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Artículo



FIRST COPROLOGICAL SURVEY OF HELMINTHS IN A WILD POPULATION OF BLACK CAPUCHIN MONKEYS (*Sapajus nigritus*) IN NORTHEASTERN ARGENTINA

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ABSTRACT. Parasites play an important role in primate ecology. Although gastrointestinal parasites have been surveyed in several primate taxa, there is still a substantial paucity of data for some species. Here we report the first coprological survey of helminths in a primate species, the wild black capuchin monkey (*Sapajus nigritus*), which is endemic to the Atlantic Forest. During three winters and one summer, we collected 665 faecal samples from 44 identified individuals of two capuchin groups in Iguazú National Park, NE Argentina, for parasitological analysis. Overall, we identified eight helminths: *Filariopsis* sp., *Strongyloides* sp., *Trichuris* sp., *Ascaris* sp., a Subuluridae, a Phylalopteridae, a Hymenolepididae cestode, and an undetermined Trematode. The Hymenolepididae (25-42%), *Filariopsis* sp. (15-42%), and *Strongyloides* sp. (11-27%) were the most prevalent parasites regardless of the survey year, group and season. On average, infected capuchins harboured 1.12-1.26 parasite taxa. The parasite community observed in the black capuchin monkeys resembled those found in other Cebidae.

RESUMEN. Primer estudio coprológico de helmintos en una población silvestre de monos caí (*Sapajus nigritus*) en el Nordeste de Argentina. Los parásitos juegan un rol importante en la ecología de los primates. Aunque los parásitos gastrointestinales han sido investigados en varios taxa de primates, todavía existe un vacío de información para algunas especies. Aquí reportamos los resultados del primer estudio coprológico de helmintos en una población silvestre de monos caí (*Sapajus nigritus*), una especie endémica del Bosque Atlántico. Durante tres inviernos y un verano, colectamos 665 muestras fecales de 44 individuos identificados pertenecientes a dos grupos de monos caí en el Parque Nacional Iguazú en el Nordeste de Argentina, para realizar análisis parasitológicos. En total identificamos ocho helmintos: *Filariopsis* sp., *Strongyloides* sp., *Trichuris* sp., *Ascaris* sp., un Subuluridae, un Spiruridae, un cestode Hymenolepididae y un Trematode indeterminado. Hymenolepididae (25-42%), *Filariopsis* sp. (15-42%) y *Strongyloides* sp. (11-27%) fueron los parásitos más prevalentes independientemente del año y la estación. En promedio, los monos caí infectados presentaron entre 1.12-1.26 taxa de helmintos. La comunidad de parásitos que encontramos presenta similitudes con la de otros Cebidae.

Key words: Atlantic Forest, parasite prevalence, parasite richness, primates.

Palabras clave: Bosque Atlántico, prevalencia de parásitos, primates, riqueza parasitaria.

INTRODUCTION

Parasites of mammals can be detrimental to their fitness and are an important ecological driver in the evolution of behaviour and social organization (Nunn & Altizer 2006). The opportunity of surveying at least some groups of parasites, such as those inhabiting the gastrointestinal tract, using non-invasive faecal sample analyses, has contributed to the remarkable increase of studies documenting primate parasites in the last decade. However, at least in the Neotropical region, there is still a significant bias towards sampling some primate genera over others. So far, most surveys and longitudinal studies have focused on howler monkeys (*Alouatta* spp.; e.g. Stoner 1994; Stuart et al. 1998; Vitazkova & Wade 2006; Trejo-Macías et al. 2007; Kowalewski et al. 2011). Although capuchin monkeys (*Cebus* spp. or gracile capuchins, and *Sapajus* spp. or robust capuchins; Lynch Alfaro et al. 2012) have been studied deeply in many aspects of their ecology and behaviour (Fragaszy et al. 2004), their parasite community is still almost unknown. The only systematic survey on gastrointestinal parasites published on *Cebus capucinus* is from Parr et al. (2013), while very few reports exist on parasites of *Sapajus* spp. (in captivity: Santa Cruz et al. 1998, 2000; in the wild: a one-point-in-time survey on a group of 10 individuals in Peru, Phillips et al. 2004) none of them based on systematic sampling. In all cases, analyses indicate that *Strongyloides* sp. and *Filariopsis* sp. are among the most common parasite taxa recovered.

