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Transmission Patterns of Pinworms in Two Sympatric Congeneric Primate Species

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Abstract Understanding pathogen transmission is essential to addressing the dynamics of infectious diseases in animal populations. Directly transmitted parasites spread in host populations via 1) contact with infected individuals and 2) contact with contaminated substrates. Although studies exist that support social or ranging effects on transmission, it is less clear how these factors interact. We test the hypothesis that a combination of social, ranging, diet, and intrinsic factors account for *Trypanoxyuris minutus* (pinworm) infections in sympatric howler species *Alouatta palliata* and *A. pigra*. We collected 211 howler fecal samples from 34 adults living in four groups, two of each species, in Tabasco (Mexico), and calculated pinworm prevalence and eggs per gram of feces (EPG). We followed each group for 80 h to determine ranging, diet, frequency of contact, and conspecific proximity. Prevalence of *Trypanoxyuris minutus* was high, with 82% of all individuals infected. Logistic modeling indicated that pinworm prevalence was positively associated with proximity and the proportion of

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group members contacted by focal individuals. Although EPG results should be interpreted cautiously owing to variable egg excretion, this index was also positively associated with proximity and the proportion of group members that were contacted, as well as with dietary diversity and use of non-tree foods. Neither intrinsic factors such as species and sex, nor group and population level variables, such as group and home range size, home range overlap, and intensity of range use, were significant predictors of pinworm infection. We conclude that both sociality and feeding behavior are key factors in infection dynamics of *Trypanoxyuris minutus* in sympatric *Alouatta palliata* and *A. pigra*, confirming that contact with infected conspecifics and contaminated substrates are important mechanisms for directly transmitted parasites.

Keywords *Alouatta palliata* · *Alouatta pigra* · Diet · Directly transmitted parasites · Ranging · Sociality · *Trypanoxyuris minutus*

Introduction

An understanding of pathogen transmission mechanisms is fundamental to addressing the dynamics of infectious diseases and the emergence of zoonotic diseases (McCallum *et al.* 2001). Transmission depends on both the likelihood of a host coming into contact with an infectious agent (i.e., exposure), and the likelihood of the host becoming infected (i.e., susceptibility) (Anderson and May 1991). Almost without exception, macroparasites are aggregated within host populations, with most individuals harboring low numbers of parasites and a few individuals harboring many. Such heterogeneities are generated by variation in the exposure and/or susceptibility of individuals (Anderson and May 1978; reviewed in Wilson *et al.* 2002), suggesting that not all animals are equally vulnerable (Ezenwa *et al.* 2006). Given that parasite transmission is not typically observable, research on transmission dynamics usually relies on the measurement of intrinsic (e.g., species, sex, age), and extrinsic (e.g., host population density, home range size), factors to investigate the likelihood of infection (colobines: Chapman *et al.* 2005).

Directly transmitted parasites (i.e., fecal–oral transmission; parasites hereafter) can spread in host populations by two mechanisms: 1) direct physical contact with infected individuals; and 2) contact with contaminated substrates (Nunn and Altizer 2006). These mechanisms influence parasite encounter rates and the number of parasite species that persist in individuals or populations (Vitone *et al.* 2004). Because social (e.g., close interactions, cohesiveness), ranging (e.g., travel routes, substrate use), and foraging behaviors (e.g., food consumption), may affect encounter probability, they are likely to influence parasite infection risk. Further, group size and composition influence these behaviors in several primate species (Chapman and Chapman 2000; Lehman *et al.* 2007), indicating that social organization may also affect parasite exposure and infection risk. Finally, sex differences in social relationships, diet, and/or habitat use, could result in differential parasite exposure for males and females (Meade 1984; Nunn and Altizer 2004, 2006).

Group-living species are predicted to be at greater risk of parasite infection (Altizer *et al.* 2003) because parasite transmission is usually density dependent and social animals experience higher local densities than solitary individuals (Dobson and

Meagher 1996). The higher risk of infectious disease among gregarious species is hypothesized to be an important cost balancing the benefits of group living (Chapman *et al.* 1995, 2012; Freeland 1976, 1979; Nunn *et al*. 2004; Schülke and Ostner 2012). Social interactions generate a network of contacts through which parasites spread within populations, with a minority of individuals being highly connected and consequently more likely to be involved in transmission events (Anderson and May 1979, 1991; Lloyd-Smith *et al.* 2005). Thus, social hosts are predicted to have higher parasite prevalence, intensity, and species richness than less social hosts (Møller *et al.* 1993), but support for this hypothesis is mixed (supportive: Clough *et al.* 2010; Freeland 1976, 1979; Phillipi and Clark 1992; partially supportive: Appleton and Henzi 1993; Chapman *et al.* 2009; Gilbert 1994; Mbora *et al.* 2009; nonsupportive: Chapman *et al.* 2007, 2012; Snaith *et al.* 2008). Nevertheless, heterogeneous interaction patterns between co-residents can mitigate simple linear relationships between group size and infection (Griffin and Nunn 2012). For example, in Japanese macaques (*Macaca fuscata yakui*), both social network centrality and grooming contact are associated with increased parasite infection, i.e., prevalence and eggs per gram of feces, indicating that individual measures of sociality may impact parasite transmission mechanisms in group-living primates (MacIntosh *et al.* 2012).

