

ECOLOGICAL ASPECTS OF NEMATODE PARASITES OF *Didelphis aurita* (DIDELPHIMORPHIA, DIDELPHIDAE) IN URBAN-SYLVATIC HABITATS IN RIO DE JANEIRO, BRAZIL

Raquel Gonzalez Boullosa Malheiro de Castro^{1,2}, Sócrates Fraga da Costa Neto^{1,2},
Arnaldo Maldonado Júnior^{1*} & Rosana Gentile¹

¹ Fundação Oswaldo Cruz (FIOCRUZ), Instituto Oswaldo Cruz, Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios. Av. Brasil, 4365, Manguinhos, Rio de Janeiro, RJ, Brasil. CEP: 21040-360

² Fundação Oswaldo Cruz (FIOCRUZ), Instituto Oswaldo Cruz, Programa de Pós-Graduação em Biodiversidade e Saúde. Av. Brasil, 4365, Manguinhos, Rio de Janeiro, RJ, Brasil. CEP: 21040-360

E-mails: raquel.castro@ioc.fiocruz.br, socrates@ioc.fiocruz.br, maldonad@ioc.fiocruz.br, rgentile@ioc.fiocruz.br

ABSTRACT

Despite the widespread occurrence and the great number of studies of the common opossum *Didelphis aurita* (Didelphimorphia, Didelphidae), there is a serious lack of information about helminth parasitism in these species. The synanthropic characteristic of these animals may influence their parasite fauna and the ecological parameters. We evaluated the abundance, intensity, prevalence and spatial aggregation of the most abundant nematodes of the large intestine and stomach, recovered from the common opossum *D. aurita*, in Pedra Branca State Park and its surroundings, which includes the FIOCRUZ Atlantic Forest Campus, Rio de Janeiro, Brazil. We investigated the effects of anthropic disturbances on the helminth populations comparing the parameters in relation to host habitat types, season and host gender in order to understand the ecological host-parasite interaction. The animals were sampled in three different habitats. We conducted eight small mammal samplings in different seasons and collected 48 individuals of the common opossum. The nematode species found in the large intestine were *Aspidodera raillieti* and *Cruzia tentaculata* while *Turgida turgida* was found in the stomach. *Cruzia tentaculata* was the species with the highest abundance, intensity and prevalence indices. The three species had a highly aggregated distribution. No species had significant difference in prevalence when compared with host habitat types, host gender or season. *Cruzia tentaculata* had higher intensity in the rainy season, which suggests that rainfall contributes to the development of the life cycle of this helminth. *Turgida turgida* had higher abundance in the disturbed forest habitat, suggesting that the presence of intermediate hosts may be favoured by the characteristics of this environment.

Keywords: Atlantic Forest; ecology; host-parasite interaction; marsupials; parasitism.

INTRODUCTION

The conservation of biological diversity is a global concern, especially because of the increasing disturbance caused by human activities in ecosystems' structure and function, which has consequently resulted in changes in the composition and abundance of species. Parasites are important organisms in ecosystems' dynamics, taking part in the regulation and structure of host populations. They play a key role in biodiversity by interfering in processes such as competition, migration, speciation and host reproduction (Combes 1996). Recent studies of the influence of parasites in complex systems have enhanced the understanding of the structure and dynamics of these

interactions (Poulin 2010, Poulin *et al.* 2013).

Among parasites, helminths have been widely used as indicators of environmental change (Gardner & Campbell 1992), which may alter the population parameters of the hosts, resulting in deleterious effects on their populations (Bush *et al.* 2001). Helminths are excellent models for studies of parasite-host interactions in natural and anthropogenic ecosystems (Simões *et al.* 2010, Cardoso *et al.* 2016) due to their great dispersal potential among species and environments, to their evolutionary history, and to their relatively short life cycles (Brandão 2007). Furthermore, seasonality can have a strong effect on helminths' abundance and intensity, and may determine their distribution. Extrinsic factors can favour the

survival of some life stages, especially for species whose eggs remain in the soil, subject to the influence of temperature, moisture or rainfall (Jiménez *et al.* 2011, Simões *et al.* 2016).

