American Journal of Primatology 70:222–230 (2008)

RESEARCH ARTICLE

Forest Fragmentation, the Decline of an Endangered Primate, and Changes in Host–Parasite Interactions Relative to an Unfragmented Forest

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Forest fragmentation may alter host–parasite interactions in ways that contribute to host population declines. We tested this prediction by examining parasite infections and the abundance of infective helminths in 20 forest fragments and in unfragmented forest in Kibale National Park, Uganda. Over 4 years, the endangered red colobus (*Procolobus rufomitratus*) declined by 20% in fragments, whereas the black-and-white colobus (*Colobus guereza*) in fragments and populations of both colobines in unfragmented forest remained relatively stable. Seven nematodes (*Strongyloides fulleborni*, *Strongyloides stercoralis*, *Oesophagostomum* sp., an unidentified strongyle, *Trichuris* sp., *Ascaris* sp., and *Colobenterobius* sp.), one cestode (*Bertiella* sp.), and three protozoans (*Entamoeba coli*, *Entamoeba histolytica/dispar*, and *Giardia* sp.) were detected. Infection prevalence and the magnitude of multiple infections were greater for red colobus in fragmented than in unfragmented forest, but these parameters did not differ between forests for black-and-white colobus. Infective-stage colobus parasites occurred at higher densities in fragmented compared with unfragmented forest, demonstrating greater infection risk for fragmented populations. There was little evidence that the nature of the infection was related to the size of the fragment, the density of the host, or the nature of the infection in the other colobine, despite the fact that many of the parasites are considered generalists. This study suggests that forest fragmentation can alter host–parasite dynamics and demonstrates that such changes can correspond with changes in host population size in forest fragments. Am. J. Primatol. 70:222–230, 2008.

Key words: *colobus*; conservation; disturbance ecology; habitat fragmentation; Kibale National Park; parasite species richness

INTRODUCTION

It is well established that forest fragmentation reduces overall species diversity and alters species abundance [Ferraz et al., 2003; Laurance & Bierregaard, 1997], often with cascading effects on ecological processes and community structure [Cordeiro & Howe, 2003; Crooks & Soule, 1999]. However, determining how specific species and processes will be affected by fragmentation has proven difficult. This is well illustrated by studies of primates inhabiting forest fragments. A synthesis of results from previous studies produces no clear generalizations regarding which primates are most susceptible to fragmentation, nor what underlying processes relate to the ability of primates to survive in fragments [Marsh, 2003; Onderdonk & Chapman, 2000; Tutin et al., 1997]. Support for patterns of ranging and diet predicting primate survival in forest fragments has been equivocal, often with an apparent regional bias. For example, studies of neotropical primates suggests that home range size and degree of frugivory are linked to species survival in fragments [Estrada & Coates-Estrada, 1996; Lovejoy et al., 1986], whereas similar studies of African primates find no relationship between these characteristics and species survival in fragments [Onderdonk & Chapman, 2000; Tutin et al., 1997]. It is possible that studies that examine the underlying

Contract grant sponsors: National Centre for Environmental Research; US Environmental Protection Agency; Contract grant sponsor: National Science Foundation; Contract grant number: SBR-990899; Contract grant sponsor: NSERC; Wildlife Conservation Society.

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Received 9 November 2005; revised 16 August 2007; revision accepted 16 August 2007

DOI 10.1002/ajp.20475
Published online 19 September 2007 in Wiley InterScience (www.interscience.wiley.com).

processes associated with the ability of primates to survive in forest fragments will improve our understanding of this interplay. One such process that remains largely unexplored is how fragmentation may alter interactions between hosts and parasites and how this may be linked to the ability of the host to survive and prosper in forest fragments.

Forest fragmentation results in a suite of alterations that may change susceptibility to parasite infection and infection risk (probability of acquiring a new infection). For example, patterns of parasitism in wildlife populations are suggested to be influenced by characteristics of the host, such as ranging patterns, density, intraspecific and interspecific contacts, and diet [Nunn & Altizer, 2006; Nunn et al., 2003], all of which are altered by fragmentation. Reduced habitat area following forest fragmentation may result in restricted ranging and crowding [Lafferty & Holt, 2003; McCallum & Dobson, 2002], increasing habitat overlap among conspecifics and predisposing individuals to a higher probability of pathogen contact. Host density is considered to be of central importance to infection rates in directly transmitted parasites [Anderson & May, 1992] and within-species studies have demonstrated that host density correlates positively with parasite prevalence and diversity [Morand & Poulin, 1998; Packer et al., 1999]. Landscape characteristics of fragment boundaries may influence the frequency and nature of contact among wildlife, human, and livestock populations, increasing the potential for the transmission of generalist pathogens [Lafferty & Gerber, 2002; McCallum & Dobson, 2002]. Conversely, fragmentation may isolate meta-populations, reducing the risk of the introduction of novel parasites from other individuals [Nunn & Altizer, 2006]. Fragmentation may also alter microclimatic features [Kapos, 1989; Murcia, 1995]. Forest edges should be less conducive to parasite transmission because they receive increased wind, increased solar radiation, and are drier than interior forest environments [Fetcher et al., 1985; Murcia, 1995]. The impact of climate on parasite infective stages was demonstrated by Larsen and Roepstorff [1999] in an experiment on the recovery rate of pig parasite eggs. They found a reduction in the number of eggs recovered in the hot, dry summer months compared with fall, spring, and winter months [see also Gillespie, 2001].