The way an individual travels through its environment determines its probability of encountering contaminated areas or individuals (tested in Chapman *et al.* 2009; Nunn and Dokey 2006; Nunn *et al*. 2011). Thus, ranging behavior can also affect the spread of parasites (Nunn *et al*. 2011). The potential for ingestion of infective stages may be especially important for gastrointestinal parasites, which involve fecal contamination of the soil or other substrates (Nunn *et al.* 2011). For instance, animals restricted to small areas (Gillespie and Chapman 2008) or that use their range more intensively may be more infected (parasite prevalence: Ezenwa 2003; parasite load: Stoner 1996) or be at a higher risk of reinfection (Freeland 1976, 1980). Ranging variables such as territoriality, home range overlap, intensity of range use, and day range length relate to parasitism patterns in some primate species (Chapman *et al.* 2009; González-Hernández *et al.* 2011; meta-analyses: Nunn and Dokey 2006; Vitone *et al.* 2004; theoretical models: Nunn *et al*. 2011).

Foraging and diet likely further affect infection risk given that many parasites have a fecal–oral transmission route, usually via the ingestion of contaminated water, plant foods, or intermediate arthropod hosts (Huffman and Chapman 2009; Nunn and Altizer 2006). Folivorous primates typically ingest larger volumes of food than frugivores and could therefore ingest more material contaminated with parasite infective stages (Gillespie *et al*. 2005; Moore 2002). The positive association between percentage of leaves in the diet and helminth parasite richness in anthropoid primates provides partial support for an effect of folivory on parasite infections (Vitone *et al*. 2004). It has also been demonstrated that folivorous howlers visit more food patches and spend more time travelling when they feed from non-tree food sources (i.e., lianas, vines, epiphytes) (Asensio *et al*. 2007; Dunn *et al*. 2012), which could increase parasite exposure as a result of increased consumption of contaminated food, more intensive home range use, and/or range overlap with other groups.

Sex differences in parasite infection exist across several vertebrate taxa, with many studies reporting higher parasite infections in males than in females (Klein 2004; Zuk and McKean 1996). This sex-biased pattern is proposed to be caused by three factors:

1) body size dimorphism requires males to consume more resources, thereby increasing their exposure; 2) males and females differ in parasite exposure due to sex differences in social relationships, diet, and/or habitat use (Meade 1984; Nunn and Altizer 2004); and 3) males generally exhibit lower immune response than females due to differences in immunosuppressive effects of reproductive hormones (Klein 2004). For instance, testosterone and cortisol levels are positively associated with parasite richness in male chimpanzees, which may indicate an increased susceptibility to infection and/or a lower immune response against parasites (*Pan troglodytes*: Muehlenbein and Watts 2010).

Although studies support social, ranging, and/or diet effects on parasite infection, it is less clear how these factors interact with each other and with intrinsic characteristics, such as species and sex (Clough *et al.* 2010; MacIntosh *et al.* 2010). We examine if and how these factors interact in sympatric mantled howlers (*Alouatta palliata*) and black howlers (*A. pigra*) in Macuspana (Tabasco, Mexico). These populations of *Alouatta palliata* and *A. pigra* are well suited to exploring how extrinsic and intrinsic factors interact to influence parasite infection patterns because they live under the same environmental conditions, allowing us to reduce the influence of potential confounding factors (Dias *et al.* 2013). Howlers (*Alouatta* spp.) are host to a wide variety of parasite taxa, including many directly transmitted parasites with a fecal–oral transmission route (Vitazkova 2009). The two species have markedly different social organizations, particularly in terms of group size (*Alouatta palliata* = 2–45 individuals; *A. pigra* = 2–16 individuals) and adult sex ratio (*A. palliata* = 1.2–4.2 females/males; *A. pigra* = 0.7–1.3 females/males: Di Fiore and Campbell 2007). Although howlers live in cohesive groups, there is variation within groups in the strength of social bonds among dyads, which presumably are the result of individual decisions (Dias *et al*. 2008, 2010; Van Belle *et al*. 2009). Spatial cohesiveness at the group level does not equal undifferentiated social relationships among group partners; therefore intragroup spatial relationships should reflect social bonding preferences (Dias *et al*. 2010). Given that sociality and ranging patterns vary as a function of group size and composition in several primate species (Chapman and Chapman 2000; Lehman *et al.* 2007), we predict that the two *Alouatta* sp. will have differences in parasite infections.