Many species of small mammals are known to act as natural reservoirs of parasites that affect humans. Opossums are noted for their high abundance, widespread occurrence and importance to public health because they are reservoirs of several zoonosis, such as trypanosomiasis (Lima *et al.* 2012), leishmaniasis (Xavier *et al.* 2014) and helminth infections, such as gnathostomiasis (Ruiz 1952) and lagochilascariasis (Artigas *et al.* 1968). The common black-eared opossum *Didelphis aurita* Wied, 1826, (Didelphimorphia, Didelphidae) occurs in the Atlantic Forest biome. It has a frugivorous / omnivorous feeding habit and can feed on items found in human garbage (Santori *et al.* 2012). These characteristics associated with its generalist use of the habitat (Fonseca 1989, Junior & Leite 2007) make this animal abundant, with high population densities, especially in areas close to human habitations (Gentile *et al.* 2000), making the common opossum a sylvatic - synanthropic animal.

The aim of this study was to analyse the parasitological parameters and the spatial aggregation of the most abundant nematodes of the large intestine and stomach of the opossum *Didelphis aurita* Wied-Neuwied, 1826 (Didelphimorphia, Didelphidae) in the Pedra Branca State Park (a forest reserve) and its surroundings. We compared the parameters in relation to habitats of the host with different levels of anthropic disturbance, season and host gender in order to understand the ecological host-parasite interactions. This study is part of a program on ecology and biodiversity of small mammal populations and communities and their parasites in the Pedra Branca Massif in the municipality of Rio de Janeiro, Brazil.

MATERIAL AND METHODS

Study area

This study was carried out in areas of the FIOCRUZ Atlantic Forest Campus of the Oswaldo Cruz Foundation (Campus FIOCRUZ Mata Atlântica - CFMA) and areas of Pedra Branca State Park

(PBSP) in the city of Rio de Janeiro. The CFMA is inserted in an expanding urban region in the Jacarepaguá Basin and is part of the buffer zone of the Pedra Branca State Park, including preserved areas of the Park. This park is considered the largest forest reserve located within an urban environment in Brazil, covering a total area of 12,492 hectares with predominance of Ombrophilous Dense Atlantic Forest vegetation. The climate of the region is humid mesothermal with hot rainy summers and mild winters.

Samples were collected in transects within the CFMA and PBSP, in three different habitat types representing areas of: 1) sylvatic-urban interface near human dwellings (peridomicile) (22°56'18"S 43°24'11"W and 22°55'57"S 43°26'34"W), 2) disturbed forest areas (22°56'28"S 43°24'34"W and 22°24'45.5"S 43°24'45.6"W), and 3) preserved forest areas (22°56'47"S 43°25'07"W and 22°55'57"S 43°26'36"W). The peridomicile areas were in the backyards of houses and had sparse understory in most of the transects, canopy ranging from 6 to 15 meters, predominance of bushes and small trees, some flooded areas, and flat to moderate slope. The disturbed forest areas were in regeneration process with a vegetation in different ecological succession stages between the areas of human occupation and the preserved areas of the Park, presenting semi-open understory, medium vegetation height ranging from 6 to 20 meters, and flat slope. The preserved forest areas were within the limits of the preserved areas of the Park and had semi-open understory, tall vegetation with canopy ranging from 10 to 40 meters, and irregular slope varying from flat to steep.

Sampling Methods

Opossums were collected from July 2012 to April 2015 every four months (except in July 2014), representing dry, rainy and intermediate seasons. Captures were carried out along transects, two at each location. Sherman® and Tomahawk® traps were placed on the ground at each point baited with a mixture of banana, peanut butter, oats and bacon.

Adult animals were euthanized for recovery of helminths and other samples, and their bionomic data were recorded (age, gender, reproductive activity, body

mass and external measures). Young animals and females with pouch young, were marked with ear tags and released at their trapping points and were not included in the analyses. The ages of the animals were estimated based on dental development and body size according to Gentile *et al.* (1995). The skulls of the animals were deposited as voucher specimens in the zoological collection of the Rio de Janeiro National Museum.

