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GASTROINTESTINAL PARASITES OF OWL MONKEYS (*AOTUS AZARAI AZARAI*) IN THE ARGENTINEAN CHACO

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Abstract

In fragmented habitats, an increase in the proportion of available forest edge has been positively correlated to parasite richness. We evaluated how the presence of forest edge may affect parasite-host dynamics in a population of wild owl monkeys (*Aotus azarai azarai*) in an unlogged gallery forest in Formosa, Argentina. We collected 53 fecal samples from groups inhabiting edge territories (n = 7 groups, 33 samples) and groups inhabiting the interior of the forest (n = 3 groups, 15 samples). We compared the number of parasite species (richness) found between the two types of groups, as well as the frequency of samples with multiple infections (more than one parasite species in the sample) and the distribution of helminths on the forest floor between habitat types. The number of parasite species, the proportion of samples with multiple infections and the helminth distribution were not significantly different across the two habitat types.

Key words: Forest fragmentation; parasite richness; owl monkeys; gastrointestinal parasites; helminths; gallery forest.

Resumen

En hábitats fragmentados, un incremento en la proporción de borde de bosque ha sido correlacionado con la riqueza de parásitos. Evaluamos cómo la presencia de borde de bosque puede afectar la dinámica de parasite-hospedero en una población silvestre de monos de noche (*Aotus azarai azarai*) en un bosque de galería no perturbado en Formosa, Argentina. Colectamos 53 muestras de heces fecales de grupos que habitaban territorios en el borde del bosque (n = 7 grupos, 33 muestras) y grupos habitando al interior del bosque (n = 3 grupos, 15 muestras). Comparamos el número de especies de parásitos (riqueza) encontrado entre los dos tipos de grupos, así como la frecuencia de muestras con múltiples infecciones (más de una especie de parásito en la muestra) y la distribución de helmintos en el suelo del bosque entre tipos de hábitat. El número de especies de parásitos, la proporción de muestras con múltiples infecciones y la distribución de helmintos no fue significativamente diferente entre los dos tipos de hábitat.

Palabras clave: Fragmentación del bosque; riqueza de parásitos; monos de noche; parásitos gastrointestinales; helmintos; bosque de galería.

Introduction

The effects of logging or other anthropogenic alterations to the landscape that result in forest fragmentation have been linked to changes in host-parasite dynamics in primates (Chapman *et al.*, 2005; Gillespie & Chapman, 2005; Gillespie & Chapman, 2008). Studies of the effect of logging on African primates have shown changes in parasite richness (e.g. total number of parasite species), as well as parasite prevalence and host density (Chapman *et al.*, 2000; Gillespie *et al.*, 2005; Chapman *et al.*, 2006a). The process of forest fragmentation affects animal communities by reducing food availability, increasing host densities and increasing risk of pathogen transmission (Milton, 1996;

Püttker *et al.*, 2006). To better understand the natural dynamics of parasite-host interactions in primates inhabiting fragmented forests it is useful to examine primate communities living in fragmented landscapes that are the result of natural processes. These studies can provide insights into the ability of animals to cope with their naturally changing environment and therefore their potential future reactions to human-induced fragmentation. The eastern Argentinean Chaco is a fragmented landscape consisting of a matrix of palm savannahs and wetlands dotted by forest islands and transected by gallery forests growing along rivers. Howler monkeys and owl monkeys live sympatrically throughout this fragmented landscape (Zunino *et al.*, 1985; Brown & Zunino, 1994; Zunino *et al.*, 2001).

Owl monkeys are medium-sized monogamous primates that live in small social groups (2–6 individuals) composed of a reproductive pair and their offspring (Fernandez-Duque, 2001). They are omnivores and forage for a variety of fruit, leaves, invertebrates and, occasionally, vertebrates (Fernandez-Duque, 2007). Taxonomists currently recognize at least eight owl monkey species, in a genus that is widely distributed from Panamá to northern Argentina (Hershkovitz, 1983; Ford, 1994). The southernmost species *Aotus azarai* is found near the Paraguayan and Argentinean borders and it is unique within the genus because of its cathemeral habits. *Aotus azarai* displays a lapse of activity during the day that varies in length and time depending on moon phase and temperature (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006). In the Eastern Chaco, the species is regularly found in gallery forests adjacent to rivers, as well as forest islands that are surrounded by grasslands. The territories of owl monkey groups have either an edge with the grassland and/or river, or have no edge because they are adjacent to other owl monkey territories. All territories overlap with neighboring territories.

