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NEWS AND PERSPECTIVES

Does home range use explain the relationship between group size and parasitism? A test with two sympatric species of howler monkeys

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Abstract Group size is related to parasite infections in primates. This relationship probably reflects the fact that group size is associated with body contact between group members and with contact with contaminated items in the environment. The latter is highly associated with range use. In the present study we hypothesized that if infection by directly transmitted parasites (DTP) is mainly determined by the exposure of individuals to parasites that accumulate in the environment, and group size correlates negatively with the intensity of home range use, then smaller groups should be more infected by DTP. Additionally, groups that share a higher proportion of their home range with other groups should be more infected. To test our hypothesis we observed and collected fecal samples of two groups of *Alouatta palliata* (large group size) and two groups of *A. pigra* (small group size) that live sympatrically in a forest fragment located in Macuspana (Mexico). Group size was positively correlated with range area size and negatively correlated with the intensity of home range use. Range use variables were not related to either DTP prevalence or load. However, there were significant differences in DTP loads between groups, which were positively correlated with group size. Our results suggest that the intensity of home range use is a poor predictor of DTP infection parameters in groups with marked differences in size. Therefore, it is possible that the individual or combined effects of other ecological (e.g., microclimate), social (e.g., contact rate), or physiological (e.g., immune function) factors are more important in the dynamics of DTP in free-ranging primates.

Keywords *Alouatta* · Directly transmitted parasites · Habitat overlap · Habitat use intensity · *Trypanoxyuris*

Introduction

Epidemiological models point to strong links between host density or local group size and the spread and diversity of directly transmitted parasites (DTP, i.e., parasites with a fecal–oral transmission route; Anderson and May 1979). This has been supported by data from comparative studies in vertebrates (e.g., Møller et al. 1993; Côte and Poulin 1995; Arneberg 2002), including primates (Vitone et al. 2004), and by a handful of empirical studies in free-ranging primate populations (e.g., Freeland 1976, 1979; Chapman et al. 2005; Gillespie and Chapman 2006; Mbora and McPeek 2009), including howler monkeys (*Alouatta*: Stuart et al. 1990; Gilbert 1994; Stoner and González-Di Pierro 2005; Trejo-Macías et al. 2007).

In primates, two alternative underlying mechanisms for the relationship between DTP infections and group size have been investigated: contact between group members and contact of individuals with contaminated items in their environment (Chapman et al. 2009). The former predicts a positive relationship between group size and DTP

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infections, whereas when group size correlates positively with home range size, the latter predicts a negative relationship.

Contact with contaminated items is strongly associated with ranging patterns, as the way a group uses its home range and travels throughout its environment should influence the probability of contacting infected areas (Chapman et al. 2009). This prediction has been supported recently by an interspecific comparative analysis of 119 primate species, which found that increases in range use intensity led to increased parasitism by DTP (Nunn and Dokey 2006). However, this finding remains to be confirmed and extended to intrageneric and intraspecific comparisons.

Transmission of DTP can be affected by the number and duration of contacts with contaminated feces (Freeland 1979; Anderson and May 1991; Ezenwa 2004). For instance, animals restricted to small areas or those that use their range more intensively may be more infected (parasite prevalence: Ezenwa 2004; parasite load: Stoner 1996) and reinfected by DTP (Freeland 1976, 1980). Therefore, repeated use of the same contaminated areas by group members or neighboring groups should lead to higher parasite prevalence (i.e., proportion of infected individuals in a group; Nunn and Dokey 2006; Chapman et al. 2009) and loads (i.e., parasite eggs per gram of feces; Stoner 1996).

