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Original Article

Variation in the prevalence and abundance of acanthocephalans in brown-nosed coatis *Nasua nasua* and crab-eating foxes *Cerdocyon thous* in the Brazilian Pantanal

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(With 2 figures)

Abstract

Host infection by parasites is influenced by an array of factors, including host and environmental features. We investigated the relationship between host sex, body size and age, as well as seasonality on infection patterns by acanthocephalan in coatis (Procyonidae: *Nasua nasua*) and in crab-eating foxes (Canidae: *Cerdocyon thous*) from the Brazilian Pantanal wetlands. Between 2006 and 2009, we collected faecal samples from these hosts and analyzed for the presence of acanthocephalan eggs. Prevalence, abundance and intensity of eggs of acanthocephalans were calculated. Egg abundance was analyzed using generalized linear models (GLM) with a negative binomial distribution and models were compared by Akaike criteria to verify the effect of biotic and abiotic factors. Prevalence of acanthocephalans was higher in the wet season in both host species but did not differ between host sexes; however, adult crab-eating foxes showed higher prevalence of acanthocephalan eggs than juveniles. In contrast, prevalence of acanthocephalan eggs found in coatis was higher in coati juveniles than in adults. Host age, season and maximum temperature were the top predictors of abundance of acanthocephalan eggs in crab-eating foxes whereas season and host sex were predictors of egg abundance in coatis. The importance of seasonality for abundance of acanthocephalan was clear for both host species. The influence of host-related attributes, however, varied by host species, with host gender and host age being important factors associated with prevalence and parasite loads.

Keywords: Acanthocephala, Carnivora, disease ecology, helminth, Pantanal.

Variação na prevalência e na abundância do parasitismo de acantócefalos em dois carnívoros silvestres do Pantanal brasileiro

Resumo

A infecção de hospedeiro por parasitos é influenciada por uma série de fatores, incluindo características do hospedeiro e ambientais. Nós investigamos a relação entre sexo do hospedeiro, tamanho corporal e idade, bem como sazonalidade nos padrões de infecção por acantocéfalos em coatis (Procyonidae: *Nasua nasua*) e em cachorro-do-mato (Canidae: *Cerdocyon thous*) do Pantanal brasileiro e quais fatores explicaram melhor a prevalência e a intensidade desses parasitos. Entre 2006 e 2009, coletamos amostras fecais desses hospedeiros e analisamos a presença de ovos de acantocéfalos. Prevalência, abundância e intensidade de ovos de acantócefálios foram calculados. A abundância de ovos foi analisada utilizando modelos lineares generalizados (GLM) com distribuição binomial negativa e os modelos foram comparados pelo critério de *Akaike* para verificar o efeito de fatores bióticos e abióticos. A prevalência de acantocéfalos foi maior na estação úmida em ambas as espécies de hospedeiros, mas não diferiu entre os sexos do hospedeiro; no entanto, os cachorros-do-mato adultos apresentaram maior prevalência de ovos de acantocéfalos do que em juvenis. Em contraste, a prevalência de ovos de acantocéfalos encontrados em coatis foi maior em juvenis do que em adultos. A idade do hospedeiro, a estação e a temperatura máxima foram os preditores de abundância de ovos de acantocéfalos em cachorro-do-mato, enquanto a estação e o sexo do hospedeiro foram preditores da abundância dos ovos do parasito em coatis. A importância da sazonalidade para a abundância do acantocéfalo foi clara para ambas as espécies hospedeiras. A influência dos atributos relacionados ao hospedeiro, no entanto, variou entre as espécies de hospedeiros, sendo o sexo e idade do hospedeiro fatores importantes associados à prevalência e às cargas parasitárias.

Palavras-chave: Acanthocephala, Carnívora, ecologia de doença, helminto, Pantanal.

