

RESEARCH ARTICLE

Life on the Edge: Gastrointestinal Parasites From the Forest Edge and Interior Primate Groups

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Humans are responsible for massive changes to primate habitats, and one unanticipated consequence of these alterations may be changes in host–parasite interactions. Edges are a ubiquitous aspect of human disturbance to forest landscapes. Here we examine how changes associated with the creation of edges in Kibale National Park, Uganda, alter the parasite community that is supported by two species of African colobines: the endangered red colobus (*Piliocolobus tephrosceles*) and the black-and-white colobus (*Colobus guereza*). An analysis of 822 fecal samples from edge and forest interior groups revealed no difference in the richness of parasite communities (i.e., the number of parasite species recovered from the host's fecal sample). However, for both species the proportion of individuals with multiple infections was greater in edge than forest interior groups. The prevalence of specific parasites also varied between edge and forest interior groups. *Oesophagostomum* sp., a potentially deleterious parasite, was 7.4 times more prevalent in red colobus on the edge than in those in the forest interior, and *Entamoeba coli* was four times more prevalent in red colobus on the edge than in animals from the forest interior. Environmental contamination with parasites (measured as parasite eggs/gm feces) by red colobus from the edge and forest interior differed in a similar fashion to prevalence for red colobus, but it did not differ for black-and-white colobus. For example, egg counts of *Oesophagostomum* sp. were 10 times higher in red colobus from the edge than in those from the interior. The less severe infections

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in the black-and-white colobus relative to the red colobus may reflect the fact that black-and-white colobus raid agricultural crops while red colobus do not. This nutritional gain may facilitate a more effective immune response to parasites by the black-and-white colobus. The fact that animals on the edge are likely not nutritionally stressed raises an intriguing question as to what facilitates the elevated infections in edge animals. We speculate that interactions with humans may be linked to the observed patterns of infections, and hence that understanding the ecology of infectious diseases in nonhuman primates is of paramount importance for conservation and potentially for human-health planning. *Am. J. Primatol.* 68:397–409, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Within the last several decades, humans have been responsible for massive, irrevocable changes to primate habitats [Chapman & Peres, 2001]. Thus, in many parts of the world today primates live in anthropogenically disturbed habitat mosaics of farmland, human settlements, forest fragments, and isolated protected areas. It has also been hypothesized that disease emergence most frequently results from a change in the ecology of the host or parasite, or both [Schrag & Wiener, 1995]. For example, in a survey of emerging pathogens in wildlife in North America, Dobson and Foufopoulos [2001] found that human involvement facilitated 55% of pathogen outbreaks, and in only 19% of the cases was there no evidence of human influence. Taken together, these observations suggest that disease may play a significant role in the population dynamics of primates that inhabit disturbed landscapes. In fact, documentation is becoming available to show that disease can pose significant conservation risks to nonhuman primate populations, many of which are already threatened or endangered by habitat loss and/or hunting [Wallis & Lee, 1999]. For example, evidence indicates that Ebola virus outbreaks have contributed to the reduction of ape population densities by more than 50% over a broad geographic scale between 1983 and 2000 [Leroy et al., 2004; Walsh et al., 2003]. Polio epidemics have caused widespread mortality in wild chimpanzee communities [Goodall, 1986].

Despite this growing evidence of the potential importance of parasites in primate populations, it is currently unclear what aspects of anthropogenic changes to the physical environment facilitate the transmission of infectious agents among wild nonhuman primates or between nonhuman primates and humans. However, to better develop conservation strategies to deal with established and changing patterns of disease, we must understand the interplay between alteration of ecosystems and disease transmission probabilities.

