International Journal of Primatology, Vol. 27, No. 1, February 2006 (© 2006)
DOI: 10.1007/s10764-005-9010-3

Coprological Surveys of *Alouatta pigra* at Two Sites in Belize

Katherine A. Eckert,[1,7] Nina E. Hahn,[2] Andrew Genz,[3] Dawn M. Kitchen,[4] Michael D. Stuart,[5] Gary A. Averbeck,[6] Bert E. Stromberg,[6] and Hal Markowitz[1]

Received September 14, 2004; revision November 23, 2004; accepted November 23, 2004; Published Online March 18, 2006

Fecal samples were collected from black howler monkeys (Alouatta pigra) in north central Belize and analyzed for evidence of endoparasite life stages. At least six types of endoparasites were found in Alouatta pigra fecal samples collected in the Lamanai Archaeological Reserve and the Community Baboon Sanctuary in 1999. These include a digenean trematode, an oxyurid nematode, a strongyle-type nematode, an ascarid presumed to be Ascaris sp., Entamoeba coli and Iodamoeba bütschlii. Higher trematode prevalence was found in adult Alouatta pigra compared to juveniles and higher prevalence of nematode larvae in all animals was found in the wet season compared to the dry season.

KEY WORDS: *Alouatta pigra*; belize; disease; parasite prevalence.

[1]San Francisco State University, Department of Biology, San Francisco, California.
[2]University of California, Berkeley Office of Laboratory Animal Care, Berkeley, California.
[3]Office of Public Health, Louisiana Department of Health & Hospitals, New Orleans, Louisiana.
[4]The Ohio State University, Department of Anthropology, Columbus, Ohio.
[5]University of North Carolina, Asheville, Department of Biology, Asheville, North Carolina.
[6]University of Minnesota, Department of Veterinary and Biomedical Sciences, College of Veterinary Medicine, St. Paul, Minnesota.
[7]To whom correspondence should be addressed at Class of 2007, Office of the Dean Student Programs, School of Veterinary Medicine, University of California, One Shields Avenue, Davis, California 95616; e-mail: kaeckert@ucdavis.edu.

INTRODUCTION

Understanding the prevalence of parasitic infection is integral to the study of primate biology and conservation. As the number of endangered primate species increases, consideration of all potential sources of information about primates has become increasingly important to make informed conservation decisions and to understand their natural history (Stuart and Strier, 1995).

Mexican (Guatemalan) black howlers (*Alouatta pigra*) live in single or multimale, multifemale social groups throughout Belize, southern Mexico and eastern Guatemala. Though a locally abundant species, they have diminished across their historic range (Horwich and Johnson, 1986; Horwich *et al.*, 2001). *Alouatta pigra* is listed as endangered (EnA4c) in the IUCN Red List of Threatened Species (Cuarón *et al.*, 2003); therefore all information relevant to their ecology or biology is important for their continued conservation and management. In addition, the tendency of the species to inhabit forest fragments in proximity to human dwellings increases the importance of monitoring the baseline parasite load of black howlers, which may help indicate changing levels of disturbance or levels of zoonotic transfer of diseases. Though there are few published reports of parasites for wild *Alouatta pigra* (reviewed by Stuart *et al.*, 1998), one study identified the digenean fluke *Controchis biliophilus* in the bile ducts of *Alouatta pigra* from Mexico (Jimenéz-Quiros and Brenes, 1958).

We report on the prevalence of parasites detected in feces from wild *Alouatta pigra* living at 2 research sites in Belize: the Lamanai Archaeological Reserve (Lamanai) and the Community Baboon Sanctuary (CBS). Both are the sites of long-term research projects on howlers (Gavazzi, 1995; Horwich *et al.*, 2001) and destination sites for ecological or archaeological tourism or both (Grossberg *et al.*, 2003; Horwich, 1990) that border human communities; therefore most subjects are habituated to human presence and exposed to a high level of anthropogenic disturbance. We compare parasite prevalence with respect to age groups, sex, and, at Lamanai, the time of year samples were collected.