Robust capuchins of genus *Sapajus* rely on an omnivorous diet including fruits, arthropods and small birds and mammals (Robinson & Janson 1987; Brown & Zunino 1990), and they use low-canopy levels, as well as the ground for foraging, drinking and playing (Terborgh 1983; Siemers 2000). They have a complex social structure and interact frequently with other individuals of their own group (Fragaszy et al. 2004). These characteristics are likely to expose them to high levels of parasitism (Nunn & Altizer 2006). Black capuchins (*Sapajus nigritus*), in particular, are endemic to the Atlantic Forest (Lynch Alfaro et al. 2012). Given the high

degrees of heterogeneity and the outstanding levels of endemism, the Atlantic Forest is one of the world's top biodiversity hotspots, harbouring 26 species of primates, 73% of which are endemic (Pinto et al. 2009). This biome has experienced a long lasting destruction and degradation and is currently reduced to 12% of the original surface (Ribeiro et al. 2011). Largely because of this habitat loss, 65% of Atlantic Forest's primate species are threatened (Pinto et al. 2009). Within this context, baseline data regarding patterns of parasitic infections in wild primate populations endemic to the Atlantic Forest are critical to providing indicators of population health and to facilitate longitudinal or cross-sectional studies of populations to assess and manage disease risks. In this study, we present the first coprological survey on helminths of wild black capuchins in Iguazú National Park, Argentina.

MATERIALS AND METHODS

Study site and subjects

We carried out the field work in Iguazú National Park, Northeastern Argentina (25° 40' S; 54° 30' W), in the southwestern section of the South American Atlantic Forest. This semi-deciduous forest is characterised by a humid subtropical climate with marked seasonality in day length and temperature (Crespo 1982). Mean annual rainfall varies between 1500 and 2000 mm without a marked dry season (Brown & Zunino 1990). There is seasonal variation in the production of fleshy fruits and arthropods, which is lower during winter months (June-August) and reaches its maximum between October and January (Janson 1996). Due to this seasonal pattern, winter is a critical time during which black capuchins depend mostly on bamboo shoots, meristems and leaf bases of epiphytes (Di Bitetti 1997). Black capuchins live in polygamous multi-male, multi-female groups of 7-30 individuals (Di Bitetti 1997). Individuals can be identified based on physical characteristics, such as facial colour patterns, body size and shape of tufts (Di Bitetti 2001).

We conducted the study on two groups, known as Macuco (N = 23-27) and Spot (N = 14-21), whose composition changed across the three years (Table 1). Macuco was exposed to a relatively high degree of contact with tourists, with interactions occasionally including physical contact and occurring during 6%-13% of the observation days in

Table 1

Age composition of Macuco (MAC) and Spot (SPO) black capuchin groups from Iguazu National Park, Misiones, Argentina, along the study seasons. We considered adults males (ADM) > 6 years old; adult females (ADF) > 5 years old, subadult males (SUBM) 5-6 years old; subadult females (SUBF) 4-5 years old, juvenile (JUV) males 1-4 and females 1-3 years old, and infants (INF) < 1 years old.

Season	Group	Sex-Age classes						TOTAL
		ADM	ADF	SUBM	SUBF	JUV	INF	
Winter 2012	MAC	5	7	2	1	7	2	24
	SPO	3	4	0	1	5	1	14
Winter 2013	MAC	7	8	3	1	5	3	27
	SPO	3	4	0	1	6	3	17
Summer 2013-14	MAC	3	7	2	2	5	5	24
	SPO	-	-	-	-	-	-	-
Winter 2014	MAC	3	8	1	2	5	4	23
	SPO	5	5	2	0	7	2	21

2013 and 2014. In addition, individuals of Macuco occasionally had access to human food. In contrast, the Spot group displayed very limited and sporadic interactions with tourists in the park, occurring between 3 and 6% of the observation days in 2013 and 2014 (Agostini unpublished data).

