GASTROINTESTINAL PARASITES OF THE GUENONS OF WESTERN UGANDA

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ABSTRACT: From January 1998 to December 2002, we collected 293 fecal samples from free-ranging individuals of the 4 guenon species of western Uganda, i.e., redtail guenons (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), l'hoesti monkeys (*Cercopithecus lhoesti*), and vervet monkeys (*Cercopithecus aethiops*), to quantify the prevalence of gastrointestinal parasites. Helminth eggs, larvae, and protozoan cysts were isolated by sodium nitrate flotation and fecal sedimentation. Helminth parasites were identified, and infection prevalence was determined for all 4 guenon species. Coprocultures facilitated identification of strongylate nematodes. For the most common species, the redtail guenon, we documented prevalence of protozoan parasites and examined the effect of season and host sex on infection prevalence. Six nematodes (*Strongyloides fulleborni*, *Oesophagostomum* sp., unidentified strongyle, *Trichuris* sp., *Streptopharagus* sp., and *Enterobius* sp.), 1 cestode (*Bertiella* sp.), 1 trematode (Dicrocoeliidae), and 5 protozoans (*Entamoeba coli*, *Entamoeba histolytica*, *Iodameoba butschlii*, *Giardia lamblia*, and *Chilomastix mesnili*) were detected. Seasonal patterns of infection were not readily apparent for any parasite species infecting redtail guenons. Although prevalence never differed between male and female guenons, only adult females were infected with *Oesophagostomum* sp. and *S. fulleborni*.

Cercopithecus spp. are the most diverse taxa of primates endemic to sub-Saharan Africa (Grubb et al., 2002). These frugivorous monkeys live in groups of 10–30 individuals and often form mixed-species associations with other primate species (Chapman and Chapman, 2000). Although guenons can be found in a wide variety of habitats, the majority inhabit tropical forests (Butynski, 2002). More than two-thirds of sub-Saharan Africa's original forest cover has been lost because of anthropogenic disturbance (World Resources Institute, 1998), and forest cover continues to decline at a rate of 0.7% annually (FAO, 1999). Largely because of resultant habitat loss, 26% of guenons are endangered (Butynski, 2002).

Although parasite infections are common in nature and low-intensity infections are often asymptomatic (Anderson and May, 1979; May and Anderson, 1979), anthropogenic change may result in a loss of stability associated with altered transmission rates, host range, and virulence (Daszak et al., 2000; Patz et al., 2000). Within this context, baseline data on patterns of parasitic infections in wild guenon populations are critical to provide an index of population health and to begin to assess and manage disease risks.

Although many studies have documented the gastrointestinal parasites of wild populations of African apes (Huffman et al., 1997; Graczyk et al., 1999; Ashford et al., 2000; Nizeyi et al., 1999; Lilly et al., 2002) and baboons (Appleton et al., 1986; Eley et al., 1989; Müller-Graf et al., 1997; Hahn et al., 2003), the gastrointestinal parasites of other African primate taxa remain poorly known. The present study identifies and quantifies the gastrointestinal helminth parasites for the 4 guenon species of western Uganda: redtail guenons (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), l'hoesti monkeys (*Cercopithecus lhoesti*), and vervet monkeys (*Cercopithecus aethiops*). For the most common species, the redtail guenon, we also report protozoan parasites and examine the effect of season and host sex on parasite prevalence.

MATERIALS AND METHODS

From January 1998 to December 2002, we collected 293 fecal samples from free-ranging guenons at forested sites in western Uganda: 235 from redtail guenons, 35 from blue monkeys, 11 from l'hoesti monkeys, and 12 from vervet monkeys. Samples from redtail guenons, blue monkeys, and l'hoesti monkeys were collected in Kanyawara, a 1,034-ha area characterized by logged and unlogged forest within Kibale National Park (766 km²; 0°13′−0°41′N, 0°19′−30°32′E; Struhsaker, 1997). Samples from vervet monkeys were collected at Lake Saka, a forest fragment 30 km northwest of the national park. The region experiences a bimodal pattern of seasonal rainfall, with peaks occurring in March–May and August–November (Fig. 1). Mean annual rainfall (1990–2001) is 1,749 mm (Chapman et al., 2002). Daily temperature minima and maxima averaged 14.9 and 20.2 C, respectively, from 1990 to 2001.