METHODS

Study Sites

The Lamanai Archeological Reserve (Lamanai; 17°46′N, 88°39′W) is a 385-ha tract of forest in the Orange Walk District of north central Belize. Lamanai's borders are the New River Lagoon to the east, milpas (small

farms) and some contiguous forest to the west, a tourist lodge and the village of Indian Church to the south, and more discontinuous forest to the north. The habitat is a combination of moist tropical lowland forest, broadleaf deciduous forest, and semi-evergreen seasonal forest (Gavazzi, 1995).

The Community Baboon Sanctuary (CBS) is located along a 32-km stretch of the Belize River (17°33N, 88°35′W) (Horwich, 1990). It is a community-owned sanctuary of 3300 ha. Samples were collected from CBS at the original 800-ha sanctuary site near the village of Bermudian Landing, *ca.* 15 km southeast of Lamanai. The land consists primarily of secondary riverine rain forest with areas of pine ridge, cohune palm, and mixed broadleaved forests as well as pastureland and milpa (Horwich and Lyons, 1988).

Subjects

Fecal samples were collected from *Alouatta pigra* at both Lamanai and CBS. Estimates of the population density of *Alouatta pigra* at Lamanai at the time of our survey ranged between 28 and 42 individuals/km^2 (Cornick and Markowitz, 2002; Treves, 2001). At CBS, the population density of *Alouatta pigra* increased from 142.86 ind/km^2 to 181.43 ind/km^2 between 1996 and 1997, the years during which we collected the fecal samples (Horwich *et al.*, 2001).

Sample Collection

Lamanai

Howler monkeys at Lamanai were categorized as adults (including subadult males), juveniles or infants using the size and behavioral guidelines established by Gavazzi (1995, see also Carpenter, 1934). Sexes were determined by visual observation of genitalia. Identification of individual animals was based on distinguishing characteristics including the presence of infants, bot fly infestation and scars. If two animals of the same sex and age class in the same troop were not clearly identifiable, samples from those animals were pooled. Troops sampled in both seasons were identified by the presence of one or more distinctive individuals, or were considered to be the same if troop composition was within one individual of the expected number and age/sex combination based on the previous season's census and home range information.

Data are reported for samples only from individuals that were identified to both age group and sex. When multiple samples were obtained from the same individual within one season, the results from each sample were combined and considered as one result for that animal in that season. For animals sampled in both seasons, the results for each season were compared separately.

Most samples were collected when troops were encountered opportunistically during trail surveys. Survey areas were selected daily based on the location of troops found that had not yet been sampled. In the absence of observed unsampled troops, surveys were conducted in parts of the reserve that had not yet been explored during that season.

When a troop was encountered, they were followed until fecal samples had been obtained from most or all of the troop members. Howler monkeys usually defecated after resting periods, and often several troop members would defecate simultaneously just after resuming activity. When defecations occurred, the location of the animal was noted and the feces underneath their location were collected. All fecal samples were collected using individual plastic bags to collect the sample, which were then inverted and labeled. Approximately one gram of feces was later placed in a 15 ml centrifuge tube containing 9ml of 10% buffered formalin. The period of time between collection of feces and preservation in formalin ranged from five minutes to several hours.

Samples were collected daily between 0530 and 1900 hrs, with troop contact time ranging between 45 minutes and eight hours per troop encounter over the course of one or two days. Dry season samples were collected over 56 days between January 24 and March 20, 1999. Wet season samples were collected over 46 days between June 4 and July 20, 1999 and over 50 days between October 4 and November 23.

CBS

The composition and home ranges of 15 troops of howler monkeys at CBS were known during this study and individuals within troops were identified using a combination of colored leg tags, size, and sex. Following defecation events of identified individuals, feces were immediately collected using a gloved hand and were preserved in a 10% formalin solution in 10 cc plastic vials upon collection.