Edges are a ubiquitous aspect of human disturbance of forest landscapes. They may cause changes in the ecology of the host or parasite, or both, and may promote greater contact among humans and wildlife. A multitude of studies have investigated the effects of edges on diversity, abundance, and ecological processes [Laurance & Bierregaard, 1997]. However, the role of edges in relation to host–parasite dynamics remains largely unknown. Primates that raid agricultural crops may develop decreased intensities of parasitism [Eley et al., 1989], since the increased nutrition may facilitate a more effective immune response. A number of studies have examined the relationship between nutrition and parasitism and

suggested that dietary stress may adversely affect resistance to parasitic infection by reducing the effectiveness of the immune system [Crompton, 1991; Gulland, 1992; Holmes, 1995; Milton, 1996; Solomons & Scott, 1994]. Alternatively, when parasites survive and reproduce in the host, heightened nutrition may provide favorable conditions for the parasite and lead to an increased burden for the host species. Weyher (unpublished data) found that a protozoan parasite benefited from the increased starch intake associated with crop raiding. Hahn et al. [2003] found that some spirurid nematodes had increased prevalence in baboon (*Papio anubis*) groups that supplemented their nutrition by feeding on refuse, while others had decreased prevalence. On the other hand, since nonhuman primates and humans are susceptible to many of the same generalist parasites [Chapman et al., 2005], monkeys ranging along forest edges may have increased parasitism stemming from frequent contact with humans.

Our study examines how anthropogenic changes associated with the creation of edges influences the ecology of the host or parasite, or both, to alter the parasite community supported by two species of African colobines: the endangered red colobus (*Piliocolobus tephrosceles*) and the black-and-white colobus (*Colobus guereza*). We compare the prevalence, proportion of multiple infections, and richness of gastrointestinal parasite species in individuals that frequent anthropogenic edges with those in animals that inhabit the forest interior. In hopes of understanding which ecological change is the most important in altering host-parasite interactions, we make comparisons with a previous investigation of how fragmentation influences the parasite community of colobus monkeys [Gillespie & Chapman, in press]. Forest fragments have significant edge components; however, they are also generally degraded i.e., trees are extracted for various reasons [Chapman et al., in press; Naughton-Treves & Chapman, 2002]. In contrast, the edges associated with Kibale National Park are abrupt transitions between relatively undisturbed forest and agricultural land [Naughton-Treves et al., 1998]. Since edges are an ever-present aspect of contemporary humanized landscapes, understanding their effects on primate diseases is vital for designing effective conservation and management plans, and improving our understanding of the interplay between ecological change and health.

MATERIALS AND METHODS

This study was conducted from August 1997 through July 2004 in Kibale National Park, Uganda. During that time 822 fecal samples from colobus monkeys were collected. The park (795 km²; 0° 13', 0° 41'N, and 30° 19', 30° 32'E) is a moist, mid-altitude (920–1,590 m) evergreen forest intermixed with swamps, secondary forests, and grasslands [Chapman & Lambert, 2000; Struhsaker, 1997]. Two types of groups were selected. First, we selected groups that were located well within the natural forest of the national park and that we knew did not range near the forest edge. Most groups ranged in areas that had undergone selective logging in the 1960s. Many of these groups are our long-term study groups [Chapman et al., 2002]. Second, we searched along the forest edge and collected samples from groups that were found within 30 m of the edge. We collected only from groups for which the edge was a transition between forest and agricultural land (i.e., we rejected groups that were adjacent to tea or eucalyptus plantations). The forest in this edge area had also been selectively logged in the 1960s. Subsequently, we compared data from the parasite communities in these two groups with published data on the parasite communities from colobus living in forest fragments [Gillespie & Chapman, in press]. These fragments are what

remains from the forest clearing that occurred in unprotected areas. By the end of the 20th century, nearly all forests outside of officially protected areas had been converted to farms, grazing areas, or tea plantations [Naughton-Treves, 1997]. Only small pockets of forest remain in areas that are unsuitable for agriculture. While the precise timing of the isolation of these forest remnants is not known, local elders describe them as “ancestral forests,” and aerial photographs from 1959 indicate that most remnant patches have been isolated from Kibale at least since that time, although many have decreased in size.

Around Kibale, people use land primarily for small-holder farming (54% of the area within 1 km) and the population density is approximately 272 individuals/km² [Naughton-Treves et al., 1998]. Farms near Kibale average 1.4 ha, of which on average 40% is under fallow [Naughton-Treves, 1998]. Farmers plant a mixture of over 30 types of subsistence and cash crops, of which bananas (*Musa* sp.), maize, beans (*Phaseolus vulgaris*), yams (*Dioscorea* spp.), and cassava (*Manihot esculenta*) cover the greatest area. Black-and-white colobus are known to regularly crop-raid, but at a low frequency, and damage only a small area of some crops. Red colobus rarely crop-raid [Naughton-Treves, 1997, 1998].