1. Introduction

Helminth parasites show a variety of transmission patterns determined by their life cycle characteristics and ecological requirements. As a result, their prevalence and abundance has been correlated with both life history characteristics of the host as well as environmental factors that act on helminth development (Mas-Coma et al., 2008). While such correlations are now well-recognized for many parasitic taxa, the relative importance these biotic and abitoc factors in explaining variability in the timing of infection is often not fully understood.

Seasonal variation in temperature and humidity and host features such as feeding habits, habitat preference, age, gender and body size can regulate the host-parasitism dynamic and are often considered in ecological studies of many parasites (Behnke et al., 2001; Ferrari, 2005; Krasnov et al., 2005; Simões et al., 2014). Such factors can determine the contact rates, and thereby influencing parasite population dynamics, parasite spatial distribution, and the risk of host infection (Bush et al., 2001; Altizer et al., 2006).

Among mammals, males tend to have higher abundance, prevalence and parasite species richness than females (Poulin, 1996; Schalk and Forbes, 1997; Soliman et al., 2001; Rossin and Malizia, 2002). These trends have been related to sex-specific host behaviors, as well as distinct androgen levels, body mass differences, and higher levels of physiological stress (Brown et al., 1994; Arneberg et al., 1998; Moore and Wilson, 2002; Morand et al., 2004; Krasnov et al., 2011). Likewise, older hosts may have higher parasite loads due to the more extensive opportunity for exposure to the parasite throughout their lives (Anderson and Gordon, 1982; Anderson and May, 1991; Cooper et al., 2012; Hudson et al., 2002).

Ecological factors associated with parasitism by endoparasites have primarily focused on nematodes of mammals (e.g. Brouat et al., 2007; Simões et al., 2012; Cardoso et al., 2016; Spickett et al., 2017). Few studies have addressed the Phylum Acanthocephala. Acathocephalans are a group of intestinal parasites with wide geographic distribution and approximately 1,300 species (Amin, 2013). Adult parasites attached to the wall of the intestine in the definitive host, causing various pathological conditions such as chronic enteritis with ulcerative lesions (Dunn, 1963; Müller et al., 2010). They typically display a two-host, indirect life cycle involving a variety of arthropods (insects and crustaceans) as intermediate hosts and vertebrates (fish, amphibians, reptiles, birds and mammals) as definitive hosts (Read, 1974; Crompton and Nickol, 1985).

The ecology of the Acanthocephala has mainly been studied in aquatic arthropods and aquatic vertebrates (Liat and Pike, 1980; Amin, 1984; Sinisalo et al., 2004; Kennedy, 2006; Steinauer et al., 2006; Franceschi et al., 2008; Amin et al., 2008; Caddigan et al., 2014; Amin, 2016), with limited research on the ecology of acanthocephalans of terrestrial mammals (Kennedy, 2006). For example, to our knowledge there have been no ecological studies of acanthocephalans from mammalian wildlife in Brazil. The aim of this study was to examine how biotic and abiotic features influence parasitological parameters of Acanthocephala found in brown-nosed coatis (*Nasua nasua*) and crab-eating foxes (*Cerdocyon thous*) in the Brazilian Pantanal.

The crab-eating fox *Cerdocyon thous* (Linnaeus, 1766) is a monogamous, sexually monomorphic canid with a social structure composed of two to five individuals, usually a breeding pair with pups and sometimes offspring from previous years (Courtenay and Maffei, 2004; Bianchi et al., 2016). In contrast, the brown-nosed coati *Nasua nasua* (Linnaeus, 1766) is a polygynous, sexually dimorphic species in which adult males are larger than females (Olifiers, 2010). Adult females and juvenile form groups of several individuals, but adults males are typically solitary outside of the reproductive season (Gompper and Decker, 1998; Bianchi et al., 2014). After the breeding season, pregnant females give birth in a nest, usually constructed on a tree, since this species is scansorial (Olifiers et al., 2009). Both species have generalist omnivorous diets, consuming fruits, gastropods, arthropods such as arachnids, insects, myriapods, as well as small vertebrates (Bianchi et al., 2014; Olmos, 1993; Pedó et al., 2006).