Samples were all collected between 0630 and 1400 hours during two study seasons, first from January to March 1996, the second from March to June 1997 during a separate behavioral study (see Kitchen, 2004). Individuals were only sampled once in each period, with the exception of one

animal in 1996 and four animals in 1997 that were sampled twice. All but three samples were collected in the dry season. Of 68 animals sampled, 11 were sampled in both 1996 and 1997.

Fecal Analysis

Approximately half of each Lamanai fecal sample was concentrated via the formalin ethyl acetate sedimentation technique (Truant *et al.*, 1981) using Fecal Concentrator Kits® (Remel Co., Lexana, Kansas). Six wet mounts were made for each sample, using 1–2 drops of fecal sediment and 22 × 22 mm cover slips. These were scanned systematically at 100X, and all material in question was viewed at 400X. In addition, one sample from each animal was used to make two trichrome-stained slides. These slides were scanned initially at 400X, using 1000X oil immersion lens for close examination. Slide observation accuracy was compared between scans of the same slide using 400X and 100X, and once competency in reading trichrome stained slides at a magnification of 100X was reached, trichrome slides were scanned at 100X.

One gram of feces from each CBS sample was washed through a 61-μm, 250 mesh sieve into a 175 ml tapered beaker and was left to allow sedimentation of the supernatant. Every 15 minutes, one-third of the supernatant was decanted. Once the liquid was clear, the sediment was centrifuged and examined under 100X magnification.

Statistical Analysis

We used nonparametric tests to examine differences in parasite prevalence between groups. We did not make comparisons for prevalence of protista, strongyle-type nematode eggs, or oxyurid nematode eggs because of low numbers of samples that were positive for these parasites. We did not make any comparisons between CBS and Lamanai because of potential sampling and analysis biases. Tests were 2-tailed and we set the α level at 0.05. We used GraphPad Instat™ and SPSS 10.0™ software in the analysis.

RESULTS

The mean minimum and maximum temperatures and humidity during the collection period for Lamanai are in Table I. Weather data were not recorded at CBS.

Table I. 1999 Weather Data for Lamanai Outpost Lodge

Season	Average humidity (%)	Average minimum temp (°C)	Average maximum temp (°C)	Percent research days with rain
Dry (Jan–May)	83.5	20.0	31.7	25
Wet (June–Dec)	88.2	22.0	31.9	83.7

Fecal samples were collected from approximately 99 individual *A. pigra* from 22 troops at Lamanai; 26 of those animals were sample in both wet and dry seasons. Fecal samples were collected from 68 *A. pigra* in 15 troops at CBS during the two study periods. The results from Lamanai are in Table II and those from CBS are in Table III. We found artifacts including insect remains and miscellaneous plant material (pollen, fibers, etc.) in samples from both sites. We reported nematode larvae, a strongyle-type nematode egg (Fig. 1), trematode eggs (Fig. 2), and oxyurid eggs (Fig. 3)based on morphology and did not identify them further (Tables II and III).

We did not see differences in trematode prevalence between seasons at Lamanai or research periods at CBS, though the prevalence of trematode infection in juveniles was lower than that of adults, including subadults, at Lamanai (Fisher's exact test, $n = 61$ adults, 20 juveniles, $p = 0.0003$) and at CBS ($n = 54$ adults, 15 juveniles, $p = 0.0517$).

Though overall parasite infection at Lamanai and trematode infection alone did not differ between the wet and dry seasons, there is a significantly higher prevalence of larval nematode infections and combined infections

Table II. Parasites in Wild *Alouatta pigra* Tabulated by Age Class, Sex, and Season During 1999 at Lamanai, Belize