The owl monkey population of the Guaycolec Ranch in the eastern Argentinean Chaco has been studied since 1997. The existing information from groups holding territories with and without edge does not suggest any profound differences in demography or behavior (Fernandez-Duque *et al.*, 2001). Although there have been some reports of gastrointestinal parasites infecting owl monkeys (Diaz-Ungria, 1965; Thatcher & Porter, 1968; Wolff, 1990; Michaud *et al.*, 2003; Phillips *et al.*, 2004), we currently have no information on the gastrointestinal parasites found in *A. azarai* from northern Argentina. We also do not know whether the edge and non-edge groups differ in the nature of their interactions with parasites.

The main goal of our study was to describe the gastrointestinal parasites found in the Guaycolec owl monkey population, and to determine if there is a difference in the host-parasite interactions between edge and non-edge territories. Given that owl monkeys live in a naturally fragmented forest where the increase or appearance of edges in the forest has been the result of a slow natural process, we hypothesize that the monkey population may have adapted accordingly. Therefore, we predict no differences in the parasitology of edge and non-edge territories. To test our prediction, we compared the total number of parasite species in each habitat, and the proportion of individuals with multiple infections (i. e. more than one parasite species per sample) between the two habitat types; parameters that have been related to mortality and morbidity of primate populations and linked to compromised nutritional status (Chapman *et al.*, 2006b). We also compared the overall distribution of helminth parasites on the forest floor using soil samples in order to test for any differences between habitat types (Gillespie *et al.*, 2005).

Methods

Area of study and subjects

The area of study is part of an undisturbed section of the ranch Estancia Guaycolec (58°11' W, 25°58' S). The Estancia Guaycolec is a 25,000-hectare cattle ranch located in the Argentinean Gran Chaco. The forest is highly seasonal with fluctuating rainfall, temperature, photoperiod, and food availability (Fernandez-Duque *et al.*, 2002). Mean temperatures range from 16°C in the winter months (May–August) to 27°C during the summer months (December–March) (Fernandez-Duque *et al.*, 2002). This forest is characterized by starkly contrasting edge habitats formed at the boundaries of forest with grasslands and the surrounding river (Fig. 1). Owl monkeys residing within this forest have been studied extensively since 1996, which facilitated the identification and location of the different owl monkey groups.

Fecal sample collection

We collected fecal samples both from individuals in social groups and from solitary individuals. During July–August 2007, we collected weekly samples from individuals within social groups and from solitary individuals opportunistically as we encountered them in the forest. These solitary individuals may travel across various territories containing or lacking edges, therefore their samples could not be used for comparisons between habitats. If the identity of the individual providing the sample was unknown, only the group identity was recorded. Otherwise, the sex, age and group composition were noted. In a few cases the identity of the individual defecating was not determined which might have led to a sampling bias of some individuals and potential pseudoreplication. Comparisons were done with and without considering the samples from unknown individuals.

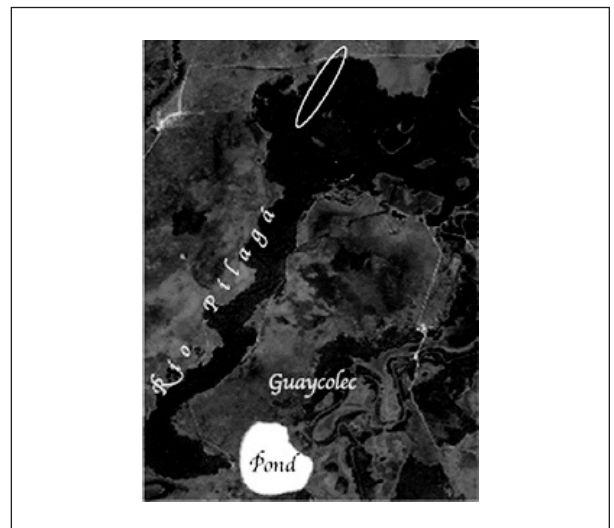


Figure 1. Area of study and sampled territories. White and black circles delineate edge and non-edge territories respectively.

To evaluate the potential relationship between parasite richness and forest structure we collected samples from individuals living in edge (n=7 groups) and non-edge groups (n=3), as well as soil samples from the corresponding territories (n=5 edge, n=2 non-edge). We defined an edge territory as a territory immediately or partially adjacent to the grasslands and/or the river boundaries. A non-edge territory on the other hand, is only adjacent to other owl monkey territories.