Faecal sampling and analysis

To obtain data on parasitism, we collected faecal samples of individuals belonging to Macuco and Spot groups during three winters and one summer: 52 days between June and August 2012; 108 days between May and August 2013 and 107 days between May and August 2014; 83 days between December 2013 and March 2014 (the latter only from Macuco group). Faecal samples were collected opportunistically from 44 identified individuals (26 from Macuco group, and 18 from Spot), and within each study period, most individuals were sampled repeatedly. We collected a total of 97 faecal samples from 33 individuals in winter 2012 (mean \pm SE samples per individual: 2.94 ± 0.21); 164 samples from 35 individuals during winter 2013 (3.90 ± 0.56); and 352 samples from 36 individuals during winter 2014 (8.38 ± 1.29) from both Macuco and Spot groups. In addition, we gathered 52 samples from 16 individuals from Macuco during summer 2013-2014 (3.25 ± 0.59). Approximately one half the subjects of each group were sampled along the study period (58% and 50% for Macuco and Spot, respectively).

We focused our sampling on adult and subadult individuals rather than on juveniles, and infants were discarded from the analyses given the difficulty of collecting their faeces. During the winters of 2013 and 2014, we ran a parallel experimental study that involved deworming of some selected individuals in both groups (Agostini et al. 2017). However, in order to describe the natural parasite community hosted by wild black capuchins, in the present survey we considered only faecal samples from untreated individuals and samples collected during the pre-treatment phase for those who were treated later in each field season.

For the analysis of gastrointestinal parasites, an aliquot of approximately 5 g of each faecal sample was stored in 15 ml of 10% formalin. Then, in the Laboratory of Parasitology of the National Institute of Tropical Medicine (INMeT) in Puerto Iguazú, Argentina, samples were processed using a semi-quantitative flotation method with a saturated sugar solution (Cox & Todd 1962). The technique consisted of weighing 3 g of each faecal sample, adding 43 ml of tap water and homogenizing it. Then, using a strainer and a funnel, the solution was poured filling a 15-ml tube, and centrifuged at 1500 rpm for 2 minutes. After discarding the supernatant, the volume of the tube was filled with a supersaturated sugar solution until forming a meniscus. Then, a cover slip of 18x8 mm was placed on top and the tube was further centrifuged at 1000 rpm during 2 minutes. Finally, the cover slip was put on a slide

and examined with the microscope. We identified eggs and larvae of helminths and took pictures using a microscope with a camera using 10x and 40x magnifiers. We counted and identified eggs and larvae at the genus or family level based on colour, shape, content and size.

Data analysis

We described parasitic infections in terms of prevalence (number of individuals infected with a given parasite/total individuals sampled) and richness (number of taxa infecting the same host) (see Bush et al. 1997). For each surveyed period, we considered an individual as infected by a given type of parasite when at least one of the faecal samples collected were positive for that parasite.

We compared prevalence of the three most common parasites between the two groups (Macuco and Spot), using the Fisher-Freeman-Halton exact test for 2x3 contingency tables (Freeman & Halton 1951), stratifying by sampling period. To evaluate if there was an inter-annual variation in prevalence of the most common parasites, we compared the frequencies of infected individuals among three consecutive winters, separately for each parasite taxon. Similarly, to determine whether parasitic prevalence varied between seasons, we compared the frequencies of infected individuals in summer vs. previous and following winter, separately for each of the most common parasites. Due to the fact that most of the capuchin individuals were repeatedly sampled along different seasons and years, to evaluate inter-annual as well as seasonal differences, we performed a Cochran's Q test for related samples (Siegel & Castellan 1988) considering only the subjects that stayed in the study groups across all study periods. This test is particularly suitable when the variables are categorical and dichotomous as in our case (presence of infection: yes/no). In case of significant difference obtained by Cochran's Q test, we evaluated specific sample pairs using post hoc Dunn's (1964) with Bonferroni adjustment. Since we had no replicates of summer sampling, the comparison between seasons should be taken with caution and cannot be generalised. All statistical tests were two tailed with α set at 0.05, and were performed with software R (v. 3.3.0; R Development Core Team 2016). To run Cochran's Q test, we used the R package *nonpar* (Sweet 2017).