We previously reported that our focal groups of *Alouatta* sp. share two parasites, the pinworm *Trypanoxyuris* sp. (believed to be *T. minutus*) and the trematode *Controrchis* sp. Here we focus on *Trypanoxyuris* sp. because it is a directly transmitted parasite, whereas trematode infection risk would not be influenced by social behavior because it requires ingestion of the intermediate host, thought to be *Azteca* sp. ants (Kowalzik *et al*. 2010). Our four focal groups (two *Alouatta palliata*, two *A. pigra*) are frequently in close proximity (10–20 m), share food patches, have significant home range overlap (40–76%), and occasionally rest in or feed from the same tree simultaneously (González-Hernández *et al*. 2011). The larger groups of *Alouatta palliata* occupied larger home ranges (*ca*. 35% larger), which they used less intensively, than the smaller groups of *A. pigra*. Group size was positively correlated with mean number of eggs per gram of feces (EPG hereafter) of *Trypanoxyuris* sp., but ranging variables did not explain mean parasite prevalence or EPG per group. These results suggested that infection with *Trypanoxyuris* sp. in this population could be associated with other factors related to group size, such as sociality patterns (González-Hernández *et al.* 2011).

We hypothesized that a combination of social, ranging, dietary, and intrinsic factors and their first-order interactions would predict patterns of infection with *Trypanoxyuris* sp. in sympatric *Alouatta palliata* and *A. pigra*. Specifically, we examined the following:

1) Social behavior: we predicted higher parasite infections in individuals that had more frequent physical contact with others, were in close proximity to others, and had more social partners than in individuals that had less physical contact, were more distant, and had less social partners. In this prediction we assumed that, if physical contact is an important transmission mechanism of *Trypanoxyuris*, individuals who are closer to other group members are more likely to come into contact with them than individuals who are usually more distant.
2) Ranging behavior: we predicted higher infections in individuals that had longer day ranges and used more trees, than in individuals with shorter day ranges and that used less trees. Here, we assumed that using more trees would increase the probability of encountering a tree/substrate with parasite infective stages, such as frequently used trees (e.g., food resource or corridors, travel routes).
3) Foraging and diet: we predicted higher infections in individuals with more folivorous and diverse diets, and who consumed more non-tree food sources than in individuals with less folivorous, specialized diets that used mainly trees as food sources. In this prediction we assumed that eating larger amounts of potentially contaminated leaf material or non-tree food sources would increase parasite encounter probability.
4) Sex: we predicted that adult males would have higher infections than adult females.

Methods

Ethical Note

Our observational study was entirely noninvasive, complied with Mexican law, and the data collection protocol was approved by the Mexican Secretary of Environment and Natural Resources SEMARNAT (permit SGPA/DGVS/03293/10).

Study Site and Groups

We conducted observations in 2010 in a 18.6-ha forest fragment in a cattle ranch in Macuspana, Tabasco, Mexico (17°38.2′N, 92°40.1′W) in the sympatric area of *Alouatta palliata* and *A. pigra* (Cortés-Ortiz *et al.* 2007; Dias *et al.* 2013). We limited our data collection to the dry season (i.e., February–June), because the field site is flooded and inaccessible in the wet season.

Both groups of *Alouatta pigra* contained six individuals, with one adult male and three adult females in group API-1 and one adult male and two adult females in group API-2. Group APA-1 of *Alouatta palliata* had 26 individuals including 4 adult males and 12 adult females, while group APA-2 of *A. palliata* consisted of 15 individuals

including three adult males and eight adult females (Table I). All adult subjects ($N = 34$) could be individually identified by facial features, scars, broken fingers, genital morphology, as well as color patterns on their feet and tail for *Alouatta palliata*. We did not collect behavioral or biological samples from infants and juveniles because of the difficulty of identifying them reliably.

Behavioral Sampling

We conducted daily behavioral observations from 07:00 to 17:00 h and collected a total of 80 h of individual focal data from each group. We observed each group over a 3-wk period in the following order: API-1, API-2, APA-1, and APA-2. We used three behavioral data sampling methods: 1) all-occurrences sampling (Altmann 1974) to record each instance of physical contact between adult group members; 2) 60-min continuous focal animal sampling (Altmann 1974) to record activity, including feeding time on tree and non-tree food sources (i.e., lianas, vines, epiphytes), during which we also collected; 3) instantaneous samples at 15-min intervals to record proximity of the focal animal to other group members (contact, <1 m, 1–5 m, 6–10 m, or >10 m following Dias and Rodríguez-Luna 2005). Focal animal samples ($N = 80$ h) were evenly distributed among individuals in each group and across time of the day for each individual. All-occurrences sampling was conducted during the same 80 h per group.