Some of the nematode specimens were fixed at 65° AFA (70% ethanol - 0.4% formalin - 100% acetic acid ratios of 93:5:2) according to Amato *et al.* (1991), and some were stored in 70% ethanol for further molecular analysis. Specimens were counted using a stereoscopic microscope and identified using a Zeiss Standard 20 light microscope. The species were identified according to Yamaguti (1961) and Vicent *et al.* (1997). Voucher specimens were deposited in the helminthological collection of the Oswaldo Cruz Institute (CHIOC numbers: *Turgida turgida* n° 38321, *Aspidodera raillieti* n° 38322, *Cruzia tentaculata* n° 38323).

Animals were captured under authorization of the Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBIO, license number 13373) and the Environmental Institute of Rio de Janeiro State (INEA, license number 020/2011). All procedures followed the guidelines for capture, handling and care of animals of the Ethical Committee on Animal Use of the Oswaldo Cruz Foundation (CEUA license number L-049/08 and LW-81/12 and LW - 39/14). Biosafety techniques and personal safety equipment were used during all procedures involving animal handling and biological sampling.

Data analysis

The parasitological parameters were calculated for each nematode species according to Combes (2001). Abundance was considered as the total number of nematodes of a species divided by the number of hosts analysed. Intensity was the total number of nematodes of a species divided by the number of animals infected by the species. Prevalence was the ratio between the number of infected animals and the total number of animals analysed. The spatial

aggregation level was calculated using the variance to mean ratio of the number of helminths per host. Nematode sex ratios were compared using the chi-square test.

Abundances, intensities and prevalences were compared in relation to habitat type where the host was captured, host gender and season for each nematode species. Prevalence rates were compared using the chi-square contingency test. Intensities and abundances were compared using generalized linear models (GLM), where the best models (models with $\Delta AICc$ less than two) were chosen using the corrected Akaike information criterion (AICc). The chi-square tests were performed using the Past Software version 3.09 (Hammer *et al.* 2001) and the analysis of GLM with PASW statistical software version 18 (SPSS Inc. 2009). The significance level used was of 5% in all the analyses.

RESULTS

Forty-eight specimens of opossums were collected, 22 in the peridomicile, 15 in the disturbed forest areas and 11 in the preserved forest areas. We found helminths species belonging to the three phyla; however, we used only three nematodes as target species to analyse the ecological effects on its populations due to their high abundance. *Turgida turgida* (Rudolphi, 1819) Travassos, 1919 (Physalopteridae, Railliet, 1893 subfam.) Leiper, 1908 was found in the stomach; and *Cruzia tentaculata* (Rudolphi, 1819) Travassos, 1922 (Kathlaniidae, Travassos, 1918) and *Aspidodera raillieti* Travassos, 1913 (Aspidoderidae, Freitas, 1956) were found in the large intestine. Forty-five percent of the opossums were infected with the three helminths analysed. We recovered a total of 319 adult worms of *T. turgida*, 3681 of *C. tentaculata*, and 966 of *A. raillieti*.

Sex ratio in *T. turgida* did not differ from 1: 1 ($\chi^2=0.127$ and $p=0.722$). *Cruzia tentaculata* and *A. raillieti* had significantly more females than males ($\chi^2=51.39$ and $p=0.0$; $\chi^2=21.35$ and $p=0.0$, respectively). *C. tentaculata* was the most abundant and prevalent species (Table 1). All species had high overall aggregation indices and when considering the infrapopulations within each habitat type, host gender

or season (Table 1). No species had significant difference in prevalence when compared among host habitat types, host gender or season ($p > 0.05$ in all cases) (Table 1).

Intensity was different among variables in *C. tentaculata* (Table 2). The best model obtained in the GLM analysis included only the season, showing that the species had higher intensity during the rainy

season (Table 2). In *T. turgida* and *A. raillieti* the best models in the analyses were the null models (without variables). However, in *T. turgida* three models were plausible, indicating that habitat, which was present in two of these three models, may also be an important variable related to intensity, which was higher in the hosts of the disturbed forest areas (Table 2).

Table 1. Abundance and intensity (\pm SD), prevalence (95% confidence interval) and aggregation indices in relation to the habitat type, host gender and season for three nematode species (*T. turgida*, *C. tentaculata*, *A. raillieti*) recovered from *Didelphis aurita* in Pedra Branca State Park and surroundings, Rio de Janeiro, Brazil.