RESULTS

We identified eight taxa of helminths corresponding to six nematodes (*Strongyloides*

sp. [Family Strongyloididae], *Trichuris* sp. [Trichuridae], *Filariopsis* sp. [Filaroididae], *Ascaris* sp. [Ascarididae], an undetermined Subuluridae, an undetermined Physalopteridae, one cestode (undetermined Hymenolepididae), and one unidentified trematode (Fig. 1). Macuco presented eight parasite taxa, whereas Spot displayed six taxa (Table 2). This difference was due to the finding of *Trichuris* sp. and a trematode in a single individual of Macuco. We also recovered some protozoan oocysts; however, since our fixation and analysis techniques were not adequate for protozoan identification, we could not determine to a further level the parasites belonging to this taxon in our capuchin study groups. Table 3 shows the measurements and a brief description of the morphology of eggs and larvae.

Parasite prevalence and richness

The overall proportion of individuals infected with at least one parasite across all survey periods ranged between 50% and 82% for Macuco and between 45% and 62% for Spot. In winter and summer, the undetermined Hymenolepididae and *Filariopsis* sp. were the most prevalent parasites, followed by *Strongyloides* sp. The other identified parasite taxa were scarcely represented (Table 2). The mean individual parasite richness ranged between 1.12 and 1.26 and modal richness was 1. In the 17 samples in which we found two parasite taxa at the same time, the most frequent combination was the pair *Filariopsis* sp.-Hymenolepididae (6/17), followed by *Filariopsis* sp.-*Strongyloides* sp. (4/17).

We did not find any significant differences in prevalence of the three most common parasites between groups in each of the three winters (Fisher-Freeman-Halton's exact test; winter 2012: $p=0.335$; winter 2013: $p=0.498$; winter 2014: $p=0.343$). We found a significant inter-annual variation in prevalence only for *Filariopsis* infection (Cochran's Q test: $\chi^2_2 = 10.71$, $p=0.005$), mostly due to higher proportions of infected individuals in winter 2014 compared to winter 2012 (post-hoc Dunn's test; $z = -3.19$, $p=0.002$), while the other pairwise comparisons of *Filariopsis* prevalence between years were not signifi-