Fecal Sample Collection and Analyses

We collected fresh fecal samples opportunistically from each adult (mean ± SEM: 6.2 ± 2.7; range: 3–9; $N = 211$) on nonconsecutive days of behavioral sampling (following Muehlenbein 2005). If we collected multiple samples from the same individual in one day, we pooled and processed the specimens as a single-day sample (Aldeen *et al.* 1993). Following Utzinger *et al.* (2001) we homogenized each sample within the plastic bag after collection to avoid intraspecimen variation in parasite egg counts. In the field, we kept samples in a cooler with frozen gel packs until arrival at the field station, at which time we preserved them in plastic vials with 10% neutral buffered formalin until they could be transported and analyzed at the Laboratory of Parasitology of Universidad Veracruzana. For each sample, we processed 3 g of wet feces using flotation with a sodium chloride solution (NaCl sp. gr. 1.20; Trejo-Macías *et al.* 2007). We systematically scanned one slide per sample for parasite eggs or cysts. We identified parasites to genus level using parasite egg size, color, and morphology (Osorio *et al.* 2009). Further, we opportunistically collected live adult helminths from the fresh fecal samples and preserved them in 70% alcohol for later taxonomic identification to the genus and species level at the Laboratory of Helminthology of the Instituto de Biología Universidad Nacional Autónoma de México.

In a previous study of these populations, we routinely found eggs of two helminths, the nematode *Trypanoxyuris* sp. and the trematode *Controrchis* sp., and found a *Cyclospora* sp. oocyst on a single occasion. *Trypanoxyuris* sp. was the only directly transmitted parasite shared by the four groups (González-Hernández *et al.* 2011). Assessment of the preserved adult nematodes ($N = 19$, all females) suggested that the pinworm was *Trypanoxyuris minutus* (Trejo-Macías *et al.* 2011).

Table I Predictions tested in this paper concerning the effects of host traits on the prevalence and eggs per gram of feces (EPG) of infection with *Trypanoxyuris minutus* in howlers (*Alouatta palliata* and *A. pigra*) and variables used to test them

Directly transmitted parasite infection increases with:	Variables	Support in the present study
Ranging factors		
Home range size	Total area (ha) of the quadrats used by each group: factor variable, four levels (API-1 = 4.31, API-2 = 2.93, APA-1 = 5.87, APA-2 = 5.25)[a]	No
Home range overlap	Percentage of quadrats shared with other groups: factor variable, four levels (API-1 = 50.7, API-2 = 76.6, APA-1 = 48.8, APA-2 = 40.4)[a]	No
Intensity of home range use	Percentage of quadrats visited once or twice: factor variable, four levels (API-1 = 62.3, API-2 = 72.3, APA-1 = 97.9, APA-2 = 86.9)[a]	No
	Number of trees visited/h by focal individual: continuous variable (min = 0.2; max = 4.0; mean = 1.2)[b]	No
Social factors		
Group size	Number of adult individuals per group: factor variable, four levels (API-1 = 4, API-2 = 3, APA-1 = 16, APA-2 = 11)[a]	No
Physical contact	Number of contacts with other individuals: continuous variable (min = 0, max = 27, mean = 8.6)[b]	No
Connectedness	Proportion of group members contacted: continuous variable (min = 0.02, max = 0.9, mean = 0.6)[b]	Yes[c]
Closeness	Mean number of individuals at <5 m: continuous variable (min = 0.8, max = 5.4, mean = 2.5)[b]	Yes[c]
Decreasing group spread	Spread index per group: factor variable, four levels (API-1 = 0.7, API-2 = 0.8, APA-1 = 0.1, APA-2 = 0.09)[a]	No
Diet		
Diet diversity	Number of plant species used as food sources/h: continuous variable (min = 0.1, max = 0.2, mean = 0.1)[b]	Yes
Folivory	Percentage of feeding time dedicated to consume leaves: continuous variable (min = 0, max = 100, mean = 61.7)[b]	No
Non-tree foods	Percentage of feeding time dedicated to consume non-tree foods: continuous variable (min = 0, max = 100, mean = 49.1)[b]	Yes
Intrinsic factors		
Sex and species	Sex, controlled by species: factor variable, four levels (*A. palliata* males = 7, *A. palliata* females = 20, *A. pigra* males = 2, *A. pigra* females = 5) [b]	No

Based on Chapman *et al.* (2009) and Nunn and Altizer (2006).

[a] Operates at group level.

[b] Operates at individual level.

[c] Connectedness and closeness as "proximity partner index."

We described infections with *Trypanoxyuris minutus* in terms of prevalence (i.e., the proportion of individuals infected with the parasite: Chapman *et al.* 2007) and the number of eggs per gram of feces (EPG: Chapman *et al.* 2007). We used a McMaster counting chamber to calculate EPG, with the same flotation media and amount of sample as described in the preceding text. After filtration through surgical gauze, we added the fecal suspension to each of the two chambers of the McMaster slide. Using ×10 magnification, we counted all parasite eggs encountered inside the grid of each chamber (MacIntosh *et al.* 2010) and calculated the number of eggs following Levecke *et al.* (2011).

