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GASTROINTESTINAL PARASITES OF THE COLOBUS MONKEYS OF UGANDA

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ABSTRACT: From August 1997 to July 2003, we collected 2,103 fecal samples from free-ranging individuals of the 3 colobus monkey species of Uganda—the endangered red colobus (*Piliocolobus tephrosceles*), the eastern black-and-white colobus (*Colobus guereza*), and the Angolan black-and-white colobus (*C. angolensis*)—to identify and determine the prevalence of gastrointestinal parasites. Helminth eggs, larvae, and protozoan cysts were isolated by sodium nitrate flotation and fecal sedimentation. Coprocultures facilitated identification of helminths. Seven nematodes (*Strongyloides fulleborni*, *S. stercoralis*, *Oesophagostomum* sp., an unidentified strongyle, *Trichuris* sp., *Ascaris* sp., and *Colobenterobius* sp.), 1 cestode (*Bertiella* sp.), 1 trematode (Dicrocoeliidae), and 3 protozoans (*Entamoeba coli*, *E. histolytica*, and *Giardia lamblia*) were detected. Seasonal patterns of infection were not apparent for any parasite species infecting colobus monkeys. Prevalence of *S. fulleborni* was higher in adult male compared to adult female red colobus, but prevalence did not differ for any other shared parasite species between age and sex classes.

Colobinae is a large subfamily of leaf-eating, Old World monkeys represented in Africa by species of 3 genera, *Colobus*, *Procolobus*, and *Piliocolobus* (Grubb et al., 2002). These folivorous monkeys live in groups of highly variable size (5–300 individuals) and often form mixed-species associations with other primates (Struhsaker, 1981; Oates, 1994; Chapman and Chapman, 2000). Colobines are forest-dependent and, consequently, are acutely threatened by human activities that reduce forest cover. 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 (Food and Agriculture Organization, 1999). Largely because of this habitat loss, 50% of African colobine species are endangered, and an additional 20% are rare (Grubb et al., 2002). Within this context, baseline data regarding patterns of parasitic infections in wild colobine populations are critical to providing an index of population health and beginning 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; Nizeyi et al., 1999; Ashford et al., 2000; 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 (see, however, Gillespie et al., 2004). The present study identifies and quantifies the prevalence of gastrointestinal helminth and protozoan parasites for the 3 colobine species of Uganda: the endangered red colobus (*Piliocolobus tephrosceles*), the eastern black-and-white colobus (*Colobus guereza*), and the Angolan black-and-white colobus (*C. angolensis*). When data are sufficient, we also examine the effect of season and host sex on parasite prevalence.

MATERIALS AND METHODS

From August 1997 to July 2003, we collected 2,103 fecal samples: 1,608 from red colobus, 476 from eastern black-and-white colobus, and 19 from Angolan black-and-white colobus. Red colobus are sexually dimorphic, with males averaging 10.5 kg and females 7.0 kg (Oates et al., 1994); they display a multimale–multifemale social structure and live in groups of 20 to more than 100 within home ranges that average 35.3 ha (Struhsaker, 1975; Gillespie and Chapman, 2001). Eastern black-and-white colobus are sexually dimorphic, with males averaging 13.5 kg and females 8.6 kg (Oates et al., 1994); they display variable social structure (1 male–multifemale or multimale–multifemale), and live in groups of 7–11 within home ranges that average 15 ha (Oates, 1974; Onderdonk and Chapman, 2000). Angolan black-and-white colobus are sexually dimorphic, with males averaging 9.7 kg and females 7.4 kg (Napier, 1985); they display a variable social structure (1 male–multifemale or multimale–multifemale) and live in groups of 5 to more than 300 within home ranges from 1 to more than 400 ha (Oates et al., 1994; T. Gillespie, pers. obs.).