The two species of howler monkeys that occur in Mexico (*Alouatta palliata* and *A. pigra*) have allopatric distributions throughout most of their distributional range, but live sympatrically in the state of Tabasco, near Macuspana (Smith 1970; Cortés-Ortiz et al. 2007). Group size varies significantly between these species, with *Alouatta palliata* groups (mean = 14.9 individuals; maximum group size = 45 individuals) being on average more than two times larger than *A. pigra* groups (mean = 6.2 individuals; maximum group size = 16 individuals; Di Fiore and Campbell 2007). This difference between closely related species that live in an area where they face similar environmental conditions offers an excellent opportunity to investigate the underlying mechanisms leading to the relationship between group size and DTP infections. To address this question, in the present study we hypothesized that if infection by DTP is mainly determined by the exposure of individuals to parasites that accumulate in the environment, and group size correlates negatively with the intensity of home range use, smaller groups should be more infected by DTP. Therefore, smaller *Alouatta pigra* groups were expected to have smaller home ranges, which they should use more intensively, and as a consequence, present higher DTP prevalence, richness, and load. Additionally, groups that share a higher proportion of their home range with other groups should be more infected.

Methods

Study site and subjects

For this study, we focused on a forest fragment located inside a private cattle farm (17°38.2′ N, 92°40.1′ W) in the Macuspana area. This fragment has a total forested area of 18.6 ha, from which ca. 60% represents suitable habitat for howlers. The remaining habitat corresponds to palm tree plantations and bushes <2 m high. The fragment is inhabited by two *Alouatta pigra* and two *A. palliata* groups. These groups are frequently in close proximity (10–20 m), and at times groups from different species rest in the same tree or feed from the same tree simultaneously.

The two *Alouatta pigra* groups had the same size (six individuals) and a similar composition. The first *Alouatta pigra* group (called API-1 hereafter) comprised one adult male, three adult females, and two juveniles. The second *Alouatta pigra* group (called API-2 hereafter) comprised one adult male, two adult females, two juveniles, and one infant. The first *Alouatta palliata* group (called APA-1 hereafter) had 25 individuals, of which four were adult males, 12 were adult females, seven were juveniles, and two were infants. The second *Alouatta palliata* group (called APA-2 hereafter) comprised 15 individuals, with three adult males, eight adult females, three juveniles, and one infant. All individuals could be identified by facial features, scars, broken fingers, and genital morphology, as well as color patterns on their feet and tail (for *Alouatta palliata*).

Use of space

From February to June 2010, each group was followed for 80 h to collect ranging data. During each observation day, we performed 60-min focal animal samples, during which we tagged and located, with a handheld global positioning system, each tree where the focal animal was observed. Focal observations were evenly distributed across all adult individuals in each group. All trees used by the focal animals were digitized as points with ARC VIEW 3.2 (Environmental System Research Institute, Redlands, CA, USA). We superimposed a 25 × 25 m grid cell system on this point map, and calculated the total number of quadrats used per group and the number of occasions each quadrat was entered by each group. Additionally, according to the number of occasions each quadrat was entered, we classified quadrats as lightly (1–2 visits), moderately (3–4 visits), or heavily (≥5 visits) used. To quantify spatial overlap between groups, we calculated the proportion of quadrats each group shared with other groups.

Fecal sample collection and laboratory analysis

Fresh fecal samples were collected immediately after defecation whenever they could be matched with individuals. Samples from juveniles and infants were not used in this study, as several individuals in these age classes could not be consistently recognized. We collected at least three fecal samples (range 3–9) from each adult (i.e., 34 individuals) on non-consecutive days. A total of 211 samples were collected.

Fecal samples were preserved in plastic vials with 10% buffered formalin until analyzed at the Laboratorio de Parasitología, Facultad de Medicina Veterinaria y Zootecnia, Universidad Veracruzana (Veracruz). Samples were processed using a flotation technique with sodium chloride solution (specific gravity 1.20; Trejo-Macías et al. 2007), using 3 g of feces. One slide per sample was systematically scanned for parasite eggs or cysts. Size, color, and morphology of parasite eggs were used to identify parasites to genus level (Osorio et al. 2009).

Infections by DTP were described in terms of parasite prevalence and load. Parasite richness was not examined in the present study, as only one genus of DTP was identified and was present in each of the four groups. Prevalence is the proportion of individuals sampled that are infected with a particular parasite (Chapman et al. 2009). Parasite egg production or load is the number of parasite eggs per gram of feces (Chapman et al. 2006a). Although this measure can be highly variable (Gillespie 2006), it may provide a quantitative description of actual infection intensity (Chapman et al. 2006a). Parasite load was determined with a McMaster counting chamber (Osorio et al. 2009).

