 were previously only described as endoparasites of snakes and amphisbaenians

Table 1. Endoparasites infecting the lizard *Strobilurus torquatus* from the Atlantic Forest, north-eastern Brazil. Infection Site (I.S): Stomach (S), Small intestine (S.I), Large intestine (L.I), Body cavity (B.C); Prevalence (P%) and Mean infection intensity (I).

Phylum	Family	Species	I.S	P%	I
Nematoda	Physalopteridae	<i>Physaloptera lutzi</i>	S/S.I/L.I/B.C	69.6	18.6
	Pharyngodonidae	<i>Spauligodon lobo</i>	S.I/L.I	51.5	9.5
	Heterakidae	<i>Strongyluris oscari</i>	S.I/L.I	15.1	6.8
Platyhelminthes	Plagiorchiidae	<i>Haplometroides odhneri</i>	S.I	3.0	4

Table 2. Diet composition, number of prey (NP) and Importance Value Index (IVI) of the prey consumed by *Strobilurus torquatus* in relation to host sex and season (dry and rainy). Niche width based on the number of prey items in pooled stomachs (Niche # A).

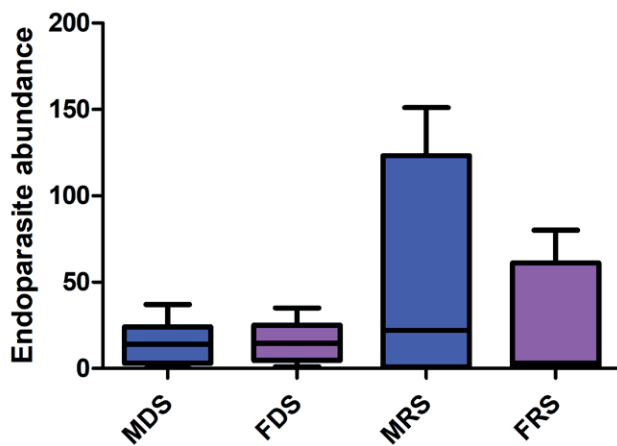
Prey category	NP / IVI			
	Dry season	Rainy season	Males	Females
Araneae	1 / 1.65	-	1 / 2.59	-
Coleoptera	19 / 13.71	3 / 7.49	17 / 20.16	5 / 6.83
Diptera	4 / 1.70	-	4 / 2.15	-
Formicidae	652 / 64.61	283 / 86.92	497 / 63.10	418 / 71.19
Hemiptera	3 / 4.27	1 / 2.49	2 / 1.07	1 / 6.85
Hymenoptera(non-Formicidae)	3 / 4.13	-	-	3 / 8.30
Acari (Ixodida)	1 / 0.83	-	1 / 1.07	-
Insect larvae	5 / 6.63	-	3 / 7.78	2 / 3.42
Scolopendromorpha	-	1 / 3.08	-	1 / 1.71
Scorpiones	3 / 2.41	-	2 / 2.03	1 / 1.66
Niche # A	1.12	1.03	1.12	1.06

(Silva and Barrella, 2002; Santos et al., 2008), however, Teixeira et al. (2018) the species *H. odhneri* parasitizing the lizard *Dryadosaura nordestina* for the first time. Recent studies have expanded the host records of this par-

asite, which has been found in different species of lizards from the families Sphaerodactylidae, Dactyloidae, Mabuyidae and Tropiduridae (Teixeira et al., 2020; 2021).

Our GLMM analysis showed that host body size directly influenced the endoparasite abundance found in *S. torquatus*. This same pattern has been observed for other lizard species of the family Tropiduridae in different biomes of the Neotropical region (Fontes et al., 2003; Anjos et al., 2012; Pereira et al., 2012; Araújo-Filho et al., 2016) and in studies conducted with fishes (Isaac et al., 2000) and amphibians (Hamann et al., 2012). Thus, these studies indicate that the positive correlation between host body size and parasitism rate does not exclusively occur in lizards.

Fontes et al. (2003), studying the tropidurid *Eurolophosaurus nanuzae* in an area of rocky outcrops in the Cerrado, observed that an increase in the infection intensity of three endoparasite species was correlated with the hosts' body size. Anjos et al. (2012), who studied another tropidurid species, *Tropidurus hispidus*, in the Caatinga area, and Pereira et al. (2012), who worked with *Tropidurus torquatus* in an area of Atlantic Forest, also obtained similar results, where host body size influenced the infection intensity of the endoparasites found.

**Fig. 3.** Interaction between endoparasites abundance, host sex and seasonality. (FDS: Female dry season, MRS: Male rainy season, FDS: Female dry season).

A host's body can be considered a parasite's habitat (Poulin et al., 2011). Thus, larger hosts have a greater adhesion area and more available nutrients to parasitic species, in addition to having greater longevity, making these individuals the best sources of resources for endoparasites (Korallo et al., 2007; Pereira et al., 2012).

However, hosts may have other ecological characteristics, in addition to body size, which can influence parasite infection rate, for example population density, social behaviour and diet composition (Morand, 2000; Poulin, 2004). All these factors affect, not only the probability of an individual acquiring endoparasites, but also the parasitic species to which the hosts may be exposed to throughout their lives.

Host sex influenced the endoparasite abundance found in *S. torquatus*, where males were more parasitised than females. Similar to our study, Brito et al. (2014b), in their research involving lizards of the families Tropiduridae and Teiidae in areas of Caatinga in Northeast Brazil, also found that sex influenced endoparasite abundance, where males were also the most parasitised. Several studies on species of the family Tropiduridae performed in different areas of the Neotropical region, have demonstrated the influence of host sex on endoparasite infection rates (Fontes et al., 2003; Pereira et al., 2012; Galdino et al., 2014; Araújo-Filho et al., 2016). In studies carried out with lizards of the families Leiosauridae (Sousa et al., 2007), Gymnophthalmidae (Oliveira et al., 2017) and Dactyloidae (Campos et al., 2021), differences in infection rates were also observed between male and female hosts.