Although both coatis and crab-eating foxes have generalist diets (Bianchi et al., 2014) and inhabit similar habitats, their distinct reproductive behavioral and sex-related morphologic features may result in different infection patterns. As a consequence, parasite load is expected to be higher in coati males than females, but not to differ by gender for the monomorphic crab-eating foxes. On the other hand, patterns of parasitism should also vary with abiotic factors in habitats with strong seasonality. For example, the Brazilian Pantanal, where both coatis and crab-eating foxes are sympatric, presents two makedly different seasons, with higher temperature and humidity during the wet season that can favor the life cycle of parasites and their intermediate hosts (e.g., for acanthocephalans: Kennedy, 2006; Amin, 1980). If abiotic factors are more important than factors intrinsic to the host in mediating the parasite-host dynamic, we expect the two parasite-host dyads to show similar quantitative relationships despite the differing ecologies of the hosts.

2. Material and Methods

2.1. Study area

The Pantanal biome is the largest wetland in the world and harbors a high density and diversity of vertebrates, particularly mammals (Tomás et al., 2010; Alho et al., 2011; Alho and Sabino, 2011). Field work was conducted at Nhumirim Ranch (18°59'S, 56°39'W), a 4,400 ha research station of the Brazilian Agricultural Research Corporation (Embrapa) in the Nhecolândia subregion of the Pantanal State of Mato Grosso do Sul, Brazil. The study area is characterized by sandy soil with mosaic vegetation of semi-deciduous forest with open grassy areas and seasonally flooded fields (Rodela, 2006). The climate is tropical with two distinct seasons: wet season (October to March) and dry season (April to September).

2.2. Capture procedures

From 2006 to 2009 we captured/recaptured *Cerdocyon thous* and *Nasua nasua* which were the subject of a broader research program conducted by Embrapa/Pantanal and the Oswaldo Cruz Foundation (FIOCRUZ-RJ). As part of this research, we collected feacal samples from known individuals for gastro-intestinal parasite diagnosis. Animals were captured every 3 to 4 months using wire box traps (1 m × 0.40 m × 0.50 m) placed in a trapping grid of 7.2 Km^2, but traps were also occasionally placed outside the grid. Traps were baited with bacon, set late in the afternoon and checked in the morning. The captured animals were anesthetized, tagged with numbered colored tag (Nasco Rototag®) and/or subcutaneous transponder (AnimalTag®), measured, weighed and sexed. Tooth eruption, condition and wear were also recorded to age individuals (Olifiers et al., 2010). Feacal samples were collected from beneath traps or via fecal loop. After sample collection, the animals were released at their capture sites. The animal capture and handling procedures were approved by the Brazilian Federal Environmental Agency (IBAMA, first license #183/2005, CGFAU/LIC; last license #11772-2) and by the University of Missouri Animal Care and Use Committee (protocol #4459).