Data analyses

We used χ^2 tests for similar expected frequencies to compare among groups: the total number of quadrats used; the proportion of lightly, moderately, and heavily used quadrats; the proportion of quadrats shared with other groups; and parasite prevalence and load. To correlate parasite prevalence and load with both ranging variables and group size, we used Spearman correlations. Statistical significance was set at $\alpha < 0.05$.

Results

Intensity of home range use

During the 320 h of observations the four groups used a total of 216 quadrats, corresponding to an area of 8.64 ha (i.e., 46.53% of the total forested area). Group API-1 used 4.31 ha, API-2 used 2.93 ha, APA-1 used 5.87 ha, and APA-2 used 5.25 ha (Fig. 1). The total number of quadrats entered at least once differed significantly among groups (Table 1), with *Alouatta pigra* groups using fewer quadrats than *A. palliata*. A similar trend was observed for lightly used quadrats, whereas the opposite occurred for

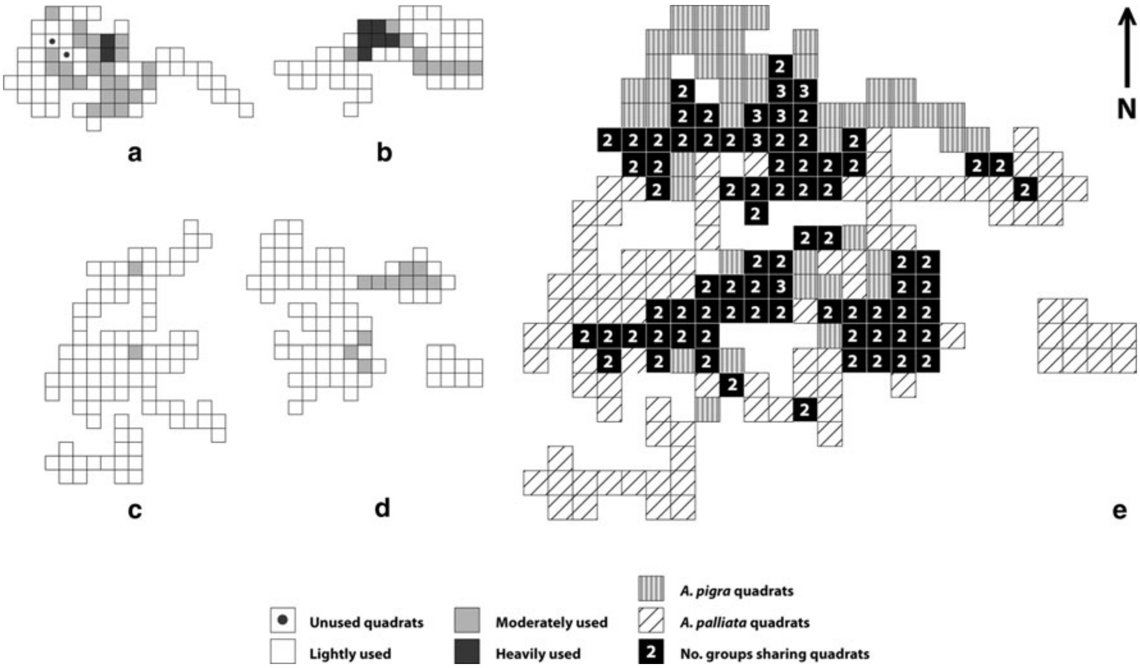

Fig. 1 Intensity of home range use by four groups of howler monkeys in a forest fragment: **a** *Alouatta pigra* (API)-1, **b** API-2, **c** *Alouatta palliata* (APA)-1, **d** APA-2, **e** all groups

Table 1 Comparisons of intensity of home range use and parasitosis among four groups of howler monkeys