Samples were collected immediately after defecation to avoid contamination and examined macroscopically for adult nematodes and tapeworm proglottids. With the exception of redtail guenons, samples represent individuals. In the case of redtail guenons, samples are the result of repeated collections from approximately 150 animals. Samples were stored individually in 5.0-ml sterile vials in 10% neutral formalin solution. Preserved samples were transported to the University of Florida where they were examined for helminth eggs, larvae, and protozoan cysts using concentration by sodium nitrate flotation and fecal sedimentation (Sloss et al., 1994). Parasites were identified on the basis of egg or cyst color, shape, contents, and size (Jessee et al., 1970). Iodine was used to facilitate protozoan identification. Measurements were made to the nearest 0.1 μm ± SD, using an ocular micrometer fitted to a compound microscope, and representatives were photographed. Mean egg sizes presented are based on measurement of 10 eggs from 10 different hosts unless otherwise noted. Coprocultures (10 per guenon species except vervets) were used to match parasite eggs to larvae for positive identification of strongylate nematodes (MAFF, 1979). Our ability to identify most parasite species from host fecal examination, even with cultured larvae, is limited. Consequently, we present the majority of our findings at the level of family or genus.

We performed chi-square tests of independence to compare the prevalence of infections between redtail guenons and blue monkeys. Small sample size precluded us from including l'hoesti and vervet monkeys in these comparisons. Chi-square tests of independence were also performed to compare prevalence between host sex for redtail guenons and to compare prevalence for the blue monkey population with previously published reports. We used Pearson correlations to test for relationships between monthly rainfall and prevalence of parasites infecting redtail guenons.

RESULTS

Nematoda

Trichuroidea: Trichuris sp. was identified on the basis of egg size and morphology (barrel-shape, yellow-brown coloration, and bipolar plugs). Eggs were found in feces of all guenon
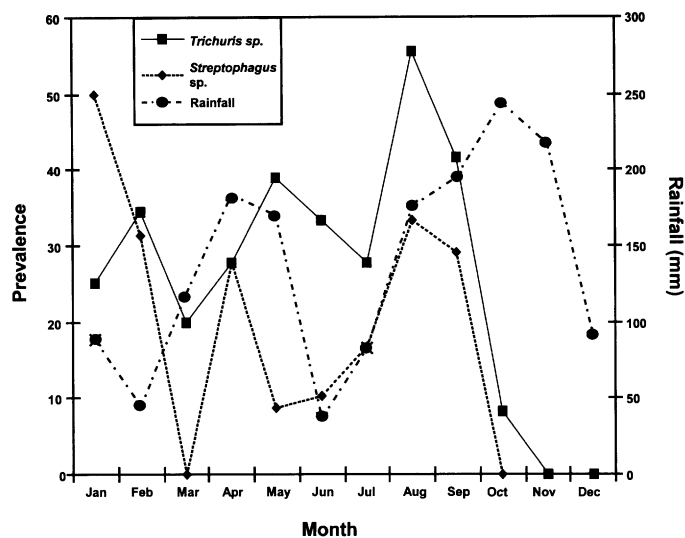
FIGURE 1. Intermonthly variation in parasite infection prevalence of redtail guenons and rainfall at Kibale National Park, Uganda.

species and measured 55.1 ± 1.2 × 27.2 ± 1.1 μm for redtail guenons, 60.0 ± 2.0 × 27.0 ± 1.4 μm for blue monkeys, 58.3 ± 1.2 × 27.1 ± 1.1 μm for l'hoesti monkeys, and 57.9 ± 1.4 × 26.7 ± 1.6 μm for vervets. Prevalence of infection with Trichuris sp. did not differ between redtail guenons (30%) and blue monkeys (26%) (P > 0.05, Table I).