Although EPG can be highly variable and may not represent actual infection intensity (Gillespie *et al.* 2005), it is a quantitative measure of parasite infection routinely used in veterinary health monitoring practices and frequently reported to describe parasite infections in studies of free ranging animal populations (Ezenwa 2003, 2004; Gulland 1992: primates; Hodder and Chapman 2012; MacIntosh *et al.* 2012; Setchell *et al.* 2007). We therefore used EPG as an index of intensity (Hodder and Chapman 2012). Intensity of infection is the number of individuals of a particular parasite species in a single infected host (Bush *et al.* 1997), and its assessment requires necropsies to collect all parasites from the infected hosts. EPG may therefore provide a quantitative description of infection and be used as a surrogate measure of intensity of parasite infection in noninvasive studies of endangered primate populations from which individuals cannot be removed (MacIntosh *et al.* 2010, 2012), such as the critically endangered *Alouatta palliata mexicana* and endangered *A. pigra* (Rodríguez-Luna *et al.* 2009). Further, a number of studies have found a linear relationship between EPG and actual number of worms in the hosts (East and Bourne 1988; Robert and Swan 1981; Seivwright *et al.* 2004; Stear *et al.* 1995); however, because it has not been demonstrated that such a relationship exists for *Trypanoxyuris minutus* infecting howlers, this intensity index should be interpreted with caution (Hodder and Chapman 2012; MacIntosh *et al.* 2012).

Data Organization and Analyses

We used the focal sampling data to examine how parasite infections varied as a function of individual range size, home range overlap, and intensity of home range use. We tagged and located all plants used by the focal individual using a handheld global positioning system and created digital maps (ArcView 5.1, Environmental System Research Institute, Redlands, CA). We superimposed a 25 × 25 m grid cell on this map and calculated group home range overlap as the proportion of quadrats each group shared with other groups. We calculated the intensity of group home range use by counting the number of times each group entered each quadrat. We previously found that the frequency of quadrat use varied between 1 and 8 (González-Hernández *et al.* 2011); thus, we calculated intensity of group home range use as the proportion of quadrats in the home range entered once or more by each group. To assess the intensity with which each individual used its group home range, we calculated an individual rate of tree use as the total number of trees used for any activity (feed, rest, travel) during its focal samples divided by the total observation time for that individual.

We used the variables listed in Table I to study the influence of social factors on parasite infection patterns. First, we calculated the frequency of physical contacts for

each individual from all occurrences sampling as the total number of contacts it had with other group members during the whole observation period per group (80 h). Second, we calculated connectedness as the mean proportion of contacted group members for each individual across all its focal samples. Therefore, connectedness expresses contact among group members independently of the frequency at which it occurred, and it varies between 0 (an individual did not contact any other group member during focal sampling) and 1 (an individual had contact with all other group members during focal sampling). Third, we calculated closeness as the mean number of group members within 5 m for each focal individual across all its instantaneous samples. Fourth, we calculated a spread index for each group from instantaneous samples:

$$C_i = \frac{\left(\sum_1^n \frac{(\text{cat1*1}) + (\text{cat2*0.5}) + (\text{cat3*0.25}) + (\text{cat4*0.125}) + (\text{cat5*0})}{\text{No.of group members}-1}\right)}{\text{No.of instantaneous samples}}$$

where C_i is the spread index for individual i, and where the proximity categories are cat1 = contact, cat2 = <1 m, cat3 = 1–5 m, cat4 = 6–10 m, and cat5 >10 m. For each instantaneous record for i, the number of individuals in each proximity category was multiplied by a weighting factor that decreased with increasing distance, and then summed. To account for differences in group size and in the number of instantaneous samples per individual, this sum was divided by the total number of group members, excluding i, and this value was then divided by the number of instantaneous samples collected for i. Mean group spread approaching 0 indicates that group members were highly separated from each other and therefore group spread was high, whereas a mean group spread index close to 1 indicates that all individuals tended to be in close proximity and group spread was low. We used this index based on the rationale that individuals that on average are closer to other group members are more likely to contact a larger number of partners than individuals that are usually more distant; if body contact is an important transmission mechanism of *Trypanoxyuris minutus*, the former should be less infected than the latter.

To avoid multicollinearity resulting from the correlation between connectedness and closeness ($r = 60$, $N = 34$, $P < 0.05$), we calculated the residuals from the regression of closeness on connectedness ($R^2 = 0.36$, $\beta = 0.60$, $F_{1,32} = 17.8$, $P < 0.001$). These residuals correlated positively with both variables (closeness = 0.60, $N = 34$, $P < 0.05$; connectedness = 0.80, $N = 34$, $P < 0.05$), indicating that with increasing residual values individuals were closer to and had more contact with more group partners. We refer to these residuals hereafter as the proximity partner index.

Each tagged plant that was used as a feeding source was identified at the species level based on phytomorphology. Diet diversity was calculated per individual as the total number of plant species used as food sources divided by the number of focal hours for each individual. We calculated folivory and use of non-tree foods for each individual as the proportion of total feeding time spent feeding from leaves and non-tree foods, respectively, across individual focal samples.