	API-1	API-2	APA-1	APA-2	χ^2_3
Total number of quadrats[a]	69	47[b]	94	84	17.05**
Lightly used quadrats (%)	62.3[b]	72.3	97.9[b]	86.9	9.26*
Moderately used quadrats (%)	34.8[b]	17.0	2.1[b]	13.1	32.95**
Heavily used quadrats (%)	2.9	10.6[b]	0	0	22.38**
Shared quadrats (%)	50.7	76.6[b]	48.8	40.4	13.55**
DTP prevalence (%)	83.3	100	80	92.3	2.76[n.s.]
DTP load (eggs/g)	156.3[b]	165.0	244.6[b]	237.5	32.54**

API *Alouatta pigra*; APA *Alouatta palliata*; DTP directly transmitted parasites; n.s. non-significant

* $P \le 0.05$, ** $P \le 0.001$

[a] Quadrat size 25 × 25 m

[b] Group contributing large proportion of non-randomness

moderately and heavily used quadrats. The percentage of shared quadrats varied significantly, with *Alouatta palliata* groups sharing less space with other groups than *A. pigra*.

Parasite infections

We found eggs of a single species of DTP, the nematode *Trypanoxyuris* sp., which was present in each of the four groups. Overall, the proportion of infected individuals in the groups was high ($\geq$80%) and no clear pattern could be identified in *Trypanoxyuris* sp. prevalence (Table 1). Parasite loads varied significantly among the groups, with *Alouatta palliata* groups showing higher loads than *A. pigra* groups. Parasite prevalence and parasite loads were not associated with ranging variables ($P > 0.05$ for the ten tests). Parasite loads were positively correlated with group size ($r_s = 0.94$, $P < 0.05$).

Discussion

Group size was correlated negatively with the intensity of home range use, as predicted in our hypothesis, because *Alouatta pigra* groups used fewer quadrats than *A. palliata* and used moderately and heavily used quadrats more than *A. palliata*. This finding converges with previous research (e.g., Milton and May 1976) and probably reflects the effects of increased within-group resource competition in larger groups (Gillespie and Chapman 2001; Chapman et al. 2009), which forces larger groups to travel further and use larger home ranges (Chapman et al. 2009). However, contrary to our hypothesis and previous interspecific comparative analyses (Nunn and Dokey 2006), smaller groups were not more parasitized than larger groups. Prevalence was similar across groups, and parasite loads were higher in *Alouatta palliata* groups. Furthermore, groups that shared a higher proportion of their home range with other groups were not more infected. Therefore, in this study, either individuals that used more intensively their home range did not contact contaminated items in their environment more often, or other mechanisms, such as increased contact between group members in the larger groups, or increased contact between individuals and parasites when the home range size is larger, may have been responsible for the observed results.

Previous studies of non-sympatric populations of *Alouatta palliata* and *A. pigra* found no differences in parasitism patterns between species, suggesting that our result is not due to species differences in vulnerability to parasitism (e.g., Vitazkova and Wade 2006; Trejo-Macías et al. 2007; Alvarado-Villalobos 2010; Cristóbal-Azkarate et al. 2010; Valdespino et al. 2010). However, the present study does not allow discarding phylogenetic history or other behavioral differences between the two species as potential predictors for the observed patterns of DTP parasitism. For instance, differences in immune function or response could explain why parasite loads differed significantly among groups (Nunn et al. 2000; Nunn 2002).

Although API-2 had significantly more shared quadrats than the other groups, all groups had overlapping home ranges. For parasites that accumulate in the external environment, physical contact between hosts is not required for successful transmission, and spatial overlap between sympatric hosts is sufficient for cross-species parasite transmission. The effect of habitat overlap on generalist parasite prevalence and abundance (i.e., load) has been demonstrated in African ungulates, where increased range overlap results in increased parasite infection rates (Ezenwa 2003). *Alouatta palliata* groups visited moderately and heavily used quadrats occupied by *A. pigra* groups on several occasions (M.G.H., personal observation). It is therefore possible that overlap zones pose higher infection risks for *A. palliata* individuals, resulting in higher infection or re-infection rates (Altizer et al. 2003). This would explain the higher parasite loads in this species, and link DTP infections with ranging dynamics. Furthermore, future research should try to disclose the effect of spatial confinement on the ranging patterns of groups. It is possible that in a larger habitat home ranges would be larger, overlapping areas would be smaller, and intensity of habitat use would be lower, resulting in different patterns of infection risk and parasitism.