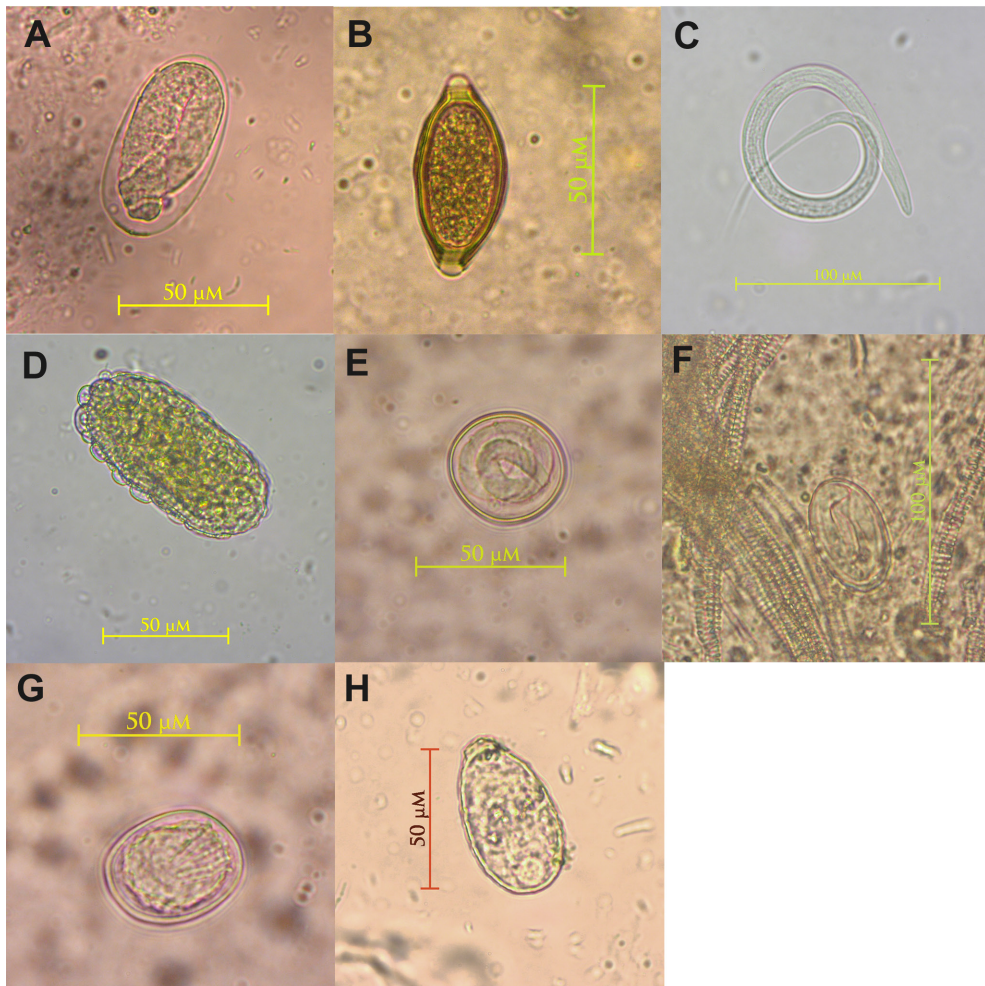


Fig. 1. Parasites from wild black capuchin monkeys in Northeastern Argentina: a) *Strongyloides* sp., b) *Trichuris* sp., c) *Filariopsis* sp., d) *Ascaris* sp., e) undetermined Subuluridae, f) undetermined Physalopteridae, g) undetermined Hymenolepididae, h) undetermined Trematode.

cantly different (winter 2012 vs. winter 2013: $z = -1.74$, $p = 0.123$; winter 2013 vs. winter 2014: $z = -1.45$, $p = 0.221$). We did not find any significant difference in the prevalence of the Hymenolepididae ($\chi^2_2 = 0.11$, $p = 0.946$) and *Strongyloides* ($\chi^2_2 = 4.00$, $p = 0.135$), across the three years. Finally, we found a significant difference between seasons (i.e. summer vs. previous winter vs. subsequent winter) only for *Filariopsis* prevalence ($\chi^2_2 = 6.22$, $p = 0.044$), and it was due to the higher prevalence shown during winter 2014 compared to the summer 2013-2014 ($z = -2.18$, $p = 0.044$), while the other

pairwise comparisons of *Filariopsis* prevalence between seasons were not significantly different (summer 2013-2014 vs. winter 2013: $z = -0.73$, $p = 0.701$; winter 2013 vs. winter 2014: $z = -1.45$, $p = 0.221$). Finally, we found no seasonal significant difference for the other two common parasites, the Hymenolepididae ($\chi^2_2 = 0.67$, $p = 0.716$) and *Strongyloides* ($\chi^2_2 = 5.25$, $p = 0.072$).

DISCUSSION

In our survey of the helminthic community of wild black capuchins, we recovered eight

Table 2

Prevalence of helminths across survey periods in two black capuchin groups, Macuco (MAC) and Spot (SPO), or as a total pooling both groups at Iguazú National Park, Misiones, Argentina. Transmission mode and intermediate host (when applicable) are indicated.