		Parasite prevalence: % infected (number of positive individuals)					
Monkey category	*n*	Trematode egg	Oxyurid egg	Nematode larvae	*Entamoeba* sp.	*Iodamoeba. bütschlii*	Multiple infections[b]
Total	99	80.8 (80)	3.6 (4)	37.4 (37)	12.1 (12)	2.0 (2)	31.3 (31)
Adults	61	93.4 (57)	3.3 (2)	41.0 (25)	14.8 (9)	1.6 (1)	37.7 (23)
Juveniles	32	62.5 (20)	6.3 (2)	31.3 (10)	9.4 (3)	3.1 (1)	21.8 (7)
Infants	6	33.3 (2)	0	33.3 (2)	0	0	16.7 (1)
Males	54	79.6 (43)	3.7 (2)	44.4 (24)	16.7 (9)	0	38.9 (21)
Females	45	82.2 (37)	4.4 (2)	26.6 (12)	6.7 (3)	4.4 (2)	22.2 (10)
Dry season[a]	48	68.8 (33)	0	16.7 (8)	10.4 (5)	2.1 (1)	10.4 (5)
Wet season[a]	77	83.1 (64)	5.2 (4)	42.8 (33)	13.0 (10)	1.3 (1)	36.4 (28)

[a] Includes animals repeated across both seasons.
[b] Concurrent infection with trematode and nonoxyurid nematode.

Table III. Parasites in Wild *Alouatta pigra* Tabulated by Age Class, Sex, and Year During Dry Seasons of 1996 and 1997 at CBS, Belize

Parasite prevalence: % infected (Number of positive individuals)					
Monkey category	*n*	Trematode egg	Nematode larvae	*Ascaris* sp.	Multiple infections[b]
Total	69	26.8 (19)	1.5 (1)[c]	4.3 (3)	4.3 (3)
Adults	54	33.3 (18)[c]	0	5.6 (3)[c]	3.7 (2)[c]
Juveniles	15[a]	6.7 (1)	6.7 (1)[c]	0	0
Males	39	30.8 (12)	2.6 (1)	7.7 (3)	7.7 (3)
Females	29	20.7 (6)	0	0	0
1996	26	26.9 (7)	0	3.8 (1)	0
1997	43	32.6 (14)	2.3 (1)	4.7 (2)	7.0 (3)

[a]Includes one distinct individual of undetermined sex.
[b]Includes infection with trematode and *Ascaris* sp. and/or nematode larvae.
[c]Includes at least 1 of 3 samples from the rainy season, collected after June 1, 1997.

with trematodes and larval nematodes in the wet season than in the dry season (Fisher's exact test, $n = 48$ individuals dry season, 77 individuals wet season, $p = 0.0031$ and 0.0015, resp.). We observed no significant difference in any parasite infection between sexes at either site.

DISCUSSION

The results of our surveys provide a baseline for future assessment of parasite prevalence in 2 populations of *Alouatta pigra* in Belize. Unfortunately, because no adult nematodes and trematodes were available, we

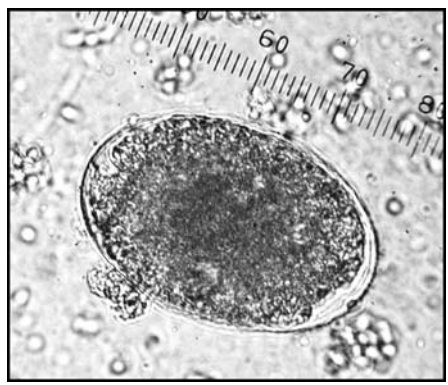

Fig. 1. Strongyle type egg from a black howler, from Lamanai. Magnification: ×400; scale: 1 unit = 2.6 μm.

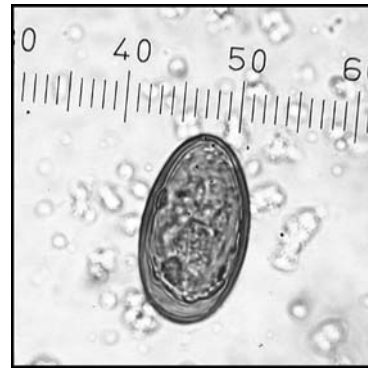

Fig. 2. Digenean trematode egg from a black howler at Lamanai. Magnification: × 400; scale: 1 unit = 2.6 μm. Egg length ranged from 31.2 to 52 μm, width from19.6 to 28.6 μm ($n = 342$).

were able to identify only the protozoan parasites to species. We identified both *Entamoeba coli* and *Iodamoeba bütschlii* in *Alouatta pigra*. Both are found in many species of primates, including humans, and generally considered to be nonpathogenic (Toft and Eberhard, 1998).