2.3. Parasitological procedures

Feces collected from each animal (1-3 g) were stored in 15 mL of 10% formalin and analyzed in the laboratory using methods for endoparasites diagnostics: flotation in sugar solution (density 1.27), sedimentation and centrifugation with formol-ether (Bowman, 1999). After sedimentation, the pellet was resuspended in 1 mL of 10% formaldehyde and a subsample of 80 µL was placed on a slide for analysis in the light microscope (Monteiro et al., 2007). Slides from the sugar flotation and sedimentation techniques were analyzed at 100x and 400x magnification. Eggs of acanthocephalans were photographed, measured, and compared with the morphology described according to Yamaguti (1963), Schmidt (1972), and Machado Filho (1950). In addition, adults specimens of acanthocephalans were collected from the intestine of three crab-eating foxes and two brown-nosed coatis found dead in the study area. The adults specimens were analysed and described/identified as the *Prosthenorchis cerdocyonis* (Gomes et al., 2015; type species CHIOC 35804 a-c) and *Pachysentis* sp. (deposit pending), respectively. Because co-infection by acanthocephalan species are apparently rare (Kennedy, 2006) and the eggs found in fecal flotation were very similar in size and shape to the eggs obtained from the female acanthocephalans recovered from the dead hosts, we suggest that we are identifying and quantifying *P. cerdocyonis* from crab-eating foxes and *Pachysenti* sp. from coatis. However, since we cannot discard the possibility of co-infection by other (perhaps undescribed) acanthocephalan species parasitizing coatis and crab-eating foxes in the study area, we classified the eggs as belonged to acanthocephalans from the Class Archiacanthocephala, Order Oligacanthorhynchida, Family Oligocanthorhynchidae. The number of acanthocephalan eggs in the faecal samples was divided by the total weight of analyzed feces and used as proxy of parasite abundance. When more than one sample for the same host was obtained in the same excursion (recaptured animals), we calculated the mean number of eggs obtained for the samples analyzed for that period.

2.4. Data analyses

We calculated the prevalence as the estimated number of infected hosts divided by the total number of analyzed hosts. Abundance was estimated as the number of eggs per gram of feces found in each individual host and the intensity was the number of eggs per gram of feces found in infected hosts (Bush et al., 1997). Prevalence was compared between sexes, age and seasons using Chi-square tests ($\alpha = 0.05$) for each host species. Mean intensity and mean abundance were also compared between species using the program Quantitative Parasitology 3.0 (QP3.0; Reiczigel and Rózsa, 2005). Confidence intervals (95% CI) for prevalence were calculated using the Clopper-Pearson interval method, and for mean and median intensity as well as mean abundance by bootstrap tests (n = 2000) using QP 3.0. The level of aggegration of both acanthocephalan species on their respective hosts was quantified by calculating the negative binomial exponent, k (Wilson et al., 2002).

To analyze the effect of biotic (age, sex, body size) and abiotic factors (season, temperature and humidity) on the abundance acanthocephalan eggs (dependent variable) we created generalized linear models (GLM) with negative binomial distributions and log link in SPSS 20, as the data showed a predominantly aggregated distribution for both parasite species (see results). Before creating the models, we checked whether abiotic variables (minimum, maximum and average temperature, relative humidity and precipitation) were correlated (Pearson correlation, $\alpha = 0.05$). The final factors used to create the models were maximum temperature (MT), relative humidity (RH) and season (dry and wet season). Abiotic data was obtained from the Instituto Nacional de Meteorologia and averaged for 30 days before the date of the fecal sample collection. Host body size (mm) was measured from the tip of the nose to the base of the tail (Olifiers, 2010). Host age was estimated based on morphometric measurements and dental condition following Olifiers et al. (2010), which allowed placement of animals into one of four age categories. We further combined classes due to small sample sizes for some age groups such that all animals were ultimately classified as juveniles (≤ 2 years old) or adults (> 2 years old).

The evaluated models consisted of all possible combinations of the six independent predictors (64 models in total); five additional models having interaction terms were included after investigation of predictor vs. response variable plots revealed possible interaction between these variables. Models were compared using the Akaike Information Criterion corrected for overdispersion (QAICc) and ranked based on the difference between the best approximating model (model with the lowest QAICc) and all others in the set of candidate models (ΔQAICc). Models with differences within two units of the top model were considered competitive models with empirical support (Burnham and Anderson, 2001). The relative importance of each predictor or interaction of predictors was quantified by calculating relative variable weights, which consists of the summed Akaike weights (QAICc weights) across all the models in which the predictor occurs. Variables weights lower than 0.40 were considered indicative of relatively low variable importance.