Fecal samples were collected, stored individually in vials in 10% formalin solution, and transported to the University of Florida or McGill University, where they were examined using concentration by sodium nitrate flotation and fecal sedimentation [Sloss et al., 1994]. Parasites were counted and identified on the basis of egg color, shape, contents, and size. Measurements were made to the nearest $0.1 \mu \pm \text{SD}$ using an ocular micrometer fitted to a compound microscope, and representatives were photographed. Coprocultures were used to match parasite eggs with larvae for positive identification [Gillespie et al., 2005a, b]. Two necropsies were conducted on animals from Kibale that died of natural causes, which allowed us to identify *Strongyloides fuelleborni*; however, because many of the other species occur only at low prevalence we were not able to identify other species (except for the larvae of *Trichuris* sp. (adults of this species are very difficult to identify) [Ooi et al., 1993]).

The parasite infections are described in terms of prevalence of infection, richness, and multiple infections. Comparisons of parasite prevalence can be a useful indicator that parasites may be impacting host populations (i.e., population declines have been correlated with increased infection prevalence). Prevalence is defined as the proportion of individuals sampled that are infected with a particular parasite. Since we could not individually recognize each animal in the population each year, we attempted to collect samples in a short period of time, and to rotate among individuals so as to avoid repeatedly sampling the same individual. However, repeat samples likely occurred, and thus this should be viewed as an index of prevalence. This is a concern because a small number of animals with consistently high infection levels and high richness could be overrepresented in the sampling scheme, particularly considering that sick animals may defecate more than healthy individuals (see Muehlenbein [2005] for a discussion of this issue). In a quantitative evaluation of this issue, Huffman et al. [1997] contrasted incidences of infection based on the number of fecal samples obtained from chimpanzees (*Pan troglodytes*) from Mahale vs. that based on the number of known individuals, and documented that individual infection rates, the preferred unit of comparison, was statistically higher than rates based on all samples.

The frequency of multiple-species infections (i.e., the proportion of a population with more than one species of parasite) can be another useful indicator that parasites may be impacting host populations, as multiple-species

infections are associated with a greater potential for morbidity and mortality. For example, in humans *Schistosoma mansoni* has an increased effect on the development of malnutrition in the presence of *Trichuris trichiura* [Parraga et al., 1996], and a range of parasites demonstrate greatly elevated pathogenic effects in the presence of HIV [Gomez et al., 1995; Kaplan et al., 1996]. Richness is defined as the number of unique intestinal species documented from the host's fecal sample [Muehlenbein, 2005]. Increases in parasite species richness may be indicative of greater morbidity and mortality. Since parasite egg production is often highly variable and thus may not be indicative of actual infection intensity, we report data only on the average number of eggs per gram of feces in infected individuals as an indication of environmental contamination (a correlate of infection risk) or potential for spillover to individuals of the same and different species.

Entamoeba histolytica and *E. dispar* have cysts that are morphologically indistinguishable, and it was only recently that *E. dispar* came to be considered a distinct species [Gatti et al., 2002]. However, *E. histolytica* is pathogenic, while *E. dispar* is not. In this work we discuss the *E. histolytica/dispar* complex.

RESULTS

Parasite Community

The parasite communities found in the red and black-and-white colobus fecal samples from both the edge and forest interior were similar in terms of the species identified. In both primates we found four species of nematodes, including *Trichuris* sp. (Superfamily Trichuroidea), *Oesophagostomum* sp. (Superfamily Strongyloidea), *Strongyloides fuelleborni* (Superfamily Rhabditoidea), and *Enterobius (Colobenterobius)* sp. (Superfamily Oxyuroidea). We also identified two protozoans: *Entamoeba coli* and *E. histolytica/dispar*.