We found oxyurids in Lamanai, but not CBS howlers. Oxyurid life cycles typically involve the adults emerging from the anus to lay eggs in the perianal area (Marquardt *et al.*, 2000); it is not uncommon for ova to be absent from the stools of infected individuals. Stuart *et al.* (1990) found that while only 22% of fecal samples from *Alouatta palliata* contained eggs of the oxyurid *Trypanoxyuris* sp., physical inspection of their perinea showed that 100% of the monkeys were infected with pinworm. It is therefore likely that we have underestimated the prevalence of oxyurids in the population at Lamanai.

The increased prevalence of nematode larvae in the wet season compared to the dry season at Lamanai is similar to results in other studies; higher humidity may promote survival of parasite intermediates (Stoner, 1995; Stuart *et al.*, 1990, 1993;).

None of the parasites in *Alouatta pigra* at Lamanai give any evidence for a role of contamination from anthropogenic sources, despite a high rate of tourism disturbance (Grossberg *et al.*, 2003; Treves *et al.*, 2001) and adjacent human settlements and agriculture. However, researchers have identified *Ascaris lumbricoides* in *Alouatta palliata* (Stuart *et al.*, 1990), so the finding of ascarid eggs in *Alouatta pigra* at CBS warrants follow-up studies to determine if it is *Ascaris lumbricoides*. Unlike the Lamanai

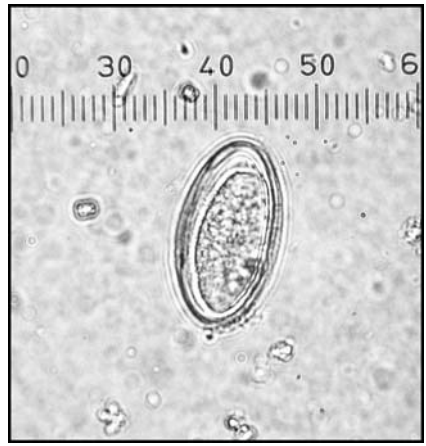

Fig. 3. Oxyurid egg seen in the feces of a black howler monkey, *Alouatta pigra* at Lamanai. Magnification: × 400; scale: 1 unit = 2.6 μm. Egg length ranged from 45.1 to 52.0 μm, width from 23.4 to 29.7 μm (n = 24).

Alouatta pigra, which one rarely sees coming to the ground, *Alouatta pigra* at CBS frequently come to the ground to travel between fragments or patches of forest (Marsh, 2000). Contact with the ground increases the likelihood of fecal–oral parasite transmission from livestock or human waste, and may be associated with contamination from those sources (Stuart *et al.*, 1990).

The higher rates of trematode infection in adults compared with juveniles in both populations of *Alouatta pigra* is somewhat surprising; younger animals are typically host to more parasites than are adults (Mueller-Graf *et al.*, 1997). However, it is consistent with the findings of Stuart *et al.* (1998), who reported a lower prevalence of infection with the trematode *Controrchis biliophilus* in juvenile *Alouatta palliata* than in adults. In our studies, this may be an artifact of sampling bias in that we sampled a smaller number of juveniles overall and there were more samples per individual in the adult category at both sites. Unfortunately, the question of variable parasite transmission in the different age categories cannot be properly addressed without a confirmed identification and information about the ecology and life cycle of the trematode we found in *Alouatta pigra*. No information is currently available that would allow any speculation on that point, because the life cycle of *Controrchis biliophilus* is still unknown, and

digenean trematodes typically have life cycles that involve one or more specific intermediate hosts.