Red colobus and eastern black-and-white colobus samples were collected from individuals inhabiting a 50 km^2 area in western Uganda consisting of a matrix of protected primary and secondary forest, forest fragments, and agricultural plots (Gillespie, 2004). Sampling effort focused on Kanyawara, a 1,034-ha area characterized by logged and unlogged forest within Kibale National Park (766 km^2; 0°13′–0°41′N, 30°19′–30°32′E) (Struhsaker, 1997) and 21 forest fragments ranging from 1 to 10 ha (total area 82 ha) located within 6.5 km of Kanyawara (Chapman et al., 2003). Red colobus density in this area ranged from 1 to 8 individuals/ha and averaged 2.3 individuals/ha (Gillespie, 2004). Eastern black-and-white colobus density in this area ranged from 0.2 to 5 individuals/ha and averaged 0.8 individuals/ha (Gillespie, 2004). Mean annual rainfall (1990–2001) was 1,749 mm (Chapman et al., 2002). Daily temperature minima and maxima averaged 14.9 and 20.2 C, respectively, from 1990 to 2001. Angolan black-and-white colobus samples were collected from 3 forest fragments ranging from 1 to 10 ha (total area 15 ha) adjacent to Lake Nabugabo in southeastern Uganda (0°20′–0°25′S, 31°50′–31°56′E). Angolan black-and-white colobus density in this area ranged from 0.5 to 3 individuals/ha and averaged 1.5 individuals/ha (Gillespie, 2004). Annual rainfall ranges from 520 to 1,970 mm (Efitre et al., 2001), and daily temperature minima and maxima average 15.2 and 27.2 C, respectively (Meteorology Department, Masaka, Uganda). All survey sites experience a bimodal pattern of seasonal rainfall, with peaks occurring in March–May and August–November.

Samples were collected from habituated and semihabituated adult and subadult males and females of each primate species. Every attempt was made to sample as widely as possible within each primate population; however, because individual recognition was not always possible, some individuals may have been sampled more than once. Samples were collected immediately after defecation to avoid contamination and examined macroscopically for adult nematodes and tapeworm proglottids. Samples were stored individually in 5.0-ml vials in 10% formalin solution. Preserved samples were transported to the University of Florida, where they were examined for helminth eggs and larvae as well as 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. Iodine was used to facilitate protozoan identification. Measurements were made to the nearest 0.1 $\mu \pm$ SD using an ocular micrometer fitted to a compound micro-

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TABLE I. The prevalence (%) of gastrointestinal parasite infections in colobus monkeys of Uganda (sample size is in parentheses following species name).

Parasite species	*Piliocolobus tephrosceles* (1.608)	*Colobus guereza* (476)	*Colobus angolensis* (19)
Strongyloides fulleborni	3.54	4.20	5.26
Strongyloides stericalis	0.44	0.00	0.00
Oesophagostomum sp.	2.80	6.09	0.00
Unidentified Strongyle	1.55	1.05	10.53
Ascaris sp.	0.12	1.26	0.00
Trichuris sp.	37.75	78.99	100.00
Colobenterobius sp.	0.44	0.63	0.00
Bertiella sp	0.06	0.21	0.00
Dicrocoeliidae sp.	0.06	0.63	0.00
Entamoeba coli	4.35	7.77	15.79
Entamoeba histolytica	3.48	7.56	10.53
Giardia lamblia	0.81	0.00	0.00
Overall	37.75	78.99	100.00

scope, and representatives were photographed. Mean egg sizes are based on measurement of 10 eggs from 10 different hosts unless otherwise noted. Coprocultures (n = 10 per primate species) were used to match parasite eggs to larvae for positive identification (Ministry of Agriculture, Fisheries, and Food, 1979; Gillespie, 2004). We present the majority of our findings at the level of family or genus, because more detailed parasite classification based on host fecal examination can be unreliable.

We performed nonparametric Kruskal–Wallis tests to compare the size of eggs and/or cultured larvae for a given parasite species among all three primate species. When two primate species were compared, MannWhitney tests were used. We performed chi-square tests of independence to compare the prevalence of infections between red colobus and eastern black-and-white colobus and between host age and sex classes for a subset of red colobus (n = 401). Small sample size precluded us from including Angolan black-and-white colobus in the species comparisons and both black-and-white colobus species in the age and sex class comparisons. We used Pearson correlations to test for relationships between monthly rainfall and prevalence of parasites infecting red colobus and eastern black-and-white colobus.