Parasite infections are common in nature and are often asymptomatic [Murray et al., 1998]. However, anthropogenic change may alter vector dynamics, transmission rates, parasite host range, and parasite virulence [Daszak et al., 2000; Gillespie et al., 2005a]. Resultant changes in host susceptibility and infection risk could result in elevated morbidity and mortality, and ultimately, the population declines. Parasites can affect host survival and reproduction directly through pathological effects and indirectly by reducing host condition [Chandra & Newberne, 1977; Coop & Holmes, 1996]. Severe infections can lead to blood loss, tissue damage, spontaneous abortion, congenital malformations, and death [Chandra & Newberne, 1977; Despommier et al., 1995]. However, less severe infections are more common and may impair nutrition, travel, feeding, predator escape, and competition for resources or mates or increase energy expenditure [Dobson & Hudson, 1992; Hudson et al., 1992]. Through these proximate mechanisms, parasites can potentially affect host population size and demographic parameters [Gregory & Hudson, 2000; Hochachka & Dhondt, 2000].

To improve our understanding of how fragmentation affects host–parasite interactions, we contrast the nature of gastrointestinal parasite infections in the endangered red colobus (*Procolobus rufomitratus*) and in the black-and-white colobus (*Colobus guereza*) between fragmented and unfragmented habitats. Concurrent censuses of colobus populations allowed us to examine relationships between patterns of infection and changes in host populations. We hypothesized that interspecific differences in the ability to survive in forest fragments will correlate with differences in patterns of parasite infection. We explore explanations for similarities and differences in patterns of parasitism between fragmented and unfragmented forest and address the implications of these findings for conservation and management.

MATERIALS AND METHODS

All research complied with protocols approved by the University of Illinois Institutional Animal Care Committee and adhered to the legal requirements of Uganda.

Research Site

We surveyed 20 forest fragments that lie within the agricultural landscape near the western boundary of Kibale National Park in the foothills of the Rwenzori Mountains in Uganda [0°13′–0°41′ N, 30°19′–30°32′; Chapman & Lambert, 2000; Fig. 1]. These fragments occurred in areas largely unsuitable for agriculture (i.e., swampy valley bottoms, steep forested rims of crater lakes), were used by local citizens to varying degrees, and were surrounded by small-scale agriculture or tea plantations. Fragments ranged from 0.8 to 130 ha in size and averaged 11.0 ha and the inter-fragment distance ranged from 50 to 300 m and averaged 121 m [Onderdonk & Chapman, 2000]. The distance from each patch to Kibale National Park ranged from 0.2 to 7.2 km and averaged 2.8 km [Onderdonk & Chapman, 2000]. Red colobus density averaged 2.1 animals per hectare and ranged from 0 to 8.33 animals per hectare [Chapman et al., 2006], whereas black-and-white colobus density averaged 2.8 animals per hectare and ranged from 0 to 11.5 animals per hectare [Onder-