Because several group level variables were correlated, we performed a principal components analysis (PCA) to reduce them to a subset of unrelated orthogonal factors

to model patterns of infection with *Trypanoxyuris minutus*. This analysis resulted in two components with eigenvalues ≥1 that explained 97% of the total variance in those variables. Component 1 explained 82.4% of the variance showing a strong positive loading ($r \geq 0.9$) for group size, home range size, and intensity of home range use and strong negative loading for group spread. Component 2 explained 15% of variance showing a negative loading with home range overlap ($r = -0.72$).

To normalize distributions and homogenize variances, we used a square root transformation for EPG and square root of the arcsine transformation for both folivory and the use of non-tree foods. Following transformation all variables showed normal distributions and homogeneous variances (Kolmogorov-Smirnov tests and Levene's tests: $P > 0.05$). We used generalized linear mixed models (GLMM) to model parasite prevalence (analyzed as the presence or absence of parasites) and EPG as a function of sociality (frequency of physical contacts, proximity partner index), ranging (components 1 and 2, as defined in the preceding text), foraging and diet (diet diversity, consumption of non-tree foods, folivory), sex and first-order interactions between these predictor variables. We nested individuals within groups and groups within species as random factors to account for intragroup variation in behavior and repeated measurements of individuals belonging to the same group, and of different groups belonging to the same species. Each model included the number of fecal samples collected from each individual as an additional control variable to test if variation in sampling effort affected our results. We used a logistic distribution for the parasite prevalence model (i.e., presence or absence of parasite per individual), and a normal distribution with a log link function for the parasite EPG model. We applied Akaike's information criterion corrected for small sample size (i.e., AIC_c: Burnham and Anderson 2010) to select the most parsimonious model that is, the combination of predictive variables that best explained each infection variable of *Trypanoxyuris minutus* (Motulsky and Christopoulus 2003). Best models (i.e., one model for parasite prevalence and one model for EPG), were those with the lowest AIC_c values (Burnham and Anderson 2010). We performed all analyses in SPSS 12.0 (SPSS Inc., Chicago, IL) using two-tailed tests and significance level set at $\alpha = 0.05$.

Results

Overall, we found no species, sex, or group differences in mean prevalence and EPG of *Trypanoxyuris minutus* (Table II). Prevalence of *Trypanoxyuris minutus* was high, with 82.4% (28/34) of all individuals being infected. In the two groups of *Alouatta pigra*, all adults were infected with the exception of a single adult female from group API-1. In the groups of *Alouatta palliata*, three females from APA-1, as well as one female and one male from APA-2, were not infected (Appendix S1). The most parsimonious model included only proximity partner index as a significant predictor of prevalence of *Trypanoxyuris minutus*, with no significant influence of species, sex, group, ranging, feeding behavior, or first-order interactions between variables (Table III). The logistic model was significant ($R^2 = 0.43$; $\chi^2_1 = 13.7$, $P < 0.001$), indicating that the probability of infection with *Trypanoxyuris minutus* increased with proximity partner index (Fig. 1).

Table II Mean parameters of infection with *Trypanoxyuris minutus* by species, sex, and group in sympatric *Alouatta palliata* and *A. pigra* during the 2010 dry season (February–June) in Tabasco, Mexico

Variable		Infection with *Trypanoxyuris minutus*		*N*
		Prevalence (%)	EPG ± SD (eggs/g)	
Species	*Alouatta pigra*	85.7	131.5 ±74.7	7
	A. palliata	81.5	213.3 ± 268.5	27
Sex	Males	88.9	194.4 ± 184.5	9
	Females	80.0	197.2 ± 264.0	25
Group	API-1	75	125.0 ± 93.5	4
	API-2	100	140.3 ± 58.4	3
	APA-1	81.3	182.3 ± 194.5	16
	APA-2	81.8	258.3 ± 356.3	11

Mean (± SD) EPG was 196.4 (± 242.8) eggs/g per individual, but was highly variable among individuals (range = 0–1150 eggs/g). The most parsimonious model of EPG (R^2 = 0.68; $t_{1,22.3}$ = 4.2, $P < 0.001$) included diet diversity ($F_{1,30.01}$ = 10.2, P = 0.001), the proportion of time dedicated to consume non-tree foods ($F_{1,32.83}$ = 8.8, P = 0.003), and proximity partner index ($F_{1,31.34}$ = 8.1, P = 0.007) as significant predictors of individual EPG (Table III). Bearing in mind that EPG should be interpreted with caution, EPG of *Trypanoxyuris minutus* increased with increasing dietary diversity, consumption of non-tree foods, and proximity partner index (Fig. 2).