3. Results

We analyzed 118 fecal samples from 55 crab-eating foxes (24 females and 31 males) and 72 fecal samples from 61 brown-nosed coatis (13 females and 48 males) throughout 10 field excursions (see Table 1 and 2). Prevalence of acanthocephalan eggs did not differ between crab-eating foxes (22.9%; n = 118) and brown-nosed coatis (29.2%; n = 72; Chi-square = 0.936; p = 0.333). Likewise, mean abundance (t-statistic = -0.607; p = 0.556) and mean intensity (t-statistic = -1.903; p = 0.061) did not differ between host species. Egg abundance was similarly aggregated in both hosts (acanthocephalan eggs in crab-eating foxes: k = 0.1031, Figure 1; acanthocephalan eggs in coatis: k = 0.1734, Figure 2).

3.1. Ecological analyses of acanthocephalan in crab-eating foxes (Cerdocyon thous)

Differences in prevalence between host sexes (Chi-square = 0.066, p = 0.797) or age categories were not significant (Chi-square = 1.771; p = 0.183). However, prevalence of eggs tended to be higher during the wet season (32.6%) than in the dry season (17.3%), although the difference was only marginally significant (Chi-square = 3.590, p = 0.058) and 95% CIs of intensity and abundance overlapped.

Four models were supported (ΔQAICc < 2) in the analysis of the abundance acanthocephalan eggs found in crab-eating foxes, but their individual QAICc weights were relatively low (from 0.05 to 0.13; Table 3). The top ranked

Table 1. Ecological parameters for *Prosthenorchis cerdocyonis* eggs in crab-eating foxes (*Cerdocyon thous*) sampled in the Brazilian Pantanal from 2006 to 2009.

Categories	N	Prevalence (%)	Mean Intensity	Median Intensity	Mean Abundance
All	118	22.9% (15.65-31.52)	6.0 (4.78-7.93)	4.0 (4.0-8.0)	1.37 (0.89-2.04)
Females	55	21.8% (12.46-34.45)	6.0 (4.67-7.92)	5.0 (4.0-8.0)	1.31 (0.67-2.20)
Males	63	23.8% (13.98-36.22)	6.0 (4.20-9.00)	4.0 (2.0-8.0)	1.43 (0.78-2.59)
Adults	70	27.1% (17.19-39.10)	6.84 (5.32-9.32)	7.0 (4.0-8.0)	1.86 (1.13-2.91)
Juveniles	48	16.7% (7.48-30.23)	4.0 (2.88-5.00)	4.0 (2.0-6.0)	0.67 (0.29-1.21)
Dry season	75	17.3% (9.56 - 27.82)	7.23 (5.15 - 11.00)	6.0 (3.0 - 8.0)	1.25 (0.67 - 2.29)
Wet season	43	32.6% (19.07-48.55)	4.86 (3.57-6.14)	4.0 (2.0-7.0)	1.58 (0.88-2.47)

Numbers between brackets are 95% confidence intervals; N = number of sampled hosts.

Table 2. Ecological parameters for *Pachysentis* sp. eggs in brown-nosed coatis (*Nasua nasua*) sampled in the Brazilian Pantanal from 2006 to 2009.

Categories	N	Prevalence	Mean Intensity	Median Intensity	Mean Abundance
All	72	29.2% (19.04-41.07)	3.81 (2.52-5.86)	2.0 (1.0-4.0)	1.1 (0.64-1.96)
Females	13	23.1% (5.03-53.82)	2.0 (1.00-2.67)	2.0*	0.46 (0.08-1.15)
Males	59	30.5% (19.18-43.87)	4.06 (2.61-6.44)	2.5 (1.0-4.0)	1.24 (0.68-2.22)
Adults	26	15.4% (4.35-34.87)	6.5 (3.50-10.75)	5.5*	1.0 (0.27-2.54)
Juveniles	46	37.0% (23.20-52.46)	3.18 (2.00-5.71)	2.0 (1.0-3.0)	1.17 (0.63-2.37)
Dry season	26	11.5% (2.44-30.16)	2.0 (1.00-2.67)	2.0*	0.23 (0.04-0.58)
Wet season	46	39.1% (25.08-54.63)	4.11 (2.67-6.33)	2.5(1.0-4.0)	1.61 (0.87-2.76)

Numbers between brackets are 95% confidence intervals; N = number of sampled hosts; *Confidence level cannot be reached because the sample size is small.