Red Colobus

We analyzed 645 red colobus samples (forest interior $n = 500$, edge $n = 145$). The richness of the parasite community found in animals from the edge did not differ from that found in animals from the forest interior (interior 0.514/individual vs. edge 0.655/individual; Mann-Whitney $P = 0.110$). However, the percentage of infected individuals with more than one species of parasite was greater in edge groups (29.6%) than in forest interior groups (13.8%; Fig. 1). Similarly, the proportion of individuals with multiple infections was greater in the edge groups than in the forest interior groups ($X^2 = 9.197$, $P < 0.005$).

The prevalence of specific parasites or groups of parasites varied between the edge and forest interior groups (statistics are presented in Fig. 2). Of particular note is that *Oesophagostomum* sp., a potentially deleterious parasite, was 7.4 times more prevalent in red colobus on the edge vs. animals in the forest interior. Similarly, *E. coli* was four times more prevalent in red colobus on the edge compared to animals in the forest interior.

Primate parasite egg output (referred to here as "environmental contamination" and measured by eggs/gram of feces) differed between the edge and forest interior in a fashion similar to that of prevalence (Fig. 3). *Oesophagostomum* sp. egg counts were 10 times higher (Mann-Whitney U-test, $P < 0.0001$) for red colobus from the edge vs. the interior, and there was a marginal trend for *Strongyloides fuelleborni* to be more abundant in samples from the edge compared to samples from the forest interior (Mann-Whitney U-test, $P = 0.067$).

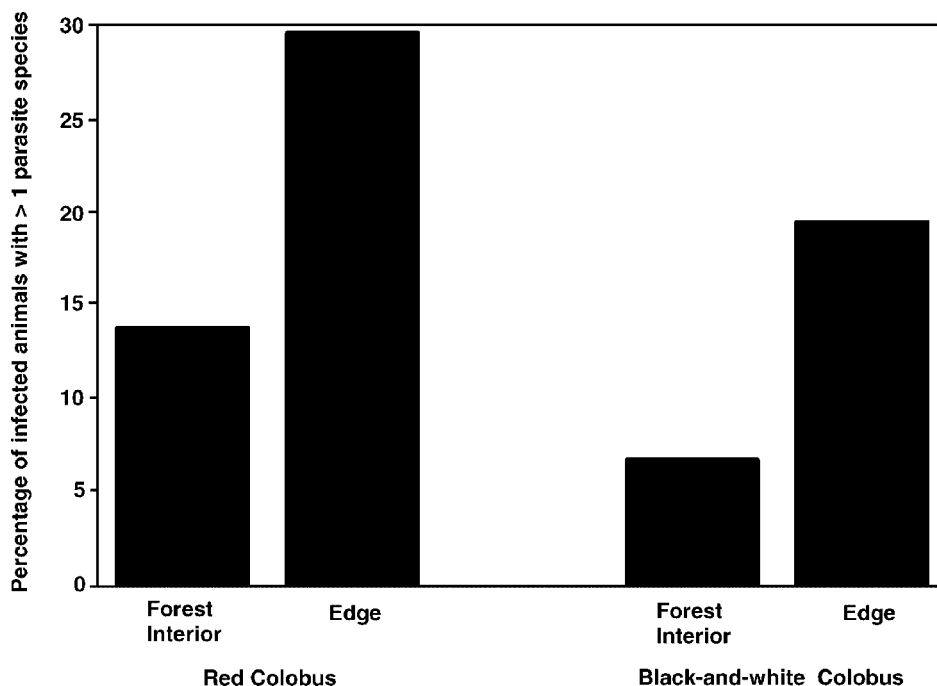


Fig. 1. The percentage of infected red and black-and-white colobus in the interior of Kibale National Park and along its forest edge, with more than one species of parasite present.

Black-and-White Colobus

We analyzed 177 samples from black-and-white colobus (forest interior $n = 103$, edge $n = 74$). There was no tendency for the richness of the parasite community on the edge to be greater than that in the forest interior (interior 1.0/individual vs. edge 0.92/individual; Mann-Whitney $P = 0.287$). However, similarly to the red colobus, the percentage of infected individuals with more than one species of parasite was greater in the edge groups (19.4%) than in the forest interior groups (6.8%; Fig. 1). Also similarly, the proportion of individuals with multiple infections was greater in the edge groups than in the forest interior groups ($X^2 = 5.414$, $P < 0.025$).