	<i>Turgida turgida</i>	<i>Cruzia tentaculata</i>	<i>Aspidodera raillieti</i>
Abundance	6.64 \pm 7.66	76.68 \pm 128.23	20.12 \pm 36.48
Peridomicile	4.04 \pm 7.05	80.18 \pm 118.99	15.50 \pm 29.88
Disturbed Forest	10.06 \pm 8.19	111.20 \pm 171.36	22.20 \pm 45.26
Preserved Forest	7.18 \pm 6.05	22.63 \pm 34.54	26.50 \pm 37.69
Male	6.51 \pm 7.19	80.92 \pm 135.48	20.29 \pm 38.06
Female	7.42 \pm 10.73	51.85 \pm 75.56	19.14 \pm 27.71
Dry Season	6.04 \pm 6.46	69.58 \pm 104.5	21.83 \pm 34.71
Rainy Season	6.90 \pm 9.26	148.00 \pm 212.27	31.20 \pm 54.02
Intermediate Season	7.50 \pm 8.75	37.92 \pm 56.96	9.28 \pm 21.19
Intensity	9.38 \pm 7.48	99.48 \pm 137.4	34.50 \pm 42
Peridomicile	6.35 \pm 7.48	103.76 \pm 116.23	26.20 \pm 34.59
Disturbed Forest	12.58 \pm 7.28	139.00 \pm 182	41.60 \pm 56.03
Preserved Forest	9.80 \pm 5.62	31.12 \pm 37.45	41.70 \pm 40.37
Male	9.20 \pm 6.89	103.68 \pm 145.82	34.66 \pm 45.29
Female	10.40 \pm 11.11	72.60 \pm 78.63	33.50 \pm 29.25
Dry Season	8.05 \pm 6.16	75.90 \pm 107.02	30.82 \pm 37.82
Rainy Season	9.85 \pm 9.44	246.6 \pm 227.65	52.00 \pm 62.89
Intermediate Season	11.66 \pm 8.58	59.00 \pm 61.80	26.00 \pm 28.19
Prevalence	70.83 (70.77-70.89)	77.08 (75.92-78.24)	58.33 (58.00-58.66)
Peridomicile	63.63 (63.54-63.72)	77.27 (75.68-78.86)	59.09 (58.70-59.48)
Disturbed Forest	80.00 (79.87-80.13)	80.00 (77.23-82.77)	53.30 (52.57-54.03)
Preserved Forest	72.72 (72.61-75.83)	72.72 (72.07-73.37)	63.60 (62.89-64.31)
Male	70.73 (70.66-70.80)	78.04 (76.72-79.36)	58.53 (58.16-58.90)
Female	71.42 (71.17-71.67)	71.42 (69.63-73.21)	57.14 (56.49-57.79)
Dry Season	75.00 (74.92-75.08)	91.66 (90.33-92.99)	70.83 (70.39-71.27)
Rainy Season	70.00 (69.82-70.18)	60.00 (55.80-64.20)	60.00 (58.93-61.07)
Intermediate Season	9.00 (8.86-9.14)	64.28 (63.33-65.23)	35.71 (35.36-36.06)
Aggregation Indices	6.31	192.97	52.6
Peridomicile	10.69	154.56	48.64
Disturbed Forest	4.12	239.21	76.63
Preserved Forest	3.57	45.07	38.08
Male	5.29	204.28	57.82
Female	14.01	95.91	29.66
Dry Season	3.95	151.29	46.86
Rainy Season	10.50	209.88	76.06
Intermediate Season	7.63	67.06	36.15

Table 2. Generalized Linear Models (GLM) for nematode intensities (*T. turgida*, *C. tentaculata* and *A. raillieti*), recovered from *Didelphis aurita* in areas of Pedra Branca State Park and surroundings, Rio de Janeiro, Brazil.