Strongyloidea: Oesophagostomum sp. was identified on the basis of egg size and morphology (elliptical and unlarvated) and cultured larvae. Eggs were found in feces of all guenon species except vervets and measured 69.1 ± 1.8 × 42.4 ± 2.0 μm for redtail guenons, 70.5 ± 2.0 × 41.3 ± 1.7 μm for blue

monkeys, and 73.1 ± 1.2 × 43.0 ± 1.4 μm for l'hoesti monkeys. Prevalence of Oesophagostomum sp. did not differ (P > 0.05) between redtail guenons (10%) and blue monkeys (9%) (Table I). Unidentified strongyle eggs were found in vervet feces (42%) and measured 72–52 × 42–35 μm. These strongyles may represent Nectator sp., Ancylostoma sp., or Oesophagostomum sp. (or all); however, coprocultures were not performed, limiting our ability to identify these parasites.

Rhabditoidea: Strongyloides fulleborni was identified on the basis of egg size and morphology (oval, thin shelled, colorless, and embryonated) and verified by cultured rhabditiform larvae. Eggs were found in feces of all guenon species and measured 50.2 ± 2.3 × 33.7 ± 4.1 μm for redtail guenons, 43.7 ± 5.0 × 35.4 ± 3.1 μm for blue monkeys, 46.5 ± 3.4 × 34.6 ± 2.3 μm for l'hoesti monkeys, and 47.1 ± 3.7 × 34.4 ± 2.6 μm for vervets. Prevalence of infection with S. fulleborni did not differ between redtail guenons (7%) and blue monkeys (6%) (P > 0.05, Table I).

Oxyuroidea: Eggs that appear to be Enterobius sp. based on egg size and morphology were found in 2 redtail guenon samples (Table I) and measured 64–66 × 36–37 μm (n = 2). This parasite is more reliably diagnosed by examination of perianal skin or by necropsy (Ashford et al., 2000). Consequently, these prevalence values may be underestimations of actual prevalence.

Spiruroidea: Eggs that most closely resemble those of Streptopharagus sp. (symmetrical, embryonated, and thick shelled) were found in feces of all guenon species except l'hoesti monkeys and measured 38.5 ± 2.1 × 24.3 ± 1.1 μm for redtail guenons, 40.1 ± 1.9 × 25.0 ± 1.3 μm for blue monkeys, and 41.7 ± 1.8 × 25.6 ± 1.5 μm for vervets. Prevalence of Streptopharagus sp. did not differ (P > 0.05) between redtail guenons (18%) and blue monkeys (14%) (P > 0.05, Table I).

TABLE I. The prevalence (%) of gastrointestinal helminth parasite infections in guenons of western Uganda, Kenya, South Africa, and Senegal. (Sample size is in parentheses following species name.)

	Western Uganda				Kenya*	South Africa†	Senegal‡
Parasite	Redtail guenon (235)	Blue monkey (35)	L'hoiste monkey (11)	Vervet monkey (12)	Blue monkey (55)	Blue monkey (121)	Vervet monkey (16)
Strongyloides fulleborni	7	6	27	42	62	0	0
Strongyloides sp.	0	0	0	0	0	6	69
Oesophagostomum sp.	10	9	9	0	47	2	0
Trichostrongylus sp.	0	0	0	0	38	0	0
Necator sp.	0	0	0	0	0	0	6
Unidentified strongyle	0	0	0	42	0	0	0
Trichuris sp.	29	26	36	58	60	56	0
Capillaria sp.	0	0	0	0	0	3	0
Streptopharagus sp.	18	14	0	17	53	81	0
Physaloptera sp.	0	0	0	0	0	0	6
Abbreviata caucasica	0	0	0	0	0	2	0
Gongylonema sp.	0	0	0	0	0	2	0
Enterobius sp.	1	0	0	0	7	0	0
Bertiella sp.	<1	0	0	0	0	17§	0
Dicrocoeliidae sp.	2	3	0	8	0	0	0
Overall	49	37	55	92	NA	NA	NA

* Munene et al. (1998).
† Appleton et al. (1994).
‡ McGrew et al. (1989).
§ Presumed (identified as anoplocephalid).