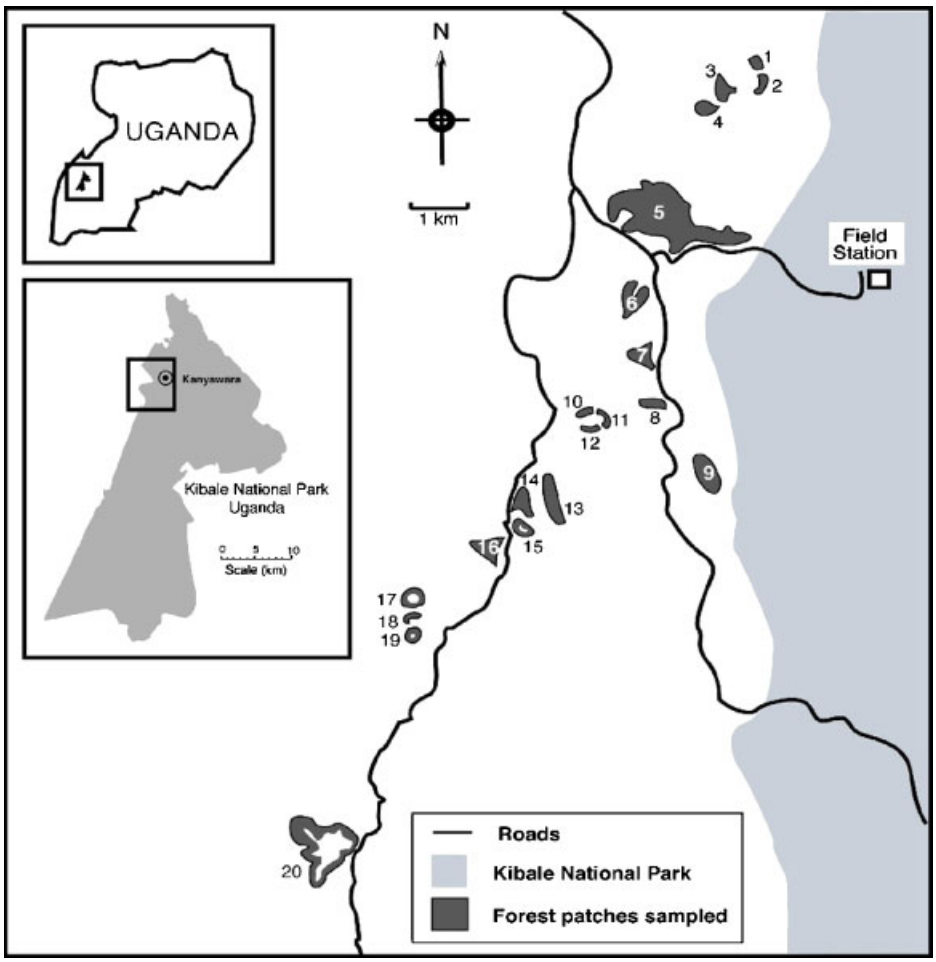

Fig. 1. Twenty forest patches surveyed near the western boundary of Kibale National Park; Uganda. 1 (Kiko #3), 2 (Kiko #4), 3 (Kiko #2), 4 (Kiko #1), 5 (Kasisi), 6 (Rusenyi), 7 (Kyaibombo), 8 (Durama), 9 (C. K.'s Durama), 10 (Rutoma #1), 11 (Rutoma #4), 12 (Rutoma #3), 13 (Rutoma #2), 14 (Nkuruba Fishpond), 15 (Nkuruba Lake), 16 (Ruihamba), 17 (Lake Nyanswiga), 18 (Dry Lake), 19 (Lake Nyaherya), and 20 (Lake Mwamba).

donk & Chapman, 2000]. Before agricultural expansion, mid-elevation, moist, and evergreen forest dominated the region [Naughton et al., 2006]. Although the precise timing of isolation of these forest remnants is not known, local elders describe them as ''ancestral forests'', and aerial photographs from 1959 confirm that most have been isolated from Kibale since at least that time.

We also surveyed compartment K-30, a 282-ha area of unfragmented forest situated within a much larger contiguous forest within Kibale National Park [795 km^2; Struhsaker, 1997]. Red colobus density in this area is 2.2 animals per hectare and black-and-white colobus density in this area is 0.18 animals per hectare [Chapman et al., 2000]. The unlogged compartment K-30 is in close proximity to the forest fragments ($<$6.5 km apart), and once belonged to the same tract of forest, minimizing the probability that differences observed are the result of inherent variation in forest structure. Elevation in the region averages 1,500 m, mean annual rainfall is 1,719 mm (1990–2006), and mean daily minimum and maximum temperatures are 14.9 and 20.2°C, respectively [Chapman & Chapman, unpublished data]. Rainfall is bimodal, with two rainy seasons generally occurring from March to May and September to November.

Fecal Sampling and Analysis

From August 1999 to July 2003, we collected 1,151 fecal samples from primates in forest fragments and the K-30 compartment of Kibale National Park; 951 from red colobus and 200 from black-and-white colobus. Every attempt was made to sample as widely as possible within each primate population; however, as individual recognition was not possible, it is likely that some individuals were sampled more than once. The populations in the forest fragments and continuous forest differed with forest fragments

having smaller groups and fewer infants per female; however, group size does not seem to influence the nature of parasite infections in the unfragmented forest [Chapman et al., in press-a].