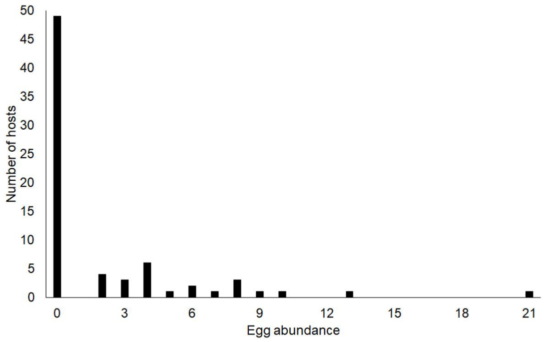

Figure 1. Distribution of acanthocephalan egg abundance (eggs/g of feces) in crab-eating foxes (*Cerdocyon thous*) from the Brazilian Pantanal wetlands.

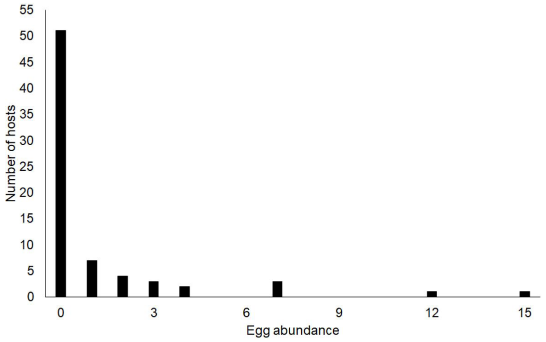

Figure 2. Distribution of acanthocephalan egg abundance (eggs/g feces) in brown-nosed coatis (*Nasua nasua*) from the Brazilian Pantanal wetlands.

model supported an interaction of season and age, followed for three models that included maximum temperature either alone or in combination with host age (Table 3). Indeed, the contributions of age (var. weight = 0.75, β = 1.08), maximum temperature (var. weight = 0.56; β = 0.197) and season (var. weight = 0.41; β_{dry} = - 0.43) to variation in abundance of the acanthocephalan eggs in crab-eating foxes were higher than all other variables.

3.2. Ecological analyzes of acanthocephalan eggs in brown-nosed coatis (Nasua nasua)

Prevalence in coati males and females did not differ (Chi-square = 0.285; p = 0.594), but prevalence was higher in juveniles than in adults (Chi-square = 3.742; p = 0.053). Egg prevalence was over 3 times higher in the wet season than in the dry season (Chi-square = 6.121; p = 0.013) (Table 2). Similarly, measures of intensity and abundance were higher during the wet season and 95% CIs were non-overlapping for the means of both.

Five top models were supported (ΔQAICc < 2) for the abundance of acanthocephalan eggs in coatis, and these models collectively contained five variables: season (var. weight = 0.88, β_{dry} = -1.816), sex (var. weight = 0.46; β_{female} = -1.316), maximum temperature (var. weight = 0.27, β= 0.114), body size (var. weight = 0.26, β = -0.005), and relative humidity (var. weight = 0.24, β = -0.019) occurred in these most-supported models (Table 4). The variable weights for season, which occurred in all five top models, and sex (which occurred in two of the top models) were higher than 0.40, suggestive of strong support.

Table 3. Ranking of the best-fitting models describing *P. cerdocyonis* egg abundance in crab-eating foxes (*Cerdocyon thous*) in the Pantanal wetlands, Mato Grosso do Sul, Brazil from 2006 to 2009.