Species	Model	AICc	AICc	WAICc
<i>Turgida turgida</i>	Null	238.619	0	5.95
	Habitat	238.896	0.277	5.18
	Host gender+Habitat	240.133	1.514	2.79
	Host gender	240.926	2.307	1.88
	Season	242.186	3.567	1.17
	Habitat+Season	242.492	3.873	3.41
	Host gender+Season	244.945	6.326	1.10
	Host gender +Habitat+ Season	245.137	6.518	0.01
<i>Cruzia tentaculata</i>	Season	468.446	0	24.63
	Host gender+Season	471.110	2.664	6.50
	Habitat+Season	472.482	4.036	3.27
	Null	473.120	4.674	2.38
	Habitat	474.854	6.408	1.23
	Host gender	475.269	6.823	1.15
	Host gender +Habitat+ Season	475.542	7.096	2.58
	Host gender+Habitat	477.436	8.990	0.01
<i>Aspidodera raillieti</i>	Null	293.072	0	29.11
	Host gender	295.589	2.517	8.27
	Season	296.910	3.838	4.27
	Habitat	297.368	4.296	3.40
	Host gender+Season	299.814	6.742	1.29
	Host gender+Habitat	300.322	7.250	1.50
	Habitat+Season	301.127	8.055	3.99
	Host gender +Habitat+ Season	303.895	10.823	0.00

Turgida turgida had higher abundances in hosts captured in the disturbed forest areas, with the best model including only host habitat (Table 3). Nevertheless, the null model and the model including host habitat and host gender were also plausible. *C. tentaculata* showed higher abundance during the rainy season, with the best model including only season, but the null model and the model including habitat were also plausible (Table 3). In *A. raillieti*, the only plausible model was the null model (Table 3), indicating no relation between abundance and the variables analysed. In all the analyses, the model effects were significant.

DISCUSSION

In parasites, female-biased sex ratios can increase the probability of mating in polygamous mating systems (Poulin 2007). The observation of a larger number of females in relation to males observed for

C. tentaculata and *A. raillieti*, which is the most common pattern in the sex ratio of nematodes, can be attributed to an ecological reproductive strategy, where an increase in egg output enhances the chances of the parasite infecting the host, and consequently, maintaining the life cycle. In counterpart, the 1:1 ratio observed for *T. turgida* can be attributed to the fact that males and females of this species spend much time adhered to each other during the reproductive phase because of the adhesive secretion produced by the prostate glands (Oliveira-Menezes *et al* 2011). Antunes (2005) also observed a 1:1 sex ratio in *T. turgida* and more females in *C. tentaculata*, agreeing with the present study; however, she observed more males in *A. raillieti*, but did not mention their mating system. Although there is a lack of information concerning the mating system of these species, we suggest that *C. tentaculata* and *A. raillieti* may have shown a polygamous behaviour in this study, which was not clearly observed for *T. turgida*.

Table 3. Generalized Linear Models (GLM) for the nematode abundances (*T. turgida*, *C. tentaculata* and *A. raillieti*) recovered from *Didelphis aurita* in areas of the Pedra Branca State Park and surroundings, Rio de Janeiro, Brazil.

Species	Model	AICc	AICc	WAICc
<i>Turgida turgida</i>	Habitat	334.876	0	10.90
	Null	336.121	1.245	5.85
	Host gender+Habitat	336.659	1.783	4.47
	Host gender	338.315	3.439	1.95
	Habitat+Season	339.654	4.778	1.49
	Season	340.451	5.575	2.15
	Host gender+Habitat+Season	341.978	7.102	1.61
	Host gender+Season	342.929	8.053	0.01
<i>Cruzia tentaculata</i>	Season	605.316	0	3.46
	Null	605.424	0.108	3.28
	Habitat	606.857	1.541	1.60
	Host gender	607.387	2.071	0.62
	Host gender+Season	607.800	2.484	2.14
	Habitat+Season	609.317	4.001	0.90
	Host gender+Habitat	609.110	3.794	4.35
	Host gender+Habitat+Season	612.051	6.735	0.01
<i>Aspidodera raillieti</i>	Null	485.083	0	8.11
	Host gender	487.356	2.273	2.60
	Season	487.451	2.368	2.48
	Habitat	488.987	3.904	1.15
	Habitat+Season	489.269	4.186	1.21
	Host gender+Season	489.642	4.559	1.11
	Host gender+Habitat+Season	489.846	4.763	2.26
	Host gender+Habitat	491.477	6.394	0.02