Parasite species	Year	Season	MAC (%)	SPO (%)	Total (%)	N (animal sampled) MAC/SPO	Transmission mode	Intermediate host
NEMATODA								
<i>Strongyloides</i> sp.	2012	Winter	27.3	27.3	27.3	22/11	Direct	-
	2013	Winter	13.6	7.7	11.4	22/13		
	2013-14	Summer	12.5	-	-	16/-		
	2014	Winter	30.0	18.8	25.0	20/16		
<i>Trichuris</i> sp.	2012	Winter	0.0	0.0	0.0	22/11	Direct	-
	2013	Winter	4.5	0.0	2.9	22/13		
	2013-14	Summer	0.0	0.0	-	16/-		
	2014	Winter	0.0	0.0	0.0	20/16		
<i>Filariopsis</i> sp.	2012	Winter	22.7	0.0	15.2	22/11	Direct (?)	-
	2013	Winter	36.4	23.1	31.4	22/13		
	2013-14	Summer	25.0	-	-	16/-		
	2014	Winter	55.0	25.0	41.7	20/16		
<i>Ascaris</i> sp.	2012	Winter	0.0	0.0	0.0	22/11	Direct	-
	2013	Winter	4.5	0.0	2.9	22/13		
	2013-14	Summer	0.0	0.0	-	16/-		
	2014	Winter	5.0	12.5	8.3	20/16		
Unidentified Subuluridae	2012	Winter	0.0	0.0	0.0	22/11	Indirect	Beetles, cockroaches
	2013	Winter	0.0	7.7	2.9	22/13		
	2013-14	Summer	0.0	-	-	16/-		
	2014	Winter	5.0	0.0	2.8	20/16		
Unidentified Physalopteridae	2012	Winter	9.1	36.4	18.2	22/11	Indirect	Beetles, cockroaches, crickets

(Table 2 cont.)

Parasite species	Year	Season	MAC (%)	SPO (%)	Total (%)	N (animal sampled) MAC/SPO	Transmission mode	Intermediate host
	2013	Winter	4.5	0.0	2.9	22/13		
	2013-14	Summer	0.0	-	-	16/-		
	2014	Winter	0.0	0.0	0.0	20/16		
CESTODA								
Unidentified Hymenolepididae	2012	Winter	50.0	27.3	42.4	22/11	Indirect (?)	Beetles
	2013	Winter	31.8	53.8	40.0	22/13		
	2013-14	Summer	25.0	-	-	16/-		
	2014	Winter	35.0	50.0	41.7	20/16		
TREMATODA								
Unidentified Trematode	2012	Winter	0.0	0.0	0.0	22/11	Indirect	Molluscs
	2013	Winter	4.5	0.0	2.9	22/13		
	2013-14	Summer	0.0	-	-	16/-		
	2014	Winter	0.0	0.0	0.0	20/16		

Number (N) of individuals sampled in Macuco (MAC) group for each season: N=22 in winter 2012 and winter 2013, N=16 in summer 2013-14, and N=20 in winter 2014. Individuals sampled in Spot (SPO) group for each season: N=11 in winter 2012, N=13 in winter 2013, N=16 in winter 2014.

Table 3

Measurements and morphological characters of larvae and eggs obtained from 665 faecal samples from two black capuchin groups at Iguazú National Park, Misiones, Argentina (n = number of eggs/larvae used for obtaining measurements).

Parasite	Measurements in μm Mean (range)	Description	
NEMATODA	<i>Strongyloides</i> sp. (n=5)	62.4 (60-65) x 39.6 (34-42)	Thin-shelled eggs, embrionated (Fig. 1a)
	<i>Trichuris</i> sp. (n=2)	58 x 29; 60 x 29	Lemon/barrel- like appearance eggs with two plugs at the extremities; wall thick brownish (Fig. 1b)
	<i>Filariopsis</i> sp. (n=4)	354.5 (337-371)	Larvae coiled with long tails (Fig. 1c)
	<i>Ascaris</i> sp. (unfertilized) (n=1)	90 x 44	Outer surface mamillated, rough, and stained brown (Fig. 1d)
	unidentified Subuluridae (n=1)	38 x 39	Spherical eggs with thin walls, containing a larva (Fig. 1e)
	unidentified Physalopteridae (n=1)	45 x 28	Embrionated eggs, elliptical with thin walls (Fig. 1f)
CESTODA	unidentified Hymenolepididae (n=22)	51 (43-56) x 42 (31-50)	Spherical eggs, contains an oncosphere of 34 x 27 enclosed in an inner envelope; 3 pairs of hooks in fan (Fig. 1g)
TREMATODA	unidentified Trematode (n=1)	60 x 33	Oval egg with operculum, thin wall (Fig. 1h)

taxa. As most other parasitic assessments on New World primates, we relied on non-invasive sampling techniques (faecal sampling) for egg identification. Since we could not access adult parasites through necropsies or performed molecular analyses on eggs, we were not able to distinguish parasites at the species level (Solórzano-García & Pérez-Ponce de León 2017). Although this is a limitation of this study, the importance of our survey lies in the fact that it is the first report of a coprological study of helminths in a wild black capuchin population. All genera and families have already been recorded for capuchin monkeys, although mainly for *Cebus* spp. (Chinchilla et al. 2007, 2010; Notarnicola et al. 2008; Parr et al. 2013).