Fecal parasite surveys of primates provide a valuable resource for studying ecological relationships between the primates and their environment. These surveys are noninvasive and can be repeated over time with minimal investment of resources. Changes in patterns of fecal parasites may reflect differences in parasite transmission both between congeneric groups and with humans, host dietary preferences, and habitat utilization (Hahn *et al.*, 2003; Stuart *et al.*, 1998). However, prevalence data represent isolated "snapshots" in time and not the actual dynamics of parasite–host interactions; changes in prevalence may be associated with changes in physiological, behavioral, or other unidentified factors. Furthermore, we cannot determine the relevance of the parasites described to the overall health of the individuals in our study. De Thoisey *et al.* (2001) describe little correlation between digestive system parasitism and clinical status in translocated red howlers, (*Alouatta seniculus*); however, their ability to examine individuals and evaluate hematological parameters were not available for either of our surveys.

The most important and necessary future work will be to identify the adult forms of the howler parasites and to confirm differences between howler adults and juveniles. To do so it will be necessary to obtain tissue and/or fecal samples containing adult organisms from Belizean *Alouatta pigra*, followed by a great deal of investigation to determine their life cycles, including the identity of any intermediate hosts. In addition, though sampling differences precluded statistical comparisons between Lamanai and CBS, perusal of the data suggests population or seasonal variability in parasites or both, which warrant further investigation.

ACKNOWLEDGMENTS

K. A. Eckert and H. Markowitz thank Oceanic Society Expeditions and M. Howells at the Lamanai Field Research Center in Belize for providing funding, research assistants, accommodations, and logistical assistance with this project. B. Cruz and C. Godoy provided field, laboratory, and manuscript preparation assistance at Lamanai; G. Antipa, G. Lum, S. Garcia, and S. Hochide at San Francisco State University (SFSU); M. Eberhard of the Centers for Disease Control in Atlanta, GA; and T. Rainwater of Texas Tech University. D. M. Kitchen and A. Genz would like to thank the residents of Bermudian Landing for friendship and access to private lands and N. Grindheim, M. Joseph, S. Kenney, C. Vögt, and

N. Weber for field assistance. For funding, K. A. Eckert thanks the Graduate Assistantship in Areas of National Need, the College of Science and Engineering, and the Department of Biology at SFSU and the SFSU Conservation Fund, which M. Vasey. Dayton & Wilkie Natural History Grants, UMN Grants for Research Abroad, UMN Department of Ecology, Evolution and Behavior provided funding for Dawn M. Kitchen. Finally we thank The Belize Forestry Department and Minister of Agriculture for allowing research at the Lamanai site and CBS management for permission to conduct research at the Bermudian Landing site.

REFERENCES

Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psych. Monogr*. 10: 1–168.

Cornick, L. A., and Markowitz, H. (2002). Diurnal vocal patterns of the black howler monkey (*Alouatta pigra*) at Lamanai, Belize. *J. Mammal*. 83: 159–166.

Cuarón, A. D., de Grammont, P. C., Cortés-Ortiz, L., Wong, G., Silva, J. C. S., Rylands, A. B., and Mittermeier, R. A. (2003). IUCN Red List of Threatened Species Assessment and Evaluation of *Alouatta pigra*. http://www.redlist.org/search/details.php?species = 914.

de Thoisey, B., Vogel, I., Reynes, J. M., Pouliquen, J. F., Carme, B., Kazanji, B., and Vie, J. C. (2001). Health evaluation of translocated free-ranging primates in French Guiana. *Am. J. Primatol.* 54: 1–16.

Gavazzi, A. (1995). Ecology of the black howler monkey (*Alouatta pigra*) at Lamanai, Belize. Masters Thesis, San Francisco State University, San Francisco, CA.

Grossberg, R., Treves, A., and Naughton-Treves, L. (2003). The incidental ecotourist: Measuring visitor impacts on endangered howler monkeys at a Belizean archaeological site. *Environ. Conserv*. 30: 40–51.