Model	Log(l)/c	QAICc	k	ΔQAICc	QAICc Weight
Season × Host age	-56.30	123.15	5	0.00	0.13
Host age + Max. temperature	-57.76	123.87	4	0.73	0.09
Max. temperature ×Host age	-57.82	123.99	6	0.84	0.09
Max. temperature	-59.46	125.13	3	1.98	0.05

Season = dry and wet seasons; Max. temperature = daily maximum temperature averaged for 30 days before the date of the fecal sample collection. Only models with ΔQAICc ≤ 2 are shown. Akaike Information Criterion corrected for overdispersion (QAICc), Akaike weights (QAICc weights).

Table 4. Ranking of the best-fitting models describing abundance of *Pachysentis* sp. eggs in brown-nosed coati (*Nasua nasua*) in the Pantanal wetlands, Mato Grosso do Sul from 2006 to 2009.

Model	Log(l)/c	QAICc	k	ΔQAICc	QAICc Weight
Season	-42.94	92.23	3	0.00	0.13
Season + Host sex	-41.95	92.50	4	0.27	0.11
Season + Humidity	-42.44	93.48	4	1.25	0.07
Season + Body size + Host sex	-41.54	93.99	5	1.76	0.05
Season + Max. temperature	-42.73	94.06	4	1.83	0.05

Season = dry and wet seasons; Max. temperature = daily maximum temperature averaged for 30 days before the date of the fecal sample collection; Humidity = daily averaged for 30 days before the date of the fecal sample collection. Only models with ΔQAICc ≤ 2 are shown. Akaike Information Criterion corrected for overdispersion (QAICc), Akaike weights (QAICc weights).

4. Discussion

In this study the overall patterns of prevalence, intensity and abundance were similar for acanthocephalans in both hosts. The samples of the present study were collected in the same study area and both definitive hosts have similar habitats and diets (Olifiers et al., 2010; Bianchi et al., 2014, 2016), which suggests these host species may have similar probabilities of contact with infected intermediate hosts. Although coatis are scansorial and therefore can climb trees, they spend most of their foraging time on the ground (Hirsch, 2009).

Prevalence of acanthocephalans in crab-eating foxes was not different between host sexes, and neither host age nor host body size appeared amongst the best-fitting models. Male and female crab-eating foxes are monomorphic in body size, and the behavioral, spatial and foraging ecology of males and females are similar (Brady, 1979; MacDonald and Courtenay, 1996; Bianchi et al., 2014; Olifiers et al., 2010). Although some studies have shown that higher androgen levels in males may lead to higher parasite intensity or prevalence (Moore and Wilson, 2002; Muehlenbein and Watts, 2010), this hypothesis does not hold for the acanthcephalans eggs found in crab-eating foxes. It seems that exposure rates to the parasite are similar between sexes and resulted in nearly equivalent parasite profiles for males and females.

In contrast to the crab-eating foxes, adult female and male coatis are behaviourally and spatially segregated during most of the year, with males usually solitary, except in the breeding season (Bianchi et al., 2014). Adult males are also larger than females and engage in agonistic behaviours during the reproductive season (Olifiers, 2010). Consequently, intersexual differences in prevalence, intensity and/or abundance of parasites are expected for this host species, especially during the breeding season, due to different testosterone levels, different consumption rates of food items, and the decreased health condition of breeding season males. Indeed, model analysis for abundance of acanthocephalan eggs in coatis indicated that host sex was an important predictor of infection; male coatis seem to be more affected by parasitism, especially during the breeding season, which may in turn favor higher parasite intensities. Olifiers et al. (2015) found similar results for *Trypanosoma evansi* infection in coatis from the same study site.

Adult crab-eating foxes had more acanthocephalan eggs than juveniles (Table 1). This result is expected, given that adults have more time to accumulate parasites than younger animals. Older hosts may have been exposed to more parasites during their lifetime, as observed in other studies in which there was a continuous increase in parasite loads with host age or age-associated body size (Anderson and Gordon, 1982; Anderson and May, 1991; Hudson and Dobson, 1995; McCormick and Nickol, 2004). However, coatis showed the opposite pattern, with prevalence (but not intensity) being higher in juveniles than in adults (Table 2). Although such result may be related to acquired immunity with age, it is not clear why this process would occur in coatis but not in crab-eating foxes.