RESULTS

Nematoda

Trichuroidea: Trichuris sp. was identified based on egg size and morphology (barrel-shape, yellow-brown coloration, and bipolar plugs). Eggs were found in feces of all colobus species and did not differ in length ($H = 4.605$, $P = 0.10$) or width ($H = 1.126$, $P = 0.57$) among colobus species (measuring 57.3 ± 1.0 × 27.0 ± 1.3 μm for red colobus, 58.2 ± 1.6 × 26.9 ± 1.2 μm for eastern black-and-white colobus, and 58.8 ± 1.2 × 27.2 ± 1.4 μm for Angolan black-and-white colobus). Prevalence of *Trichuris* sp. was higher in eastern black-and-white colobus than red colobus ($\chi^2 = 249.94$, df = 1, $P < 0.001$) (Table I).

Strongyloidea: Oesophagostomum sp. was identified on the basis of egg size and morphology (elliptical and unlarvated) and was verified by cultured third-stage larvae. Eggs were found in feces of all colobus species except Angolan black-and-white colobus, and they did not differ in length ($U = 45.50$, $P = 0.739$) or width ($U = 40.50$, $P = 0.481$) between colobus species (measuring 70.0 ± 1.4 × 41.8 ± 1.6 μm for red colobus and 70.2 ± 1.8 × 41.6 ± 1.6 μm [n = 2] for eastern black-and-white colobus). Cultured third-stage larvae of *Oesophagostomum* sp. did not differ in length ($U = 36.50$, $P = 0.334$) between red colobus (905.0 ± 4.7 μm) and eastern black-and-white colobus (904.5 ± 3.6 μm). Prevalence of *Oesophagostomum* sp. was higher in eastern black-and-white colobus than in red colobus ($\chi^2 = 11.40$, df = 1, $P < 0.001$) (Table I).

Unidentified strongyle eggs were found in feces of all colobus species and differed in length ($H = 6.6$, $P = 0.037$) and width ($H = 6.678$, $P = 0.035$) among colobus species (measuring 59.6 ± 5.6 × 38.2 ± 4.1 μm for red colobus, 63.7 ± 4.8 × 40.1 ± 4.5 μm [n = 5] for eastern black-and-white colobus, and 68.4 ± 2.0 × 40.3 ± 2.3 μm [n = 2] for Angolan black-and-white colobus). These strongyles may represent *Necator* sp., *Ancylostoma* sp., and/or *Oesophagostomum* sp.; however, coprocultures were not performed, limiting our ability to identify these parasites to the genus level. Prevalence of unidentified strongyles did not differ among colobus species ($P > 0.1$) (Table I).

Rhabditoidea: Strongyloides fulleborni was identified based on egg size and morphology (oval, thin-shelled, colorless, and larvated) and verified by cultured third-stage larvae. Eggs were found in feces of all colobus species and did not differ in length ($U = 36.00$, $P = 0.315$) or width ($U = 37.00$, $P = 0.353$) between red colobus and eastern black-and-white colobus (measuring 45.7 ± 1.7 × 34.8 ± 2.0 μm for red colobus, 46.7 ± 2.2 × 35.2 ± 2.2 μm for eastern black-and-white colobus, and 47.0 × 35.4 μm [n = 1] for Angolan black-and-white colobus). Cultured third-stage larvae of *S. fulleborni* did not differ in length ($U = 43.50$, $P = 0.667$) between red colobus (634.9 ± 3.1 μm) and eastern black-and-white colobus (635.5 ± 2.7 μm). Prevalence of *S. fulleborni* did not differ among colobus species ($P > 0.1$) (Table I).