Our findings are similar to those reported by Santa Cruz et al. (2000) for a captive *Sapajus* spp. colony from Argentina, and by Parr et al. (2013) for wild *Cebus capucinus* from Costa Rica. In those studies, *Filariopsis* sp. and *Strongyloides* sp. were among the most prevalent species. Since reports of infections with *Strongyloides* in New World primates commonly indicate *Strongyloides cebus* (Kaur & Singh 2009; Corrêa et al. 2016), this is likely to be the species infecting our capuchin study population. Other reports of the presence of *Filariopsis* in *Sapajus* or *Cebus* identify this nematode as *Filariopsis barretoii* (= *F. arator*), whose life cycle is still unknown (Rego & Schaeffer 1988; Santa Cruz et al. 1998; Parr et al. 2013). Considering the phylogenetic relatedness with *Filaroides* spp., which have a direct life cycle and immediately infective larvae shed in host faeces, it is likely that *Filariopsis* can also be directly transmitted through consumption of contaminated soil or food (Parr et al. 2013).

Another prevalent parasite found herein is the Hymenolepididae cestode. Although we cannot have certainty about the identification without molecular analyses or access to adult worms, egg morphology resembles to some *Hymenolepis* species (Yamaguti 1959; Thienpont et al. 1979). These eggs are circular to slightly oval, possess a thin wall, an embriophora without striations (in contrast to *Taenia* spp.) and the oncosphera holds six hooks displayed in fan. They are similar in shape and size to those found in wild *Cebus capucinus* by Parr

et al. (2013), who classified them as belonging to the Anoplocephalidae family. However, these authors probably misinterpreted the egg morphology and erroneously classified them. In fact, eggs of Anoplocephalidae are different in shape and size. They are oval, with an oncosphera presenting either a pyriform apparatus like in *Bertiella* sp. or parallel hooks as is the case for *Railletina* sp. and *Mathevotaenia* sp. Furthermore, measurements of eggs of Anoplocephalidae differ from those reported in Parr et al. (2013), which are similar to ours (Navone 1988; Ezquiaga et al. 2009; Mollericono et al. 2013). Our eggs are morphologically similar to those of *Hymenolepis diminuta*, a human parasite, but differ in size (43-56 x 31-50 µm in our samples vs. 60-79 x 72-86 µm in human samples; Thienpont et al. 1979). In Brazil, *Hymenolepis cebidarum* has been reported parasitizing *Callicebus nigrifrons* (Travassos 1965; Schmidt 1986) without mentioning the size or the morphology of the eggs. With the exception of *Himenolepis nana*, all other Hymenolepididae, such as *H. diminuta*, which could be consistent with the cestode we found, are characterised by indirect life cycles that include insects as intermediate hosts (Dunn 1963; Keymer 1981). This suggests that the relatively high prevalence found in our *S. nigritus* groups is due to the heavy reliance of these monkeys on arthropods as one of the major items in their diets. In fact, invertebrates in general, represent annually 40% to 57% of feeding time of this capuchin population at our study site (Brown & Zunino 1990; Agostini unpublished data). Moreover, since capuchins at our site groom each other frequently (Di Bitetti 1997), ingesting fleas containing the Hymenolepididae's cysticeroid larvae in grooming context may enhance the chances of becoming infected with this cestode.