We collected fecal samples immediately after defecation and preserved them in 10% formalin. We gathered qualitative information about the fecal sample (e.g. color, consistency) at the time of collection. The fecal samples were processed using flotation and sedimentation techniques (Sloss *et al.*, 2004) at the Parasitology Laboratory in the National University of the Northeast (UNNE) in Corrientes, Argentina. Each sample was evaluated for presence or absence of parasites based on morphological characteristics. Color, size and shape of ova, cysts, larvae or adult parasites were some of the parameters used to identify each parasite species. In cases where multiple samples from the same individual were collected, parasitic diversity was compared among samples to determine any possible intra-specific variation. Soil samples were collected using V-shaped transects and analyzed immediately for helminth larvae and ova using both sedimentation and flotation techniques (Sievers *et al.*, 2007).

Data analyses

We used the following three parameters to evaluate potential differences between edge and non-edge territories; 1) mean number of parasite species (i.e. parasite diversity, Mann-Whitney U test), 2) number of samples with multiple parasitic infections (i.e. more than one gastro-intestinal parasite found, Chi-square test) and 3) number of soil samples containing helminths (Chi-square test).

Results

We collected and processed 32 fecal samples from 23 individuals and 16 samples from several unidentifiable individuals from 10 social groups. We also collected five fecal samples from five solitary individuals. The majority of the samples (92%, n=49) contained parasites and more than half of them (60%, n=32) had multiple infections. When the samples from unknown individuals were excluded from the analyses the percentages did not change markedly: 94% of samples contained parasites and 58% of them had multiple infections. Five of the 7 individuals sampled more than once showed intra-specific variation in parasitic diversity with a tendency to higher parasitic diversity in early winter. The parasite diversity consisted of four helminth and six protozoan species (Table 1). Diversity was different between social groups and solitary individuals. Fecal samples collected from social groups presented all four helminths and protozoa species, whereas samples from solitary individuals did not contain any *Uncinaria* sp, *Blastocystis* sp and *Taenia* sp. This apparent difference may be a result of the uneven sampling of social and solitary individuals.

There were some qualitative differences in the parasite species found in 15 samples from individuals living in edge territories (n=9 individuals from n=7 territories) and in 33 samples from non-edge ones (n=14 individuals from n=3 territories). *Entamoeba* sp was only associated with edge territories, whereas *Taenia* sp and the unidentified amoeba were found only in samples from individuals living in non-edge territories. The mean number of parasite species in edge and non-edge groups did not differ significantly (U=215, n₁=7, n₂= 3, z=-0.75, p=0.45) and the lack of statistical difference persisted when we excluded samples from unknown individuals (U=124, p=0.94). Qualitative differences of parasite diversity also remained unchanged after excluding samples from unknown individuals.

Table 1. Parasite count and percentage of samples containing each parasite species.

Parasite	Social/edge	Social/non-edge	Solitary	Total samples (percent)
<i>Strongyloides</i> sp.	6	9	1	16 (30%)
<i>Uncinaria</i> sp.	8	1	0	9 (17%)
<i>Taenia</i> sp.	1	0	0	1 (2%)
<i>Trypanoxyrius</i> sp.	5	6	1	12 (23%)
<i>Entamoeba</i> sp.	0	11	1	12 (23%)
<i>Blastocystis</i> sp.	2	12	0	14 (26%)
<i>Isospora</i> sp.	7	14	3	24 (45%)
<i>Giarda</i> sp.	1	2	1	4 (8%)
<i>Endolimax nana</i>	3	7	2	12 (23%)
Unspecified amoeba	1	0	1	2 (4%)
Total (number of samples)	34	62	10	106

Edge and non-edge territories did not differ significantly in the presence of parasite species per sample nor in the number of samples with multiple infections. More than half of the samples collected from edge and non-edge territories had multiple infections (60% and 58% respectively; $\chi^2 = 0.25$, $df = 1$, $P = 0.565$). These comparisons remained unchanged when "Unknown" samples were excluded (62% and 50% respectively; $\chi^2 = 0.43$, $df = 1$, $P = 0.512$). The percentage of soil samples with helminths was not different in edge (36%, $n = 15$) and non-edge territories (27%, $n = 8$) ($\chi^2 = 0.039$, $df = 1$, $P > 0.843$).