Hahn, N. E., Proulx, D., Muruthi, P. M., Alberts, S. A., and Altmann, J. (2003). Gastrointestinal parasites in free-ranging Kenyan baboons (*Papio cynocephalus* and *P. anubis*). *Int. J. Primatol*. 24: 271–279.

Horwich, R. H. (1990). How to develop a community sanctuary: An experimental approach to the conservation of private lands. *Oryx* 24: 95–102.

Horwich, R. H., and Johnson, E. D. (1986). Geographical distribution of the black howler (*Alouatta pigra*) in Central America. *Primates* 27: 53–62.

Horwich, R. H., Brockett, R. C., James, R. A., and Jones, C. B. (2001). Population growth in the Belizean black howling monkey (*Alouatta pigra*). *Neotrop. Primates* 9: 1–7.

Horwich, R. H., and Lyons, J. (1988). Experimental technique for the conservation of private lands. *J. Med. Primatol.* 17: 169–176.

Jimenéz-Quiros, O., and Brenes, R. R. (1958). Nota sobre el Trematodo *Controrchis caballeroi* Jimenéz y Brenes, 1957. *Rev. Biol. Trop*. 6: 189–190.

Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: Effect of numeric odds, male companion behaviour, and reproductive investment. *Anim. Behav.* 67: 125–139.

Marquardt, W. C., Demaree, R. S., and Grieve, R. B. (2000). *Parasitology and Vector Biology*, Harcourt/Academic Press, Orlando, FL, pp. 445–458.

Marsh, L. K. (2000). Ecological effect of the black howler monkey (*Alouatta pigra*) on fragmented forests in the Community Baboon Sanctuary, Belize. Doctoral dissertation, Washington University, St. Louis, MO.

Mueller-Graf, C. D. M., Collins, D. A., Packer, C., and Woolhouse, M. E. J. (1997). *Schistosoma mansoni* infection in a natural population of olive baboons (*Papio*

cynocephalus anubis) in Gombe Stream National Park, Tanzania. *Parasitology* 115: 621–627.

Stoner, K. E. (1995). Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: Implications for conservation biology. *Conserv. Biol.* 10: 539–546.

Stuart, M. D., Greenspan, L. L., Glander, K. E., and Clarke, M. R. (1990). A coprological survey of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. *J. Wildl. Dis*. 26: 547–549.

Stuart, M. D., Pendergast, V., Rumfelt, S., Pierberg, S., Greenspan, L., Glander, K. E., and Clarke, M. R. (1998). Parasites of wild howlers (*Alouatta* spp.). *Int. J. Primatol.* 19: 493–512.

Stuart, M. D., and Strier, K. B. (1995). Primates and parasites: A case for a multidisciplinary approach. *Int. J. Primatol*. 16: 577–593.

Stuart, M. D., Strier, K. B., and Pierberg, S. M. (1993). A coprological survey of parasites of wild muriquis, *Brachyteles arachnoides*, and brown howling monkeys, *Alouatta fusca*. *J. Helminthol. Soc. Wash.* 60: 111–115.

Toft II, J. D., and Eberhard, M. L. (1998). Parasitic diseases. In Bennet, B. T., Abee, C. R., and Henrickson, R. (eds.), *Nonhuman Primates in Biomedical Research: Diseases*. Academic Press, San Diego, CA, pp. 116–117.

Treves, A. (2001). Reproductive consequences of variation in the composition of howler monkey groups. *Behav. Ecol. Sociobiol*. 50: 61–71.

Treves, A., Drescher, A., and Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behav. Ecol. Sociobiol*. 50: 90–95.

Truant, A., Elliot, S. H., Kelly, M. T., and Smith, J. H. (1981). Comparison of formalin-ethyl ether sedimentation, formalin-ethyl acetate sedimentation, and zinc sulfate flotation techniques for detection of intestinal parasites. *J. Clin. Microbiol*. 13: 882–884.