According to Poulin (1996), the biological differences (physiological, morphological and behavioural) between hosts of different sexes can make one sex more susceptible to parasitic infections than the other. Differences in endoparasite abundance between sexes may be related to host diet, habitat use and reproductive period (Goldberg and Bursley, 1989; Pereira et al., 2012; Brito et al., 2014b; Araújo-Filho et al., 2016). The males of *S. torquatus* present more territorial behaviour than females (Rodrigues et al., 1989), which may have influenced the fact that these individuals were more parasitized than females. Lizards that present this type of behaviour spend more time patrolling or participating in territorial disputes, raising stress levels that can compromise an individual's immune system. Additionally, during the reproductive period, this type of behaviour tends to intensify due to an increase in testosterone levels, and very high levels of testosterone can cause immunosuppression in the animal, making these individuals more susceptible to infections (Folstad and Karter, 1992). However, due to the lack of studies on the ecology of *S. torquatus* and information about the differences that may exist between sexes, and

since we found that the males and females did not differ in terms of diet, we cannot say for sure which factors contributed to the increase in the endoparasites abundance in male *S. torquatus* individuals.

We observed that the highest levels of infection occurred during the rainy season. The endoparasite species that showed the highest prevalence were *P. lutzi*, *S. lobo* and *S. oscar*. Despite presenting different life cycles, heteroxene and monoxenes, respectively, all of these species depend on increased humidity and precipitation in the environment in order for their eggs and larval stages to persist longer in the environment (Anderson, 2000).

In a study by Brito et al. (2014b) in the semi-arid Caatinga, the environmental conditions during the rainy season influenced the endoparasite abundance in *Tropidurus hispidus*. The authors emphasized that seasonal variation in parasite abundance may have occurred because the identified endoparasites have a monoxenous (direct) life cycle and may encounter the best environmental conditions during the rainy season. Araújo-Filho et al. (2016) analysed populations of *T. hispidus* in Caatinga, Restinga and Atlantic Forest habitats, and observed different seasonal variations. In the Caatinga, the highest infection rates occurred during the rainy season, while in the Restinga areas the highest endoparasite abundance was observed during the dry season, and in the Atlantic Forest region no variation was observed. These publications have shown the importance of performing studies on the same species in different environments, as they can generate relevant information about seasonal and geographic differences in the infection process and variation in the endoparasites abundance.

According to Gambhir et al. (2012), temperature and precipitation are the main climatic factors that influence both the distribution of host species and the survival of parasites. Temperature can influence the transmission, development and mortality rates of endoparasite larval stages, and therefore, acts as a regulatory agent of endoparasite populations in hosts (Esch et al., 1977; Altizer et al., 2006). Rainfall intensity, in particular, is a critical factor because excessive rainfall can sweep eggs and larvae deposited in the environment away during runoff, thus limiting the probability of transmission to potential hosts (Stromberg, 1997).

In the present study, the increase in precipitation associated with humidity during the rainy season may have mainly favoured nematodes, whose transmission occurs through the ingestion of eggs or free-living juvenile stages by *S. torquatus*, because during the rainy season the humidity and temperature conditions are optimal for parasites eggs to persist longer in the environment. (Lafferty and Kuris, 2005).

The differences in infection prevalence and intensity between male and female hosts are usually attributed to the different types of diets observed in these individuals (Goldberg and Bursey, 1989). However, in our analysis, male and female lizards did not differ in terms of diet, and the same was observed when comparing dietary data between seasons (Table 2). We observed a high niche overlap 0.999, indicating that male and female *S. torquatus* consumed practically the same prey during the study period. Despite this high niche overlap, endoparasite abundance varied in relation to sex and seasonality. According to Fontes et al. (2003) and Galdino et al. (2014) the differences in infection parameters observed between sexes may be due to other factors that are complementary to the diet.

The life cycles of the endoparasites found in *S. torquatus*, were associated with seasonal variation in the environment and the behavioural and physiological differences between male and female hosts may have influenced the endoparasite abundance observed here. The nematode *P. lutzi* uses insects as intermediate hosts (Anderson, 2000), which, in turn, are the main food source of *S. torquatus* (Rodrigues et al., 1989). Although *S. torquatus* is an arboreal species, these individuals tend to forage at various heights along tree trunks and occasionally on the ground (Rodrigues et al., 1989). During the collections, individuals were found in treetops, standing tree trunks, fallen trunks (at various elevations), and in pitfall traps at ground level. The presence of *S. torquatus* on the ground, and at the different types of elevations, may explain how these individuals may have come into contact and became infected with the eggs of *S. lobo* and *S. oscari*.

Due to the low prevalence of *H. odhneri* and the general lack of information regarding the parasitic fauna of *S. torquatus*, we believe that the occurrence of this species of Trematoda parasitizing a single specimen of *S. torquatus* was accidental. However, further studies on the parasitic fauna of *S. torquatus* would be needed in order to confirm whether this species also acts as a definite host for *H. odhneri*. This is the first study analysing seasonal influence on the diet and endoparasites of *S. torquatus*, in addition to providing the first record of the trematode *H. odhneri* parasitizing this lizard species. We emphasize that, in addition to seasonal variation, other factors can influence the parasitic infection processes, such as host sex and body size, as well as the behaviour and diet of individuals and should be considered in future studies.

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