Strongyloides stercoralis was identified based on larvae size and morphology (rhabditiform esophagus, prominent genital primordium, and short buccal cavity). Larvae of *S. stercoralis* were found only in the feces of red colobus and measured 242.4 ± 4.5 μm in length.

Ascaroidea: Ascaris sp. was identified based on egg size and morphology (round or oval, thick-shelled, brown or yellow brown, and mammillated albuminous covering). Eggs were found in feces of red colobus and eastern black-and-white colobus and did not differ in length ($U = 4.50$, $P = 0.615$) or width ($U = 3.00$, $P = 0.429$) between colobus species (measuring 65.2 ± 1.3 × 55.8 ± 1.1 μm [n = 2] for red colobus and 63.9 ± 1.4 × 54.4 ± 1.0 μm [n = 6] for eastern black-and-white colobus). Prevalence of *Ascaris* sp. was higher for eastern black-and-white colobus than for red colobus ($\chi^2 = 10.71$, df = 1, $P < 0.005$) (Table I).

Oxyuroidea: Colobenterobius sp. was identified based on egg size and morphology (elliptical and thick-shelled). Eggs were found in feces of red colobus and eastern black-and-white colobus and did not differ in length ($U = 7.50$, $P = 0.517$) or width ($U = 9.50$, $P = 0.833$) between colobus species (measuring 64.8 ± 1.6 × 36.4 ± 1.4 μm [n = 7] and 65.3 ± 1.2 × 36.6 ± 1.6 μm [n = 3], respectively). Prevalence of *Colobenterobius* sp. did not differ between colobus species ($P > 0.1$)

(Table I). This parasite is more reliably diagnosed by examination of perianal skin or by necropsy (Ashford et al., 2000). Consequently, these prevalence values likely are an underestimation of prevalence.

Cestoda

Eggs that most closely resemble *Bertiella* sp. (spherical, colorless, and fully developed oncosphere) were found in feces of red colobus and eastern black-and-white colobus and measured 40.3 × 48.8 μm (n = 1) and 41.2 × 50.0 μm (n = 1), respectively. No proglottids were detected through macroscopic inspection of feces. Prevalence of *Bertiella* sp. did not differ between colobus species ($P > 0.1$) (Table I). Because eggs of this species are passed in proglottids, they are not mixed heterogeneously in feces. Consequently, these prevalence values may underestimate actual prevalence.

Trematoda

A dicrocoeliid liver fluke was identified based on egg size and morphology (ellipsoid, operculated, and golden-brown coloration). Eggs were found in feces of red colobus (46 × 24 μm, n = 1) and eastern black-and-white colobus (43.8 ± 1.1 × 23.6 ± 1.4 μm, n = 3). Prevalence of this trematode was higher for eastern black-and-white colobus than red colobus ($\chi^2 = 5.34$, df = 1, $P < 0.025$) (Table I). These eggs may represent *Dicrocoelium colobusicola*, *Brodenia* spp., and/or *Concinnum* sp.; however, they cannot be differentiated to the genus level based on egg morphology alone.

Protozoans

Multinucleate cysts most closely resembling *Entamoeba coli* were found in the feces of all colobus species and did not differ in diameter among colobus species ($H = 1.693$, $P = 0.429$; measuring 18.1 ± 1.0 μm for red colobus, 17.4 ± 1.4 μm for eastern black-and-white colobus, and 17.6 ± 1.3 μm [n = 3] for Angolan black-and-white colobus). Prevalence of *E. coli* was higher for eastern black-and-white colobus than for red colobus ($\chi^2 = 4.28$, df = 1, $P < 0.05$) (Table I).

Cysts most closely resembling *Entamoeba histolytica* were found in the feces of all colobus and did not differ in diameter among colobus species ($H = 2.464$, $P = 0.292$; measuring 13.2 ± 1.1 μm for red colobus, 12.5 ± 1.8 μm for eastern black-and-white colobus, and 12.7 ± 1.6 μm [n = 2] for Angolan black-and-white colobus). Prevalence of *E. histolytica* was higher for eastern black-and-white colobus than for red colobus ($\chi^2 = 14.68$, df = 1, $P < 0.001$) (Table I).