For black-and-white colobus there were fewer differences in the prevalence of specific parasites or groups of parasites when the edge and forest interior groups were compared (statistics are presented in Fig. 2). The only difference was the prevalence of *E. coli*, which was significantly higher in animals on the edge compared to animals in the forest interior.

Environmental contamination with primate parasites (eggs/gram of feces) was highly variable, and did not differ between the edge and forest interior with respect to any of the parasites or groups of parasites considered (Fig. 3). This suggests that for black-and-white colobus, environmental contamination is similar between habitats. However, considering that many of the parasites we investigated are directly-transmitted generalists and are found in both black-and-white and red colobus, the infection risk from *Oesophagostomum* sp. and *Strongyloides fuelleborni* (marginal difference) may still be higher on the edge, since red colobus on the edge have higher loads of those species.

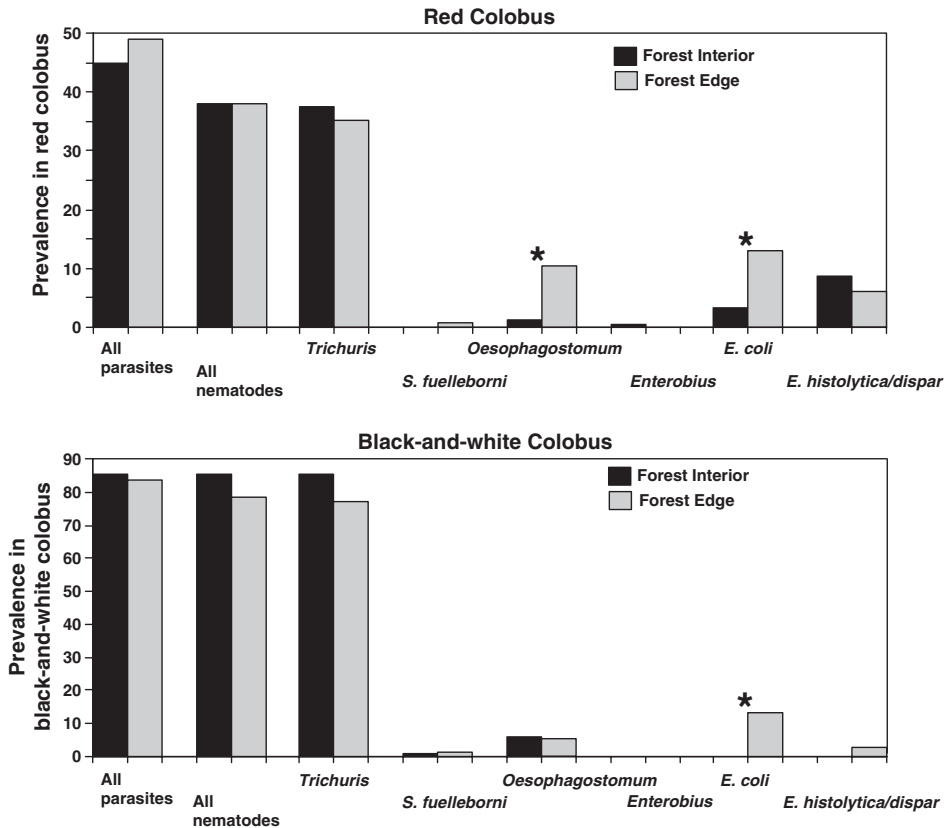


Fig. 2. The prevalence of various parasites or groups of parasites found in red colobus and black-and-white colobus from either the forest interior or the forest/agricultural land edge in Kibale National Park, Uganda (* indicates a difference at $P < 0.05$).

DISCUSSION

This study reveals significant differences in the percentage of infected individuals with more than one species of parasite, the proportion of individuals with multiple infections, the prevalence of specific species, and environmental parasite contamination between colobus that frequent forest edges and those that are found only in the forest interior. Given that edges are a ubiquitous aspect of human disturbance of forest landscapes, it is critical to understand what specific aspects of living on the edge contributed to these differences if these observations are going to be used in the construction of informed management plans.