Table III Results of models investigating variation in prevalence of *Trypanoxyuris minutus* and eggs per gram of feces (EPG) in *Alouatta palliata* and *A. pigra* during the 2010 dry season (February–June) in Tabasco, Mexico

Model	Δ_i [a]
Prevalence	
Proximity partner index	0
Proximity partner index + physical contact + non-tree foods	2.06
Proximity partner index + component 1	6.36
Component 1 + non-tree foods + Proximity partner index	6.47
EPG	
Diet diversity + non-tree foods + proximity partner index	0
Diet diversity + non-tree foods + proximity partner index + component 1	3.01
Proximity partner index + non-tree foods + physical contact	3.58
Diet diversity + non-tree foods + proximity partner index + folivory	4.32
Diet diversity + non-tree foods + folivory + sex and species	5.36
Diet diversity + non-tree foods + sex and species	6.90

[a] AIC differences between models. Only models with $\Delta_i < 7$, i.e., those receiving high to moderate support (Burnham and Anderson 2002) are presented. $\Delta_i = 0$ indicates the most parsimonious, best models.

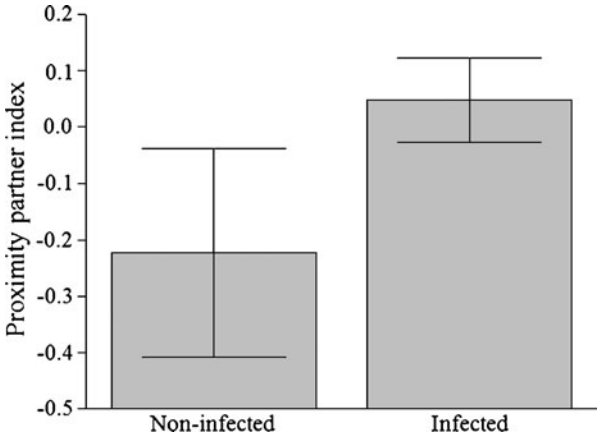

Fig. 1 Variation (mean ± SD) in prevalence of *Trypanoxyuris minutus* according to proximity partner index in sympatric *Alouatta palliata* and *A. pigra* during the 2010 dry season (February–June) in Tabasco, Mexico.

Discussion

Individual behavior, but not group or population level variables, was the best predictor of infection with *Trypanoxyuris minutus* in sympatric populations of *Alouatta palliata* and *A. pigra*. The probability of being infected with *Trypanoxyuris minutus* was higher for individuals that were closer to and had physical contact with a higher proportion of the group. Although EPG should be interpreted with caution (Gillespie *et al*. 2005), the importance of individual sociality in infection with *Trypanoxyuris minutus* was

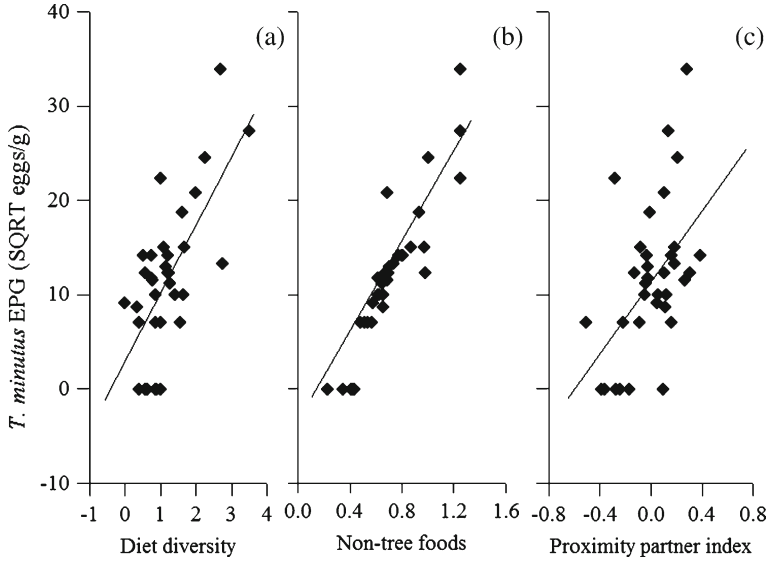

Fig. 2 Relationships between mean individual eggs per gram (EPG) of feces of *Trypanoxyuris minutus* and dietary diversity **(a)**, time spent consuming non-tree foods **(b)**, and proximity partner index **(c)** in sympatric *Alouatta palliata* and *A. pigra* during the 2010 dry season (February–June) in Tabasco, Mexico.

supported by the positive association of proximity partner index and EPG. In addition, EPG was also significantly associated with diet: individuals that used more plant species and non-tree plants as food sources were more heavily parasitized. Therefore, both sociality and feeding behavior are important factors influencing the dynamics of infection with *Trypanoxyuris minutus* in these populations.