In forest fragments, edge effects frequently result in higher within-fragment variations in vegetation structure, which in turn, affect microclimate (e.g., Didham and Lawton 1999). Differences in microclimate, particularly humidity and temperature, could have a strong effect on the survival of infective stages of parasites in the environment (Stuart and Strier 1995), and consequently, in transmission probabilities via contact with contaminated substrates (Snaith et al. 2008). For instance, quadrats with high humidity could pose a higher infection risk (Stoner 1996). Additionally, spatial variation in the distribution of parasites in the environment may account for variation in host infection (Møller et al. 1993). Such an effect has been proposed to explain differences in parasite infections in primate groups inhabiting the edges versus interiors of fragments in Africa (Chapman et al. 2006b). We did not record microclimate data for our study area, so further research will have to be conducted to assess whether microclimate variation affects the relationship between group size, space use intensity, and DTP infections.

Among primates, time spent being social (Dunbar 1991) and the number of social interactions often increase with group size (Chapman et al. 2009). If DTP are transmitted during social behavior then individuals living in larger social groups may on average be more infected by DTP than individuals living in smaller groups (Møller et al. 1993). For instance, empirical evidence for a positive effect of group size and increased physical contact on protozoa richness has been reported in mangabeys (*Cercocebus albigena*; Freeland 1979). It is possible that increased sociality is responsible for the higher parasite loads observed in the larger groups of *Alouatta palliata* in the present study. Our results are in accord with the hypothesis that social contact between group members is the dominant mechanism driving the relationship between group size and parasitism.

In conclusion, our results suggest that the intensity of home range use is a poor predictor of DTP infection parameters in groups with marked differences in size, as in the present case of sympatric *Alouatta palliata* and *A. pigra*. However, parasite loads were positively correlated with group size. Therefore, it is possible that the individual or combined effects of other ecological (e.g., microclimate), social (e.g., contact rate), or physiological (e.g., immune function) factors are more important in the dynamics of DTP in free-ranging primates.

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References

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JRC (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. Annu Rev Ecol Evol Syst 34:517–547

Alvarado-Villalobos MA (2010) Prevalencia e intensidad de parásitos intestinales de *Alouatta pigra* en fragmentos de selva en Playas de Catazajá, Chiapas. BSc dissertation, Universidad Autónoma de Ciudad Juárez, Chihuahua. p 103

Anderson RM, May RM (1979) Population biology of infectious diseases: part 1. Nature 280:361–367

Anderson RM, May RM (1991) Infectious diseases of humans. Aust J Public Health 16:208–212

Arneberg P (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. Ecography 25:88–94

Chapman CA, Gillespie TR, Speirs ML (2005) Parasite prevalence and richness in sympatric colobines: effects of host density. Am J Primatol 67:259–266

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006a) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anthropol 131:525–534

Chapman CA, Speirs ML, Gillespie TR, Holland T, Austad KM (2006b) Life on the edge: gastrointestinal parasites from the forest edge and interior primate groups. Am J Primatol 68:397–409

Chapman CA, Rothman JM, Hodder SAM (2009) Can parasite infections be a selective force influencing primate group size? A test with red colobus. In: Huffman MA, Chapman CA (eds) Primate parasite ecology: the dynamics and study of host–parasite relationships. Cambridge University Press, Cambridge, pp 423–440

Cortés-Ortiz L, Duda TF, Canales-Espinosa D, García-Orduña F, Rodríguez-Luna E, Bermingham E (2007) Hybridization of large-bodied new World primates. Genetics 176:2421–2425

Côte IM, Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. Behav Ecol 6:159–165

Cristóbal-Azkarate J, Hervier B, Vegas-Carillo S, Osorio-Sarabia D, Rodríguez-Luna E, Vea JJ (2010) Parasitic infections of three Mexican howler monkey groups (*Alouatta palliata mexicana*) living in forest fragments in Mexico. Primates 51:231–239

Di Fiore A, Campbell CJ (2007) The Atelines: variation in ecology, behavior and social organization. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, Oxford, pp 155–185