Edges differ from continuous forest in a number of ways that may influence the probability of transmission and infection. Compared to the forest, the edge receives higher solar radiation, has higher daytime temperatures, and is less moist (in terms of air and soil moisture, and vapor pressure deficit [Kapos, 1989; Murcia, 1995]). These conditions would be expected to negatively impact the infection rate of many of the parasites that infect the colobus. For example, *E. histolytica* outbreaks are associated with heavy rains [Hunter, 2003], and cysts are readily killed by desiccation and high temperatures [Schmidt & Roberts, 1977]. Similarly, in chimpanzee [Huffman et al., 1997] and bonobo [Dupain et al.,

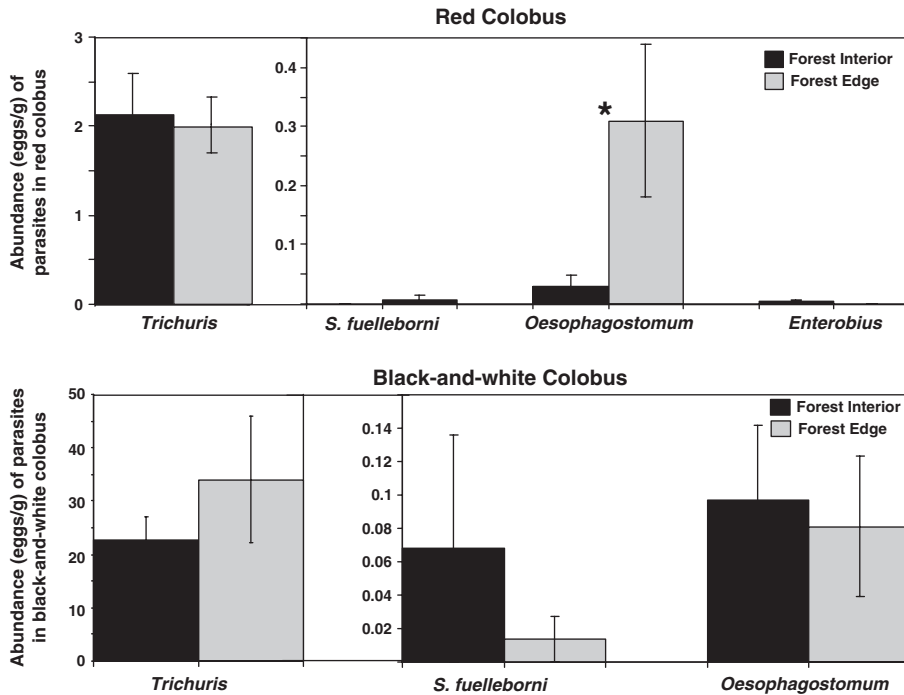


Fig. 3. Environmental contamination with various parasites found in red colobus and black-and-white colobus from either the forest interior or the forest/agricultural land edge in Kibale National Park, Uganda (* indicates a difference at $P < 0.05$).

2002] populations there is a sharp rise in the occurrence of new infections of *Oesophagostomum* sp. after the rains begin, which suggests that new infections may be promoted by moister conditions (*Oesophagostomum* sp. at the infective L3 stage actually can survive long periods of desiccation by shrinking to a fraction of its original size, but when water is available it will swell and resume activity [Polderman & Blotkamp, 1995]). These descriptions of the microclimate on edges, the ability of some parasites to infect hosts during periods of desiccation, and seasonal infection patterns in chimpanzees and bonobos all lead us to suspect that transmission probabilities would be reduced along the edge. However, our study documented an increased prevalence of some parasites on the edges, and thus it seems unlikely that changes in microclimate are driving the differences we documented between the parasite communities in edge and forest colobus.

Edges may be associated with changes in the nutritional status of the host, which could influence its ability to resist parasite infections. Weyher (unpublished data) found that wild foraging baboons had a higher output of helminths than crop-raiding animals [see also Eley et al., 1989; Hahn et al., 2003], and suggested that crop-raiding animals are in better physical condition as a result of the crops they obtain and are thus more able to fight off parasite infections compared to wild, foraging animals. The black-and-white colobus crop-raid, while red colobus do not, and thus they may be benefiting in a similar manner, as indicated by the facts that there were fewer differences in the prevalence of specific parasites, and that parasite loads (eggs/gram) of black-and-white colobus from the edge and the forest interior did not differ, while they did for red colobus. However, the ability of crop-raiding black-and-white colobus to resist parasite

infections does not seem to outweigh other negative aspects of being on the edge, since a number of other indices of parasite infections were elevated in these animals.