The rainy season seemed to promote an increase in the intensity of *C. tentaculata* in the opossums and, less evidently, in abundance. This result may be related to the life cycle characteristics of this helminth. *C. tentaculata* has a direct life cycle, so that embryonated eggs remain latent in the soil until they are ingested by the host (Jiménez *et al.* 2011). During such periods, soil temperature and moisture must be constant and adequate for the eggs remain infective (Anderson 2000). Thus, drought periods can impair the development of the free-living stages of this species in the environment. The same might apply to *A. raillieti*, because this species also has a direct life cycle (Anderson 2000, Jiménez *et al.* 2011), and also showed greater abundance and intensity during the rainy season. However, the modelling results for this species did not indicate season as a significant variable, so further investigation is needed. Although *C. tentaculata* and *A. raillieti* occur in the same microhabitat, the large intestine, we did not observe any association (positive or negative) between them

(unpublished data of the laboratory), indicating no evidence of competition or synergism between these species in this study.

The greater abundance and intensity of *T. turgida* in opossums of the disturbed forest area can be explained by the ecological characteristics of this area. The vegetation of these areas presents different stages of ecological succession, and is close to human dwellings as well as to the more preserved forest. These features could provide a larger abundance of the intermediate hosts of this nematode, which are possibly arthropods. These constitute one of the main items of the opossum diet (Santori *et al.* 2012), causing infection by ingesting the nematode eggs or larvae. *T. turgida* has a heteroxenous life cycle, where the arthropods, which are present in the opossum diet, may act as intermediate hosts when infected with the nematode larvae (Anderson 2000, Jiménez *et al.* 2011, Acosta-Virgem *et al.* 2015). Thus, the generalist and synanthropic characteristics of the opossum may have favoured the transmission of this helminth.

Most studies of parasitism have only investigated the occurrence of parasite species in the hosts. The scarcity of parasitological studies of small mammal host with ecological focus, especially in Brazil, reinforces the importance of the present report and the need for further studies on this topic. Ecological approaches have a key role in the understanding of host-parasite interactions, and thus understanding the functional importance of parasites in the stability of ecosystems (Lebarbenchon *et al.* 2009). Parasites can also be considered as biological parameters in biodiversity conservation programs (Poulin 1999). The present report is a preliminary study and the first to evaluate parasitism by nematodes in small mammals in the sylvatic-urban interface of the largest urban forest in Brazil, Pedra Branca State Park. We concluded that the host's behaviour might be an important characteristic for the maintenance of these parasites' life cycles in the different environments. There was no clear evidence that *A. railieti* was affected by habitat type of the hosts' captures, season or host gender. Rainfall seems to facilitate the life cycle development of the nematode *C. tentaculata*. *T. turgida* seems to be favoured by characteristics of more heterogeneous areas within the interface of the sylvatic-urban environment, which may enable the occurrence of its intermediate hosts.

ACKNOWLEDGMENTS

We would like to thank the staff and students of Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Laboratório de Hantavírus e Rickettsioses, Laboratório de Biologia de Tripanossomatídeos e Laboratório de Pesquisa Clínica em Dermatose from Fiocruz who helped in the field work; to Dr. Paulo D'Andrea for the ICMBio and INEA licences and for supporting the general project; to the coordinator of Fiocruz Atlantic Forest Campus, Gilson Antunes, for providing local facilities and supporting the general project; to the equip of Fiocruz Atlantic Forest Campus, especially to Marta L. Brandão and José L. P. Cordeiro for local facilities and help in the field work; to Marcelo F. Freitas for helping in the field work in all campaigns; to Instituto Estadual do Meio Ambiente (INEA) for the collecting licence and for local facilities. This project was financially supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq (306352/2014-1), Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro-FAPERJ (E-26/111.296/2014), and Instituto Oswaldo Cruz (Fiocruz). RGBMC received grants from CNPq and SFCN from CAPES.