Cestoda

Eggs that most closely resemble those of *Bertiella* sp. (spherical, colorless, fully developed oncosphere) were found in feces of only 1 redtail guenon and measured 40–43 × 48–51 μm (n = 4), and no proglottid was detected through macroscopic inspection of feces (Table I). Because eggs of this species are passed in proglottids, they are not mixed heterogeneously in feces. Consequently, these prevalence values may be gross underestimations of actual prevalence.

Trematoda

A dicrocoeliid liver fluke was identified on the basis of egg morphology (ellipsoid, operculated, and golden-brown coloration). Eggs were found in feces of all guenon species except l'hoesti monkeys and measured 45.8 ± 1.1 × 24.2 ± 1.0 μm for redtail guenons, 44 × 24 μm for blue monkeys, and 46 × 24 μm for vervets. Prevalence of this trematode did not differ (*P* > 0.05) between redtail guenons (2%) and blue monkeys (3%) (Table I).

Protozoans

Cysts of 3 amoebae and 2 flagellates were identified from 235 fecal samples from redtail guenons. Cysts most closely resembling *Entamoeba coli* were multinucleate with a mean diameter of 17.8 ± 1.1 μm. Cysts most closely resembling *Entamoeba histolytica* had a mean diameter of 12.9 ± 2.1. Cysts most closely resembling *Iodameoba butschlii* had a single nucleus, distinct glycogen vacuole, and a mean diameter of 11.2 ± 2.1. Cysts most closely resembling *Giardia lamblia* were ovoid with a mean diameter of 11.4 ± 1.4. Cysts most closely resembling *Chilomastix mesnili* were lemon-shaped with a mean diameter of 7.5 ± 1.1. Prevalence in redtail guenons was relatively low for all protozoans: *E. coli* (11%), *E. histolytica* (10%), *I. butschlii* (10%), *G. lamblia* (4%), and *C. mesnili* (1%).

Correlation between season and host sex with infection prevalence

Although prevalence did not correlate with monthly rainfall for any parasite species infecting redtail guenons (*P* > 0.496), seasonal fluctuations did occur (Fig. 1). Although prevalence did not differ between male (n = 12) and female (n = 98) redtail guenons for any shared parasite species (*P* > 0.05), *Oesophagostomum* sp. (n = 24) and *S. fulleborni* (n = 16) infections were only detected in adult females.

Variation in prevalence among sites throughout Africa

Previous studies have investigated the gastrointestinal parasites of blue monkeys from South Africa (Appleton et al., 1994) and Kenya (Munene et al., 1998). Comparisons with the current study demonstrate great similarity in helminth faunas of blue monkeys among sites. However, prevalence varied greatly among sites (Table I). *Trichuris* sp. prevalence was lower in blue monkeys in Uganda than in Kenya and South Africa (χ^2 = 11.96, *P* < 0.005). Prevalence of *Oesophagostomum* sp. in blue monkeys was higher in Kenya than in Uganda and higher in Uganda than in South Africa (χ^2 = 64.03, *P* < 0.001). *Stron-*

gyloides sp. prevalence was higher in blue monkeys in Kenya than in Uganda and South Africa (χ^2 = 93.85, *P* < 0.001). Prevalence of *Streptopharagus* sp. in blue monkeys was higher in South Africa than in Kenya and prevalence in Kenya was higher than in Uganda (χ^2 = 54.66, *P* < 0.001). Infections of an anoplocephalid, thought to be *Bertiella* sp., were documented for blue monkeys in South Africa and Uganda, and prevalence was higher in blue monkeys in South Africa than in Uganda (χ^2 = 32.35, *P* < 0.001).