Discussion

This is the first report on the gastrointestinal parasites of free-ranging *Aotus azarai* from Formosa, Argentina. The study includes data on parasites already described for *Aotus* such as *Strongyloides* sp., *Giardia* sp., *Trypanoxyrius* sp., *Entamoeba* sp., *Endolimax nana*, *Isoospora* sp. (Tantalean & Gozalo, 1994), and the first report for *Blastocystis* sp. As predicted our data did not show any marked quantitative differences between edge and non-edge territories in the number of parasite species found. This result could be due to a relatively small sample size, but it is also possible that the dramatic variation in rainfall characteristic of the region that regularly leads to the flooding of sections of the forest far from the river may reduce differences between the two habitats we compared.

The parasite richness in the population was relatively high when compared with other primates of similar size. A survey of the gastrointestinal parasites of six primate species of Tambopata National Park in Perú showed that medium to small-sized primates (*Callicebus brunneus*, *Cebus albifrons*, *Cebus apella*, *Saguinus fuscicollis*, *Saimiri sciureus*, and *Aotus vociferans*) had a maximum of 5 parasite species (Phillips *et al.*, 2004). A similar study of the sympatric howler monkeys (*Alouatta caraya*) found that this gregarious species living in a series of highly fragmented and continuous gallery forests had lower parasite richness (Santa Cruz *et al.*, 2000) than the one we report here for owl monkeys. Howler monkeys are larger than owl monkeys and live in large multi-male multi-female groups. It is possible that howlers experience a higher parasitic diversity because they provide a larger variety of niches for parasites and they have a higher risk of transmission and infection due to their sociality (Kuris *et al.*, 1980; Moller *et al.*, 1993; Altizer *et al.*, 2003). It has been proposed that leaf-eating primates, such as howler monkeys, may experience a higher parasitic diversity because the large volumes of plant matter ingested contain infective-stage pathogens (Vitone *et al.*, 2004).

To date, most studies that have examined the relationships between host body mass, host sociality and parasite diversity have yielded conflicting results because of the complex effects of phylogeny in these interactions (Arneberg *et al.*, 1998; Morand & Poulin, 1998; Nunn *et*

al., 2003; Cote & Poulin, 1995). In the future, further sampling of additional groups in the population, of other populations in the region and of other sympatric mammals in the area will contribute to better understand the possible sources of relatively high parasite diversity in owl monkeys.

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References

- Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M., and Pulliam, J. R. C. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. S.* 34: 517–547.
- Arneberg, P., Skorping, A., Grenfell, B., and Read, A. F. 1998. Host densities as determinants of abundance in parasite communities. *P. R. Soc. Lon. B. Bio.* 265: 1283–1289.
- Brown, A. D., and Zunino, G. E. 1994. Hábitat, distribución y problemas de conservación de los primates de la Argentina. *Vida Silvestre Neotropical* 3:30–40.
- Chapman, C. A., Gillespie, T. R., and Goldberg, T. L. 2005. Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions? *Evol. Anthropol.* 14: 134–144.
- Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., and Struhsaker, T. T. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14: 207–217.
- Chapman, C. A., Speirs, M. L., Gillespie, T. R., Holland, T., and Austad, K. M. 2006a. Life on the edge: Gastrointestinal parasites from the forest edge and interior primate groups. *Am. J. Primatol.* 68: 397–409.
- Chapman, C. A., Wasserman, M. D., Gillespie, T. R., Speirs, M. L., Lawes, M. J., Saj, T. L., and Zeigler, T. E. 2006b. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *Am. J. Phys. Anthropol.* 131: 525–534.