Didham RH, Lawton JH (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17–30

Dunbar RIM (1991) Functional significance of social grooming in primates. Folia Primatol 57:121–131

Ezenwa VO (2003) Habitat overlap and gastrointestinal parasitism in sympatric African bovids. Parasitology 126:379–388

Ezenwa VO (2004) Host social behavior and parasitic infection: a multifactoral approach. Behav Ecol 15:446–454

Freeland WJ (1976) Pathogens and the evolution of primate sociality. Biotropica 8:12–24

Freeland WJ (1979) Primate social groups as biological islands. Ecology 4:719–728

Freeland WJ (1980) Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination. Ecology 61:1297–1303

Gilbert KA (1994) Endoparasitic infection in red howling monkeys (*Alouatta seniculus*) in the central Amazonian Basin: a cost of sociality? PhD dissertation, Graduate School, New Brunswick Rutgers, State University of New Jersey

Gillespie TR (2006) Noninvasive assessment of gastrointestinal parasite infections in free-ranging primates. Int J Primatol 27:1129–1143

Gillespie TR, Chapman CA (2001) Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraint model. Behav Ecol Sociobiol 50:329–338

Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conserv Biol 20:441–448

Mbora DN, McPeek MA (2009) Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. J Anim Ecol 78:210–218

Milton K, May ML (1976) Body weight, diet and home range area in primates. Nature 259:459–462

Møller AP, Dufva R, Allander K (1993) Parasites and the evolution of host social behavior. Adv Stud Behav 22:65–102

Nunn CL (2002) A comparative study of leukocyte counts and disease risk in primates. Evolution 56:177–190

Nunn CL, Dokey ATW (2006) Ranging patterns and parasitism in primates. Biol Lett 2:351–354

Nunn CL, Gittleman JL, Antonovics J (2000) Promiscuity and the primate immune system. Science 290:1168–1170

Osorio D, García-Hernández J, García-Prieto L, Romero-Callejas E (2009) Métodos de diagnóstico parasicológico mediante técnicas no invasivas en antropoides no humanos. Instituto de Biología. UNAM Press, Mexico city, pp 1–10

Smith JD (1970) The systematic status of the black howler monkey, *Alouatta pigra* Lawrence. J Mamm 51:358–369

Snaith TV, Chapman CA, Rothman JM, Wasserman MD (2008) Bigger groups have fewer parasites and similar cortisol levels: a multi-group analysis in red colobus monkeys. Am J Primatol 70:1–9

Stoner KE (1996) Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implications for conservation. Conserv Biol 10:539–546

Stoner KE, González-Di Pierro AM (2005) Intestinal parasitic infections in *Alouatta pigra* in tropical rainforest in Lacandona, Chiapas, Mexico: implications for behavioral ecology and conservation. In: Estrada A, Garber PA, Pavelka MSM, Luecke L (eds) New perspectives in the study of mesoamerican primates: distribution, ecology, behavior and conservation. Springer, New York, pp 215–240

Stuart MD, Strier KB (1995) Primates and parasites: a case for a multidisciplinary approach. Int J Primatol 16:577–593

Stuart MD, Greenspan LL, Glander KE, Clarke MR (1990) A coprological survey of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. J Wildl Dis 25:547–549

Trejo-Macías G, Estrada A, Mosqueda-Cabrera MA (2007) Survey of helminth parasites in populations of *Alouatta palliata mexicana* and *A. pigra* in continuous and in fragmented habitat in southern Mexico. Int J Primatol 28:931–945

Valdespino C, Rico-Hernández G, Mandujano S (2010) Gastrointestinal parasites of howler monkeys (*Alouatta palliata*) inhabiting the fragmented landscape of the Santa Martha mountain range, Veracruz, Mexico. Am J Primatol 72:539–548

Vitazkova SK, Wade SE (2006) Parasites of free-ranging black howler monkeys (*Alouatta pigra*) from Belize and Mexico. Am J Primatol 68:1089–1097

Vitone ND, Altizer S, Nunn CL (2004) Body size, diet and sociality influence species richness of parasitic worms in anthropoid primates. Evol Ecol Res 6:183–199