Contact rates among individuals within populations can vary greatly and social interactions among group members are rarely homogeneous (Fenner *et al.* 2011; Gompper 2004). There is abundant evidence that individuals more highly connected in the social network are at greater risk of becoming infected (Godfrey *et al.* 2009; Johnson *et al.* 2011; Shirley and Rushton 2005; Tompkins *et al.* 2011). For instance, in Japanese macaques (*Macaca fuscata yakui*), both network centrality and direct contact were positive predictors of parasite infection (MacIntosh *et al.* 2012). In the current study, proximity partner index was a good predictor of both parasite prevalence and EPG, highlighting the importance of social factors in the transmission dynamics of *Trypanoxyuris minutus* in sympatric *Alouatta palliata* and *A. pigra* and possibly other parasites as well. Closeness and contact with group partners could promote reinfection and thus higher infection intensity. In the larger groups of *Alouatta palliata* only a few individuals had contact with a majority of adult group members (APA-1, one individual contacted 53.8% of all group members; APA-2, two individuals contacted 72.7% of all group members), while most individuals contacted fewer than five partners. All highly social individuals were infected with *Trypanoxyuris minutus* and had high EPG counts even though they represented only a few individuals. Thus, as observed in humans (Lloyd-Smith *et al.* 2005), free-ranging primates (MacIntosh *et al.* 2012), and other mammals (*Canis familiaris*: Brunker *et al.* 2012; *Peromyscus maniculatus*: Clay *et al.* 2009), infections in *Allouatta palliata* are strongly skewed toward the most social individuals. These superspreaders are usually individuals central in their social network and are far more likely to receive and transmit a pathogen than more peripheral individuals (Lloyd-Smith *et al.* 2005; MacIntosh *et al.* 2012).

We found that six individuals were not infected with *Trypanoxyuris minutus*. It is possible that limited sample size could affect our ability to detect the pinworm. However, we followed Muehlenbien's (2005) collection protocol because he concluded that three or four samples collected on nonconsecutive days was an efficient sampling effort to assess parasite richness in short study periods where seasonal effects are not taken into consideration, as in the present study.

Considering that noninfected individuals from different groups were consistently negative in their samples (even those with six or seven samples, Appendix S1), it is possible that 1) autoinfection, such as direct fecal–oral self-contamination via fingernail contact, or retroinfection (larvae hatch from egg in anal mucosa and migrates into the sigmoid colon: Cook 1994) may also be important transmission modes of *Trypanoxyuris minutus* in *Alouatta* sp.; 2) noninfected individuals were in the prepatent infection period (Bogitsh *et al.* 2013); or 3) eggs were not released into the fecal bolus (Stuart *et al.* 1990) and therefore pinworm infection went undetected.

We found that individuals that fed on a more diverse diet had higher EPG of *Trypanoxyuris minutus* in *Alouatta palliata* and *A. pigra*. In howlers, diet diversity is positively associated with folivory (Dias and Rangel-Negrín in press) and ranging distances (Estrada 1984). Leaves consumed by howlers have higher toxin concentrations than other plant parts (Milton 1980), and individuals may avoid toxic overload

caused by plant secondary compounds by diversifying their diets (Glander 1978). This diversification should result in increased ranging (Oates 1977) owing to heterogeneities in the spatial distribution of tree species in tropical forests (Condit *et al.* 2000). However, we did not find such relationships between diet diversity, folivory, and ranging (data not shown). In contrast to previous research (Freeland 1980; Moore 2002; Nunn and Dokey 2006), parasite prevalence and EPG were explained neither by folivory nor by ranging behavior in these populations of howlers. This could be a consequence of higher dietary diversity caused by foraging on plant growth forms that use trees for support, such as lianas, vines, and epiphytes; foraging on such non-tree foods was a significant predictor of EPG of *Trypanoxyuris minutus* (but not prevalence). Although foraging on these growth forms may have behavioral costs (Dunn *et al.* 2012), it may boost dietary diversity without greatly increasing ranging costs because within-tree displacements are sufficient for finding food from multiple plant species. Our analyses suggest that the use of such non-tree foods has physiological consequences, as individuals that used more non-tree plants in their diet were more parasitized.

In conclusion, we found a positive relationship between infection with *Trypanoxyuris minutus* and sociality, diet diversity, and use of non-tree foods in two species of sympatric howlers. Our results support the hypothesis that increased sociality and contact with contaminated substrates are important factors influencing infection patterns of a directly transmitted parasite, likely resulting from increased exposure to parasites. *Trypanoxyuris minutus* is a common parasite in howlers and, as with other nematodes, is thought to have low virulence because nematodes have no extraintestinal migration and they do not feed on tissue or host food (Stuart *et al.* 1998; Vitazkova 2009). Instead, they consume bacteria in the posterior gut of their host (Adamson 1994), which may have a limited impact on host health and only marginally decrease digestive efficiency. However, mortality caused by a hyperinfection with *Trypanoxyuris minutus* has been reported in brown howlers (*Alouatta guariba*: Amato *et al.* 2002), suggesting that under certain circumstances intense pinworm infection may affect the health status and fitness of primates.

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