Contrasting these results with those obtained by studying colobus in forest fragments [Gillespie & Chapman, in press] allows us to consider which specific aspects of life on the forest edge are negative. The prevalence and richness of gastrointestinal helminth and protozoan parasite infections, as well as the magnitude of multiple infections, were greater for red colobus in fragmented vs. undisturbed forest, but these parameters did not differ between areas for black-and-white colobus. The major difference between the forest edges studied here and the forest fragments is that the fragments are being rapidly degraded, while the edges are not [Chapman et al., 2004; Onderdonk & Chapman, 2000]. The average size of the fragments that supported black-and-white colobus populations was 3.7 ha, and in these fragments the density of stumps averaged 98/ha (range = 0.16–338/ha; the fragment with the fewest stumps was the site of a community-based conservation project). The average size of the fragments with red colobus was 4.1 ha and the density of stumps averaged 84/ha (range = 0.16–337/ha). In contrast, the cutting of trees within the forest park is illegal and occurs very rarely [Chapman et al., in press]. While the richness values of the parasite community in the edge and fragments were similar, there were differences in the prevalence of some species, with fragments always having a higher prevalence (Fig. 4), with the exception that *Oesophagostomum* sp. had a higher prevalence in red colobus along the edge than in the forest fragment. The extraction of trees in the fragments is removing food trees from the colobus monkeys, which suggests that animals in the fragments may be nutritionally stressed and thus their immune system may be compromised. As a result they may not be able to fight off a parasitic infection. Dietary stress has been documented to adversely affect resistance to parasitic infection by reducing the effectiveness of the immune system [Crompton, 1991; Holmes, 1995; Milton, 1996; Solomons & Scott, 1994].

Colobus monkeys on the edge are likely not nutritionally stressed because the forest they inhabit is not being degraded, and the black-and-white colobus may be benefiting nutritionally by crop-raiding. Why then do colobus on the edge have more severe intestinal infections than animals in the interior? There are a number of possibilities: 1) One might think that colobus on the edge have increased contacts with infective-stage larvae since they are on the ground more than interior animals, and that this might explain their increased prevalence. However, if this were the case, black-and-white colobus groups on the edge that frequently crop-raid would be expected to have more severe infections than red colobus, but we documented the opposite pattern. 2) It is possible that the stress that can accompany life on the edge may lead to a suppressed immune response. Primates on the edge are sometimes harassed by people attempting to prevent crop-raiding (e.g., by throwing stones), and along the edges primates interact with local dogs, which have been reported to kill colobus monkeys. Research has documented that human interaction can elevate glucocorticoid stress in wildlife [Creel et al., 2002]. This may lead to a suppressed immune system, which can exacerbate the clinical consequences of parasitic infection [Holmes, 1995]. 3) One thing that forest edges and fragments have in common is that the primates that inhabit them frequently interact with people. People are often at the edge tending their crops, and often guard the crops against crop-raiding animals [Naughton-Treves, 1997]. People also enter the forest to collect deadfall and to engage in a variety of illegal activities, such as setting snares. When in the forest, people often