REFERENCES

Acosta-Virgem, K., López-Caballero, Jorge, García-Pietro, L., & Mata-López, R. 2015. Helminths of three species of opossums

- (Mammalia, Didelphidae) from Mexico. *ZooKeys*, 511, 131-152. DOI: 10.3897/zookeys.511.9571
- Amato, J. F. R., Boeger, W. A., & Amato, S. B. (Eds.). 1991. *Protocolo para laboratório - coleta e processamento de parasitas do pescado*. Rio de Janeiro: Imprensa Universitária, UFRJ: p. 81.
- Anderson, R. C. 2000. *Nematode parasites of vertebrates: their development and transmission*. 2nd ed. Wallingford, OXON: CABIPublishing: p. 650. DOI: 10.1079/9780851994215.0000
- Antunes, G. M. 2005. Diversidade e potencial zoonótico de parasitos de *Didelphis albiventris* Lund, 1841 (Marsupialia, Didelphidae). Faculdade de Veterinária da Universidade Federal do Rio Grande do Sul. p. 122.
- Artigas, P. T., Araujo, P., Romiti, N., & Ruivo, M. 1968. Sobre um caso de parasitismo humano por *Lagochilascaris minor* Leiper 1902, no Estado de São Paulo, Brasil. *Revista do Instituto de Medicina Tropical de São Paulo*, 10(2), 78-83.
- Brandão, M. L. 2007. Helminths of mammals from the Parque Nacional Serra da Capivara, Sudeste do Piauí: diversidade e influências antrópicas. Escola Nacional de Saúde Pública da Fundação Oswaldo Cruz. p. 165. Retrieved from <http://www.arca.fiocruz.br/handle/icict/5237>
- Bush, A. O., Fernández, J. C., Esch, G. W., & Seed, J. R. 2001. *Parasitism: the diversity and ecology of animal parasites*. 1st ed. New York, NY: Cambridge University Press: p. 580.
- Cardoso, T. S., Simões, R. O., Luque, J. L. F., Maldonado, A., & Gentile, R. 2016. The influence of habitat fragmentation on helminth communities in rodent populations from a Brazilian Mountain Atlantic Forest. *Journal of Helminthology*, 90(4), 460-468. DOI: 10.1017/S0022149X15000589
- Combes, C. 1996. Parasites, biodiversity and ecosystem stability. *Biodiversity and Conservation*, 5(8), 953-962. DOI: 10.1007/BF00054413
- Combes, C. 2001. *Parasitism: The ecology and evolution of intimate interactions*. 1st ed. Chicago, IL: University of Chicago Press: p. 552.
- Fonseca, G. A. B. 1989. Small mammal species diversity in Brazilian tropical primary and secondary forest of different sizes. *Revista Brasileira de Zoologia*, 6(3), 381-422. DOI: 10.1590/S0101-81751989000300001
- Gardner, S. L., & Campbell, M. L. 1992. Parasites as probes for biodiversity. *Journal of Parasitology*, 78(4), 596-600. DOI: 10.2307/3283534
- Gentile, R., D'Andrea, P. S., Cerqueira, R., & Maroja, L. S. 2000. Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study. *Studies on Neotropical Fauna & Environment*, 35(1), 1-9.
- Gentile, R., D'andrea, P. S., & Cerqueira, R. 1995. Age structure of two marsupials in a Brazilian Restinga. *Journal of Tropical Ecology*, 11(4), 679-682. DOI: 10.1017/S0266467400009226
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4, 1-9.
- Jiménez, F. A., Catzefflis, F., & Gardner, S. L. 2011. Structure of parasite component communities of didelphid marsupials: insight from a comparative study. *Journal of Parasitology*, 97(5), 779-787. DOI: 10.1645/GE-2711.1