Prevalence of acanthocephalans was higher during the wet season for both host species (Table 1 and 2) and all the best-fitting models had the variable "season" or "maximum temperature" (Table 3 and 4). Thus, acanthocephalans from brown-nosed coatis and crab-eating foxes are likely more available to hosts during the wet season. This availability may reflect an increased abundance in intermediate hosts and changes in exposure rates. Furthermore, model analysis revealed higher parasite abundance for acanthocephalan eggs in coatis feces just after a humid month, while abundance of acanthocephalan eggs in crab-eating foxes was higher just after months with higher maximum temperature. Chubb (1982) and Kennedy (2006) showed seasonal cycles in prevalence and abundance of acanthocephalans that were correlated with temperature. Likewise, Amin et al. (2008) also suggested a seasonal pattern of acanthocephalan infection and showed that prevalence of acantocephalans may increase during the summer in freshwater fishes from Lake Malawi, due to the sexual maturity and breeding activity in the end of winter and early spring. In addition, Amin (1980, 1987) and Kennedy (2006) analyzed the ecology of intermediate hosts and showed that in warm temperatures, parasite development increases as cystachanths (the infective stage to the definitive host) in the intermediate host; a greater proportion of gravid female worms are found in the definitive host during the summer; and the definitive host consumed more infected intermediate host in the summer, resulting in higher transmission rates.

Although the intermediate hosts of the acanthocephalans studied here are unknown in the Pantanal, arthropods are more abundant in the warmer wet season (Santos Filho et al., 2008), and both host species may have higher consumption rates of these potential intermediate hosts during the wet season. However, while a primary food item consumed by both host species in the study area were coleopterans, which can be intermediate hosts for acanthocephalans, these were more frequently found in fecal samples of these animals in the dry season (Bianchi et al., 2014). The pre-patent period for acanthocephalans (infection of the intermediate hosts by cystacants and the development to adults) and the patent period can vary from weeks to months in acanthocephalans (Nicholas, 1967; Kennedy, 2006). If we consider the pre-patent period of acanthocephalans from mammals as 30 to 100 days (Nicholas, 1967; Crompton and Nickol, 1985), the acanthocephalan eggs would be more abundant in coati and fox feces in the wet season if those hosts were actually infected by mid-late dry season. However, the lack of knowledge regarding the life cycle and intermediate host species for these acanthocephalans precludes fully informed inferences regarding the mechanisms driving seasonal variation in parasite loads.

Overall, while the importance of seasonality for acanthocephalan was clear in both host species, the influence of host-related attributes varied for parasite-host interactions. Nonetheless, both host gender and host age appear to be important factors determining prevalence and parasite intensity of these acanthocephalans. The fact that general patterns of prevalence in the Pantanal did not differ between host species, and were similar for both genders in coatis and crab-eating foxes may indicate that differences in features such as body size and social behavior are relatively less important for predicting infection rates by acanthocephalans when compared to the availability and consumption rates of infected intermediate hosts by definitive hosts. Parasites loads, in turn, may shaped more by features related to host health and immune system function, which are in turn potentially affected by host age and gender.

Despite the study using survey approaches that focus on eggs rather than larval or adult stages, we were able to detect important patterns in acanthocephalan ecology, perhaps due to our relatively large sample sizes. We believe that using egg counts is a potentially powerful tool when sample sizes are large and when it is possible to obtain replicates from the same hosts. Morover, fecal egg counts represent a minimally invasive method for estimating parasite loads (Hämäläinen et al., 2015). The study of parasite dynamics in large animals using egg counts is particularly useful considering that many large host species show decreasing abundance and are already threatened by extinction (IUCN, 2008), which precludes host collection for parasite quantification.

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