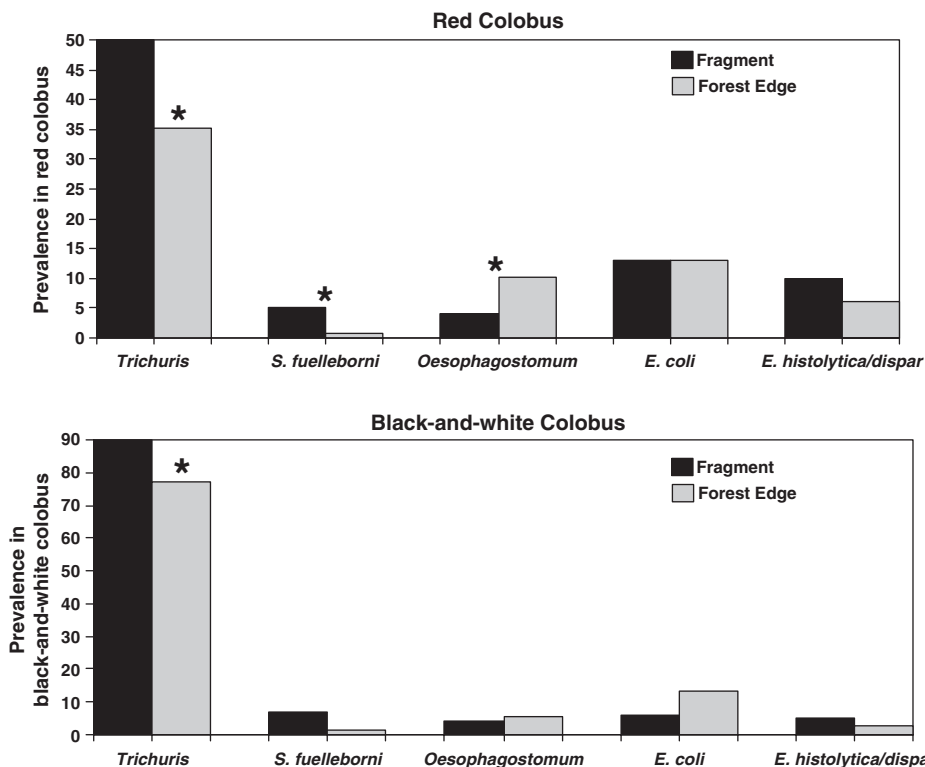


Fig. 4. The prevalence of various parasites found in red colobus and black-and-white colobus from either the forest edge or a forest fragment near Kibale National Park, Uganda (* indicates a difference at $P < 0.05$).

use it as a latrine. Thus, an alternative explanation for elevated indices of parasite infection involving generalist direct lifecycle parasites for colobines living on the forest edge is that there is direct transmission between humans and nonhuman primates. To verify this speculation, more detailed studies (including the identification of all parasites to the species level) are needed. With most of the species described here (i.e., *Trichuris* sp., *Oesophagostomum* sp., and *Strongyloides fuelleborni*), this will likely require extremely detailed morphological analyses of adults and/or molecular studies. A number of previous studies that used only fecal analyses identified *Trichuris trichiura*, *Oesophagostomum* sp., and *Strongyloides fuelleborni* [Jones-Engel et al., 2004; Legesse & Erka, 2004; Muriuki et al., 1998; Phillips et al., 2004; Rothman & Bowman, 2003]. These studies suggested that transmission may be occurring between nonhuman primates and humans, and discussed the implications of this for human health. However, recent molecular studies of *Oesophagostomum bifurcum* indicate that such suggestions should be made with caution. While early molecular studies using relatively simple approaches for genetic differentiation suggested that the *Oesophagostomum* from humans and Mona monkeys were the same species [de Gruijter et al., 2002], more recent studies using high-resolution DNA fingerprinting clearly show clear genetic groupings, with humans being separate from nonhuman primates [de Gruijter et al., 2005]. Similarly, morphological studies that used light and scanning electron microscopy on adult parasites identified as

Trichuris trichiura showed morphological differences between specimens collected from nonprimates and humans [Ooi et al., 1993].

Given that monkeys and apes can share parasites with humans, and that current patterns of land clearance can change the interactions among primates and their parasites, we suggest that understanding the ecology of infectious diseases in nonhuman primates is of paramount importance for both conservation and human-health planning [Chapman et al., 2005]. The challenge that remains for conservation is to connect the patterns we have documented to the demography of primates that frequent edges vs. those that inhabit the interior forest. Several of the parasites that infect colobus in the Kibale region have the capacity to cause substantial damage at high prevalence [Gillespie & Chapman, in press]. Heavy infections of *Oesophogostomum* sp. and *Strongyloides* sp. are associated with mucosal inflammation, ulceration, dysentery, weight loss, and death. Even moderate burdens of *Oesophogostomum* sp. have proved to be clinically important in stressed captive primates [Crestian & Crespeau, 1975]. However, other parasites, such as *Trichuris* sp. and *E. coli*, are typically asymptomatic and may not affect the demography of these populations.

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