McGrew et al. (1989) reported on the gastrointestinal parasites of vervet monkeys in Senegal. Although *Trichuris* sp. infections were not documented, and another spiruroid nematode, *Physaloptera* sp., replaced *Streptopharagus* sp., the overall helminth fauna was similar to that of vervets in our study (Table I).

DISCUSSION

To our knowledge, this is the first report on gastrointestinal helminth parasites from wild populations of redtail guenons and l'hoesti monkeys and the first report on gastrointestinal helminth parasites from blue and vervet monkeys from Uganda.

The similarities in gastrointestinal parasite faunas among the guenons of western Uganda suggest that generalist parasites predominate, supporting the contention that in communities comprising closely related species, i.e., *Cercopithecus* spp., cross-species interaction may be an important source of infection risk (Ezenwa, 2003). This may be 1 reason why redtail guenons associate with unrelated red colobus monkeys far more than with other guenon species (Chapman and Chapman, 2000).

Seasonal patterns of infection were not readily apparent for any of the parasite species infecting redtail guenons. This result is unexpected because previous studies of primate parasite infections from tropical forest sites have documented an increase in prevalence during the rainy season (Freeland, 1977; Huffman et al., 1997). It is difficult to ascertain why seasonal differences were not seen in this study. However, fluctuation in infection prevalence was high, warranting future investigation of the mechanism behind these differences (Fig. 1).

Although no difference in prevalence of infection was apparent between male and female guenons for shared parasite species, only adult females were infected with *Oesophagostomum* sp. and *S. fulleborni*. This may reflect energy and nutrient stress associated with producing and raising infants, which may result in an increased susceptibility to infection (Gulland, 1992; Milton, 1996).

Studies that have investigated the gastrointestinal parasites of blue monkeys revealed similar helminth faunas among sites (Appleton et al., 1994; Munene et al., 1998). This might be expected because of the recent origin of blue monkeys (Leakey, 1988; Ruvolo, 1988). However, parasite prevalence varied greatly among sites. In general, helminth prevalence was highest for Kenyan blue monkeys, with the exception of *Streptopharagus* sp., which had the highest prevalence for South African blue monkeys. In most cases, intermediate prevalence was seen in Ugandan compared with Kenyan and South African blue monkeys. Kenyan forests are small and fragmented compared with those sampled in Uganda and South Africa (Appleton et al., 1994), and evidence suggests that primates living in forest fragments may be more susceptible to infection and dem-

onstrate higher prevalence compared with conspecifics inhabiting large, undisturbed forests (Gillespie, 2004; but see Stuart et al., 1993). This may explain the high prevalence of infection in Kenyan blue monkeys compared with the other 2 sites.

The helminth fauna of vervets was similar in Uganda and Senegal (McGrew et al., 1989). However, small sample size precluded comparisons of prevalence.

Freeland (1977) reported on the protozoan parasites of several primate species in Kibale National Park. His study identified 2 protozoans from redtail guenons, which were not found in our study, i.e., *Entamoeba hartmanni* and an unidentified flagellate. Although Freeland (1977) did identify *C. mesnili* cysts from several species, they were not identified from redtail guenons. Despite these differences, the overall protozoan fauna of redtail guenons reported by Freeland (1977) and our study was similar. Unfortunately, Freeland (1977) does not provide data on prevalence.

Our study contributes baseline data on the patterns of parasitic infection in wild guenons, providing a first step toward an index of population health and disease risk assessment for conservation and management plans of threatened guenon populations. Our study also reveals that many of the gastrointestinal parasites of the guenon species examined may be zoonotic. Accordingly, future studies are needed to determine risks of cross-transmission. Mechanisms to reduce such risks would promote human health, livestock production, and local support for conservation.

Gastrointestinal parasite classification by fecal analyses is weak by its very nature. However, it is the only responsible method to approach threatened species. Future studies using molecular analyses and opportunistic necropsies are needed to improve our classification of the gastrointestinal parasites of guenons, as well as to improve our understanding of the risks of epizootic and zoonotic transmission.