Ovoid cysts most closely resembling *Giardia lamblia* were found only in the feces of red colobus. These cysts had a mean diameter of 11.9 ± 1.8 μm (Table I).

Effect of season and host age and sex on infection prevalence

Prevalence did not correlate significantly with monthly rainfall for any parasite species infecting red colobus ($P > 0.077$) or eastern black-and-white colobus ($P > 0.081$). Variation, however, was evident over the year.

Prevalence of *S. fulleborni* was higher in adult males compared to adult females ($\chi^2 = 6.19$, df = 2, $P < 0.05$). Prevalence, however, did not differ for any other shared parasite species between age and sex classes ($P > 0.05$).

DISCUSSION

To our knowledge, this is the first comprehensive survey of the gastrointestinal helminth and protozoan parasites of any African colobines. Our results demonstrate high overlap among parasites infecting the sampled colobine species. With the exception of unidentified strongyles, we found no differences in egg or larvae size for any given parasite between colobus species, suggesting that generalist parasites predominate. This supports the contention that in communities comprised of closely related species, cross-species interaction may be an important source of infection risk (Ezenwa, 2003). Many of the species infecting colobines in Uganda occur at high frequency in human and other nonhuman primates in the region (National Environmental Management Authority 1997; Gillespie et al., 2004). Consequently, zoonotic, epizootic, and/or anthropozoonotic transmission may occur and be promoted by various forms of anthropogenic disturbance.

Despite the great correspondence in parasite faunas among colobines, prevalence varied between red colobus and eastern black-and-white colobus. In general, prevalence was higher for eastern black-and-white colobus compared to red colobus. Prevalence likely is affected by complex interactions among environmental, demographic, genetic, and behavioral factors, making it difficult to explain this variation in prevalence.

Seasonal patterns of infection were not readily apparent for any of the parasite species infecting red colobus or eastern black-and-white colobus. This result is unexpected, because previous studies of parasite infections from tropical forest frugivorous monkeys and apes—that is, *Lophocebus albigena* (Freeland, 1977) and *Pan troglodytes* (Huffman et al., 1997)—have documented an increased prevalence during the rainy season. It is difficult to determine why seasonal differences were not seen in these foloivores. Fluctuation in infection prevalence was high, however, warranting future investigation of the mechanism behind these differences.

Prevalence of *S. fulleborni* was higher in adult male compared to adult female red colobus. Perhaps this reflects energy and nutrient stress associated with maintaining social dominance (Hausfater and Watson, 1976), which may result in an increased susceptibility to infection (Gulland, 1992; Milton, 1996). If this is the case, however, then it is not clear why infection prevalence is not higher for other parasite species in males compared to females.

Freeland (1977) provided a survey of the protozoan parasites of primate species in Kibale National Park that failed to document the presence of any protozoan in colobus feces based on examination of a small number of samples for red colobus (n = 5) and eastern black-and-white colobus (n = 7). This differs from our results, which demonstrate that colobines are susceptible to protozoan infection. Our results, however, reveal that protozoan prevalence for colobines is low compared with that in other primate species examined by Freeland (1977), such as chimpanzees and baboons. Accordingly, greater sampling effort during this earlier study likely may have yielded findings similar to our own.

The present study contributes baseline data regarding the patterns of parasitic infection in wild colobus monkeys, providing a first step toward an index of population health and disease risk assessment for conservation and management plans of threatened and endangered colobus populations. Our study also reveals that many of the gastrointestinal parasites of the colobines examined may be zoonotic, epizootic, or anthropozoonotic. Accordingly, future studies are needed to determine the risks of cross-transmission. Mechanisms to reduce such risks may 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 for approaching threatened species. Future studies employing molecular analyses and opportunistic necropsies are needed to improve our classification of the gastrointestinal parasites of colobines as well as to improve our understanding of the risks of transmission.

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