- Cote, I. M., and Poulin, R. 1995. Parasitism and group size in social animals: A meta-analysis. *Behav. Ecol.* 6: 159–162.
- Diaz-Ungria, C. 1965. Nematodes de primates Venezolanos. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 25: 393–398.
- Fernandez-Duque, E. 2003. Influences of moonlight, ambient temperature and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behav. Ecol. Sociobiol.* 54: 431–440.
- Fernandez-Duque, E. 2007. *Aotinae*: Social monogamy in the only nocturnal haplorhines. In: *Primates in Perspective*, C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder (eds.), pp 139–154. New York, Oxford Univ Press.
- Fernandez-Duque, E., and Erkert, H. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. *Folia Primatol.* 77: 123–138.
- Fernandez-Duque, E., Rotundo, M., and Sloan, C. 2001. Density and population structure of owl monkeys (*Aotus azarai*) in the Argentinean Chaco. *Am. J. Primatol.* 53: 99–108.
- Fernandez-Duque, E., Rotundo, M., and Ramirez-Llorenz, P. 2002. Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the Argentinean Chaco. *Int. J. Primatol.* 23: 639–656.
- Ford, S. M. 1994. Taxonomy and distribution of the owl monkey. In *Aotus: The Owl Monkey*, J. F. Baer, R. E. Weller, and I. Kakoma (eds.), pp 1–57. San Diego, Academic Press.
- Gillespie, T. R., and Chapman, C. A. 2005. Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. *Cons. Biol.* 20: 441–448.
- Gillespie, T. R., and Chapman, C. A. 2008. Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interaction relative to an unfragmented forest. *Am. J. Primatol.* 70: 22–230.
- Gillespie, T. R., Chapman, C. A., and Greiner, E. C. 2005. Effects of logging in gastrointestinal parasite infection and infection risk in African primates. *J. Appl. Ecol.* 42: 699–707.
- Hershkovitz, P. 1983. Two new species of night monkeys, genus *Aotus* (Cebidae, Primates): A preliminary report on *Aotus* taxonomy. *Am. J. Primatol.* 4: 209–243.
- Kuris, A. M., Blaustein, A. R., and Alio, J. J. 1980. Hosts as islands. *Am. Nat.* 116: 570–586.
- Michaud, C., Tantalean, M., Ique, C., Montoya, E., and Gozalo, A. 2003. A survey for helminth parasites in feral New World non-human primate populations and its comparison with parasitological data from man in the region. *J. Med. Primatol.* 32: 341–345.
- Milton, K. 1996. Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler (*Alouatta palliata*) population in Panama. *J. of Zool.* 239: 39–63.
- Moller, A. P., Dufva, R. and, Allender, K. 1993. Parasites and the evolution of host social behavior. *Adv. Stud. Behav.* 22:65–102.
- Morand, S., and Poulin, R. 1998. Density, body mass and parasite species richness of terrestrial mammals. *Evol. Ecol.* 12: 717–727.
- Nunn, C. L., Altizer, S., Jones, K. E., and Sechrest, W. 2003. Comparative tests of parasite richness in primates. *Am. Nat.* 162: 597–614.
- Phillips, K. A., Haas, M. E., Grafton, B. W., and Yrivarren, M. 2004. Survey of the gastrointestinal parasites of the primate community at Tambopata National Reserve, Perú. *J. of Zool.* 264: 149–151.
- Püttker, T., Meyer-Lucht, Y., and Sommer, S. 2006. Effects of fragmentation on parasite burden (nematodes) of generalist and specialist small mammal species in secondary forest fragments of the coastal Atlantic forest, Brazil. *Ecol Res* 23: 207–215.
- Santa-Cruz, A. C. M., Toribio-Borda, J., Patiño, E. M., Gomez, L., and Zunino, G. E. 2000. Habitat fragmentation and parasitism in howler monkeys (*Alouatta caraya*). *Neotrop. Primates* 8:146–148.
- Sievers, G., Amenabar, A., and Gadick, P. 2007. Comparación de cuatro sistemas de muestreo de tierra para determinar contaminación de áreas con huevos de *Toxocara canis*. *Parasitología Latinoamericana* 62: 67–71.
- Sloss, M. W., Kemp, R. L., and Zajac, A. M. 1994. *Veterinary clinical parasitology*. Ames, Iowa State University Press.
- Tantalean, M., Gozalo, A. 1994. Parasites of the *Aotus* monkey. In *Aotus: The Owl Monkey*, J. F. Baer, R. E. Weller, and I. Kakoma (eds.), pp 354–373. San Diego, Academic Press.
- Thatcher, V. E., and Porter, J. A. 1968. Some helminth parasites of Panamanian primates. *T. Am. Microsc. Soc.* 87: 186–196.
- Vitone, N.D., Altizer, S., and Nunn, C. L. 2004. Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. *Evol. Ecol. Res.* 6: 183–199.
- Wolff, P. L. 1990. Parasites of new world Primates: A review. *P. Am. Assoc. Zoo Vet.*: 87–94.
- Zunino, G. E., Galliari, C. A., and Colillas, O. J. 1985. Distribución y conservación del mirikina (*Aotus azarae*), en Argentina: resultados preliminares. *A Primatologia no Brasil* 2: 305–316.
- Zunino, G. E., Gonzalez, V., Kowalewski, M., and Bravo, S. P. 2001. *Alouatta caraya*: Relations among habitat, density and social organization. *Primate Report* 61: 37–46.