We found *Ascaris* sp. eggs in both Macuco and Spot groups, although at low prevalence. A record of this parasite was also reported for one individual of *Sapajus macrocephalus* in Tambopata National Reserve, Peru (Phillips et al. 2004). Given the rarity of *Ascaris* in New World monkeys, contrasting with the relative high prevalence recorded in humans (Michaud et al. 2003), it is likely that situations

of close contact between humans and monkeys increase the probability of anthroponotic exchange of this parasite (Stuart et al. 1990; Michaud et al. 2003; but see Phillips et al. 2004). The other parasite taxa recovered in this study (i.e. *Trichuris* sp., the physalopterid, the subulurid, and the unknown trematode) had low overall prevalence and their presence was discontinuous across the four survey periods. As suggested by Parr et al. (2013), we should be cautious about including low-prevalence parasites, since they could have been accidentally acquired during the ingestion of some animal prey or animals' faeces. Nevertheless, there are records of physalopterids, subulurids, and trematodes recovered from necropsies of Neotropical primates (Stoner & González-Di Piero 2005; Nunn & Altizer 2006; Santos et al. 2010; Corrêa et al. 2016). Therefore, the presence of these species with low prevalence in Neotropical primates could indicate that they correspond to satellite parasite species.

Overall, the most common parasites found in our capuchin population have relatively low pathogenicity. *Filariopsis* sp. is known to form fibrous nodules containing worms and provoking small lesions on pulmonary tissues in capuchin monkeys (Rego & Schaeffer 1988). However, despite the high intensity of infection and significant pulmonary lesions found in lungs during necropsy, there has been no record of corresponding clinical signs of pulmonary disease in capuchin monkeys (Rego & Schaeffer 1988; Santa-Cruz et al. 1998; Parr et al. 2013). Cestodes belonging to Hymenolepididae are usually present in large numbers, however, infection with these parasites are rarely associated to clinical disease or enteric lesions. The principal clinical signs of infections with Hymenolepididae are diarrhoea and abdominal pain (Abee et al. 2012). Probably, the only parasite that may cause more severe clinical signs is *Strongyloides*. Infections with this parasite may provoke haemorrhagic or mucoid diarrhoea in nonhuman primates, as well as dermatitis, urticarial, anorexia, debilitation, vomiting, cough, and prostration among other signs. Occasionally, fatal cases of strongyloidiasis have been reported for nonhuman primates (reviewed by Abee et al. 2012).

We found similar prevalence of the most common parasites between our capuchin study groups, and temporal variation was evident only for *Filariopsis*, whose prevalence increased in the last winter study period compared to the previous sampling periods (both summer and winters). It is well known that seasonal changes can affect hosts and pathogens in ways that alter the rate at which infected hosts are produced (Altizer et al. 2006). The increase in prevalence recorded for *Filariopsis* could have been caused by particular climatic conditions, such as the high level of precipitation recorded in winter 2014 (937 mm; www.meteored.com.ar), compared to winter 2013 (656 mm) and winter 2012 (490 mm), that could have favoured the proliferation and transmission of this parasite among the study capuchins at Iguazú. Furthermore, as experimentally demonstrated by Agostini et al. (2017) in the same black capuchin study groups, an increase in food availability determines a decrease in the probability of infection, especially with the two most common parasites, *Filariopsis* and the Hymenolepididae, and a decrease in individuals' overall parasite richness and probability of multiple infections. Thus, seasonal as well as inter-annual variations in food availability could be driving the observed changes in *Filariopsis* prevalence. However, other factors could have contributed to the observed rise in prevalence. We recorded changes in demography occurred in the two study groups during the last period, including immigration of new and potentially infected individuals into the groups that could have spread the parasite within the groups. Finally, during the 2014 winter period, we recorded events of frequent aggressions and social instability within both study groups. For the Macuco group, in particular, this instability later led to a male takeover. As it is known, situations of increased social stress can reduce immune-competence of individuals, making them more susceptible to become infected with parasites (Solomon 1969; Sheldon & Verhulst 1996).

In conclusion, our results provide an important baseline for future investigations of gastrointestinal parasites in *Sapajus nigritus* and related species. Further effort should

be devoted to sampling other endoparasites, such as protozoa, which are the second most diverse group of parasites reported from wild primates (Nunn & Altizer 2006), and that can be at least partially recovered by non-invasive faecal sampling. In addition, future parasite surveys should include molecular analyses to facilitate more accurate species identification, thus providing a more precise evaluation of their zoonotic potential, their implications for primate conservation and management and for public health (Solórzano-García & Pérez-Ponce de León 2017).

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