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LITERATURE CITED

ANDERSON, R. M., AND R. M. MAY. 1979. Population biology of infectious diseases. Nature **280:** 361–367.

APPLETON, C. C., S. P. HENZI, A. WHITTEN, AND R. BYRNE. 1986. The gastro-intestinal parasites of *Papio ursinus* from the Drakensberg Mountains, Republic of South Africa. International Journal of Primatology **7:** 449–456.

———, R. C. KRECEK, A. VERSTER, M. R. BRUONTON, AND M. J. LAWES. 1994. Gastro-intestinal parasites of the Samango monkey, *Cercopithecus mitis*, in Natal, South Africa. Journal of Medical Primatology **23:** 52–55.

ASHFORD, R. W., G. D. F. REID, AND R. W. WRANGHAM. 2000. Intestinal parasites of the chimpanzee *Pan troglodytes*, in Kibale Forest, Uganda. Annals of Tropical Medicine and Parasitology **94:** 173–179.

BUTYNSKI, T. M. 2002. Conservation of the guenons: an overview of status, threats, and recommendations. *In* The Guenons: Diversity and adaptation in African monkeys, Mary E. Glenn and Marina Cords (eds.). Kluwer Academic/Plenum Publishers, New York, p. 411–424.

CHAPMAN, C. A., AND L. J. CHAPMAN. 2000. Interdemic variation in mixed-species association patterns: Common diurnal primates of Kibale National Park, Uganda. Behavioral Ecology and Sociobiology **47:** 129–139.

———, ———, AND T. R. GILLESPIE. 2002. Scale issues in the study of primate foraging: Red colobus of Kibale National Park. American Journal of Physical Anthropology **117:** 349–363.

DASZAK, P., A. A. CUNNINGHAM, AND A. D. HYATT. 2000. Wildlife ecology—Emerging infectious diseases of wildlife-threats to biodiversity and human health. Science **287:** 443–449.

ELEY, R. M., S. C. STRUM, G. MUCHEMI, AND G. D. F. REID. 1989. Nutrition, body condition, activity patterns and parasitism of free-ranging baboons (*Papio anubis*) in Kenya. American Journal of Primatology **18:** 209–219.

EZENWA, V. O. 2003. Habitat overlap and gastrointestinal parasitism in sympatric African bovids. Parasitology **126:** 379–388.

[FAO] FOOD AND AGRICULTURE ORGANIZATION. 1999. State of the world's forests. Food and Agriculture Organization of the United Nations, Rome, Italy, 22 p.

FREELAND, W. J. 1977. Dynamics of primate parasites. Ph.D. Dissertation. University of Michigan, Ann Arbor, Michigan, 202 p.

GILLESPIE, T. R. 2004. Effects of human disturbance on primate-parasite dynamics. Ph.D. Dissertation. University of Florida, Gainesville, Florida, 99 p.

GRACZYK, T. K., L. J. LOWENSTINE, AND M. R. CRANFIELD. 1999. *Capillaria hepatica* (Nematoda) infections in human-habituated mountain gorillas (*Gorilla gorilla beringei*) in the Parc National de Volcans, Rwanda. Journal of Parasitology **85:** 1168–1170.

GRUBB, P., T. M. BUTYNSKI, J. F. OATES, S. K. BEARDER, T. R. DISOTELL, C. P. GROVES, AND T. T. STRUHSAKER. 2002. An assessment of the diversity of African primates. IUCN/SSC Primate Specialist Group, Washington, D.C., 57 p.

GULLAND, F. M. D. 1992. The role of nematode parasites in Soay sheep (*Ovis aries* L.) mortality during a population crash. Parasitology **105:** 493–503.

HAHN, N. E., D. PROULX, P. M. MURUTHI, S. ALBERTS, AND J. ALTMAN. 2003. Gastrointestinal parasites in free-ranging Kenyan baboons (*Papio cynocephalus* and *P.anubis*). International Journal of Primatology **24:** 271–279.