- Junior, V. C., & Leite, Y. L. R. 2007. Uso de habitats por pequenos mamíferos no Parque Estadual da Fonte Grande Vitória, Espírito Santo, Brasil. *Boletim do Museu de Biologia Mello Leitão*, 21, 57-77.
- Lebarbenchon, C., Poulin, R., & Thomas, F. 2009. Parasitism, biodiversity, and conservation biology. In: F. Thomas, J.-F. Guégan & F. Renaud (Eds.), *Ecology & evolution of parasitism*. pp. 149-160. Oxford: Oxford University Press.
- Lima, M. M., Sarquis, O., Oliveira, T. G., Gomes, T. F., Coutinho, C., Daflon-Teixeira, N. F., Toma, H. K., Britto, C., Teixeira, B. R., D'Andrea, P. S., Jansen, A. M., Bóia, M. N., & Carvalho-Costa, F. A. 2012. Investigation of Chagas disease in four periurban areas in northeastern Brazil: epidemiologic survey in man, vectors, non-human hosts and reservoirs. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 106(3), 143-149. DOI: 10.1016/j.trstmh.2011.10.013
- Oliveira-Menezes, A., Lanfredi-Rangel, A., & Lanfredi, R. M. 2011. The first description of eggs in the male reproductive system of *Physaloptera bispiculata* (Nematoda: Spiruroidea). *Journal of Helminthology*, 85(2), 142-145. DOI: 10.1017/S0022149X10000374
- Poulin, R. 1999. The functional importance of parasites in animal communities: many roles at many levels? *International Journal for Parasitology*, 29(6), 903-914. DOI: 10.1016/S0020-7519(99)00045-4
- Poulin, R. 2007. *Evolutionary ecology of parasites*. 2nd ed. Princeton: Princeton University Press: p. 332.
- Poulin, R. 2010. Network analysis shining light on parasite ecology and evolution. *Trends in Parasitology*, 26(10), 492-498. DOI: 10.1016/j.pt.2010.05.008
- Poulin, R., Krasnov, B. R., Pilonosof, S., & Thielges, D. W. 2013. Phylogeny determines the role of helminth parasites in intertidal food webs. *Journal of Animal Ecology*, 82(6), 1265-1275. DOI: 10.1111/1365-2656.12101
- Ruiz, J. M. 1952. Sobre um novo *Gnathostoma* assinalado no Brasil. *Memórias do Instituto Butantan*, 24(1), 37-44.
- Santori, R. T., Lessa, L. G., & Astúa, M. D. 2012. Alimentação, nutrição e adaptações alimentares de marsupiais brasileiros. In: N. C. Cáceres (Ed.), *Os marsupiais do Brasil: biologia, ecologia e conservação*. pp. 383-404. Campo Grande: UFMS.
- Simões, R., Gentile, R., Rademaker, V., D'Andrea, P. S., Herrera, H., Freitas, T., Lanfredi, R., & Maldonado Jr., A. 2010. Variation in the helminth community structure of *Thrichomys pachyurus* (Rodentia, Echimyidae) in two sub-regions of the Brazilian Pantanal: the effects of land use and seasonality. *Journal of Helminthology*, 84(3), 266-275. DOI: 10.1017/S0022149X09990629
- Simões, R. O., Luque, J. L., Gentile, R., Rosa, M. C. S., Costa-Neto, S., & Maldonado Jr., A. 2016. Biotic and abiotic effects on the intestinal helminth community of the brown rat *Rattus norvegicus* from Rio de Janeiro, Brazil. *Journal of Helminthology*, 90(1), 21-27. DOI: 10.1017/S0022149X14000704
- SPSS Inc. 2009. *PASW Statistics for Windows, Version 18.0*. Chicago: SPSS Inc.
- Vicente, J. J., Rodrigues, H. O., Gomes, D. C., & Pinto, R. M. 1997. Nematóides do Brasil. Parte V: nematóides de mamíferos. *Revista Brasileira de Zoologia*, 14(1), 1-452. DOI: 10.1590/S0101-81751997000500001
- Yamaguti, S. (Ed.). 1961. *Sistema helminthum: nematodes of vertebrates parts I and II*, vol. 3. New York: Interscience Publishing, Inc.: p. 1261.
- Xavier, S. C. C., Roque, A. L. R., Bilac, D., De Araújo, V. A. L., Costa-Neto, S. F., Lorosa, E. S., Silva, L. F. C. F., & Jansen, A. M. 2014. Distantiae transmission of *Trypanosoma cruzi*: a new epidemiological feature of acute Chagas disease in Brazil. *PLoS Neglected Tropical Diseases* (Online), 8(5), e2878. DOI: 10.1371/journal.pntd.0002878

Submitted: May 25, 2016

Accepted: September 7, 2016