HUFFMAN, M. A., S. GOTOH, L. A. TURNER, M. HAMAI, AND K. YOSHIDA. 1997. Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania. Primates **38:** 111–125.

JESSEE, M. T., P. W. SCHILLING, AND J. A. STUNKARD. 1970. Identification of intestinal helminth eggs in old world primates. Laboratory Animal Care 20: 83–87.

LEAKEY, M. 1988. Fossil evidence for the evolution of guenons. *In* A primate radiation: Evolutionary biology of the African guenons, A. Gautier-Hion, F. Bourliere, and J. P. Gautier (eds.). Cambridge University Press, Cambridge, U.K., p. 54–78.

LILLY, A. A., P. T. MEHLMAN, AND D. DORAN. 2002. Intestinal parasites in gorillas, chimpanzees, and humans at Mondika Research Site, Dzanga-Ndoki National Park, Central African Republic. International Journal of Primatology **23:** 555–573.

[MAFF] MINISTRY OF AGRICULTURE, FISHERIES, AND FOOD. 1979. Manual of veterinary parasitology laboratory techniques. Her Majesty's Stationary Office, London, U.K., 72 p.

MAY, R. M., AND R. M. ANDERSON. 1979. Population biology of infectious diseases. Nature **280:** 455–461.

MCGREW, W. C., C. E. G. TUTIN, AND S. K. FILE. 1989. Intestinal parasites of two species of free-living monkeys in far western Africa, *Cercopithecus (aethiops) sabaeus* and *Erythrocebus patas patas*. African Journal of Ecology **27:** 261–262.

MILTON, K. 1996. Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler (*Alouatta palliata*) population in Panama. Journal of Zoology **239:** 39–63.

MÜLLER-GRAF, C. D., D. A. COLLINS, C. PACKER, AND M. E. WOOLHOUSE. 1997. *Schistosoma mansion* infection in a natural population of olive baboons (*Papio cynocephalus anubis*) in Gombe Stream National Park, Tanzania. Parasitology **15:** 621–627.

MUNENE, E., M. OTSYULA, D. A. N. MBAABU, W. T. MUTAHI, S. M. K. MURIUKI, AND G. M. MUCHEMI. 1998. Helminth and protozoan gastrointestinal tract parasites in captive and wild-trapped African nonhuman primates. Veterinary Parasitology **78:** 195–201.

NIZEYI, J. B., R. MWEBE, A. NANTEZA, M. R. CRANFIELD, G. R. N. N. KALEMA, AND T. K. GRACZYK. 1999. *Crytosporidium* sp. and *Giardia* sp. infections in mountain gorillas (*Gorilla gorilla beringei*) of the Bwindi Impenetrable National Park, Uganda. Journal of Parasitology **85:** 1084–1088.

PATZ, J. A., T. K. GRACZYK, N. GELLER, AND A. Y. VITTOR. 2000. Effects of environmental change on emerging parasitic diseases. International Journal for Parasitology **30:** 1395–1405.

RUVOLO, M. 1988. Genetic evolution in the African guenons. *In* A primate radiation: Evolutionary biology of the African guenons, A. Gautier-Hion, F. Bourliere, and J. P. Gautier (eds.). Cambridge University Press, Cambridge, U.K., p. 127–139.

SLOSS, M. W., R. L. KEMP, AND A. M. ZAJAC. 1994. Veterinary clinical parasitology, 6th ed. Iowa State University Press, Ames, Iowa, 198 p.

STRUHSAKER, T. T. 1997. Ecology of an African rain forest: Logging in Kibale and the conflict between conservation and exploitation. University of Florida Press, Gainesville, Florida, 402 p.

STUART, M. D., K. B. STRIER, AND S. M. PIERBERG. 1993. A coprological survey of parasites of wild muriquis (*Brachyteles arachnoids*) and brown howling monkeys (*Alouatta* fusca). Journal of the Helminthological Society of Washington **60:** 111–115.

WORLD RESOURCES INSTITUTE. 1998. World resources 1998–99. Oxford University Press, New York, 384 p.