All samples were collected immediately after defecation to avoid contamination. Samples were stored individually in 5.0 mL sterile vials in a 10% formalin solution. Preserved samples were examined for helminth eggs and larvae and protozoan cysts using concentration by sodium nitrate flotation and fecal sedimentation [Gillespie, 2006]. Parasites were counted and 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 μm ± SD using an ocular micrometer fitted to a compound microscope. Unknown parasites were photographed for later identification. Coprocultures ($n = 10$ per primate species) and opportunistic necropsies of animals found dead in the forest ($n = 2$ per species) were used to match parasite eggs to larvae and adult worms for positive identification [Gillespie, 2006]. As taxonomic accounts of the gastrointestinal parasites of most wild primates remain unavailable, we often identified parasites to the genus level. *Entamoeba histolytica* and *Entamoeba dispar* have cysts that are morphologically indistinguishable and it was only recently that *E. dispar* was considered a distinct species [Gatti et al., 2002]. However, *E. histolytica* is pathogenic, whereas *E. dispar* is not. Here, we discuss the *E. histolytica*/*dispar* complex. Descriptions of taxa, mode of infection, and associated pathology (largely based on captive animals) for each parasite species recovered are given in Table I. Without using the appropriate immunofluorescent or enzyme-linked immunosorbent assay detection kits [Salzer et al., 2007], accurately determining the presence or absence of protozoan in a sample is difficult, so results on protozoans should be considered as a minimum prevalence.

Infection Risk Assessment

To obtain an index of infection risk, we determined infective-stage parasite densities for canopy vegetation, ground vegetation, and soil plots from fragmented and unfragmented forest. From January to August 2002, we collected 29 1-m^3 vegetation plots at a height of 12 m from canopy trees used within the previous 2 hr by red colobus: 15 from forest fragments and 14 from unfragmented forest. Canopy access for plot collection was facilitated by a single rope-climbing technique [Houle et al., 2004; Mitchell, 1982]. Twenty-nine 1-m^3 ground vegetation plots were collected below all trees sampled for canopy plots. Soil plots (0.05 m^3 surface scratches) were collected within randomly selected ground vegetation plots, 10 from forest fragments and 10 from unfragmented forest. We used a modified sedimentation technique to recover infective-stage parasites from vegetative plots [Sloss et al., 1994]. Soil plots were examined using a modified Baermann method [Sloss et al., 1994]. Samples from all plots were examined by dissection and compound scope, and infective-stage individuals of the two most prevalent parasites, *Trichuris* sp. (eggs) and *Oesophagostomum* sp. (L3 larvae), were counted.

Colobus Surveys

Colobus populations in each forest fragment were surveyed between May and August 2000, and again between May and August 2003. Observers move throughout these small fragments attempting to locate groups and once found, group counts were made. These counts often took many hours and involved observers waiting until the whole group moved across openings in the forest canopy. Our repeated censuses of red colobus and black-and-white colobus over the past three decades within the K-30 compartment of Kibale National Park provide comparable data for these colobus populations [Chapman et al., 2000].

RESULTS

Infection Prevalence and Richness in Fragmented and Unfragmented Forests

Seven nematodes (*Strongyloides fulleborni*, *Strongyloides stercoralis*, *Oesophagostomum* sp., an unidentified strongyle, *Trichuris* sp., *Ascaris* sp., and *Colobenterobius* sp.), one cestode (*Bertiella* sp.), and three protozoans (*Giardia* sp., *Entamoeba coli*, and cysts most closely resembling *E. histolytica*/*dispar*) were detected (Table I). Prevalence of infection with *Trichuris* sp., *Oesophagostomum* sp., *E. coli*, and *E. histolytica*/*dispar* was higher for red colobus from forest fragments compared to red colobus from unfragmented forest, but prevalence did not differ for *S. fulleborni* or *Colobenterobius* sp. (Table II). Only red colobus from forest fragments were infected with *S. stercoralis, Ascaris* sp., *Bertiella* sp., *Giardia* sp., and the unknown strongyle nematode (Table II). There were no species of parasites found only in unfragmented forest. The number of parasite species infecting individual red colobus was greater in forest fragments compared to unfragmented forest ($t = -5.785$, $P < 0.001$, fragmented forest mean = 0.662, unfragmented forest mean = 0.417). There were no relationships between prevalence, load (eggs per gram), or richness of parasite infections in the red colobus and the size of the fragment or density of red colobus or all colobus (red+black-and-white colobus; $P > 0.10$ in all cases), with the exception of a negative relationship between fragment size and *Trichuris* sp. prevalence [$r = -0.621$, $P = 0.024$; for a similar finding with fewer fragments see Gillespie &

TABLE I. Mode of Infection, Morbidity, and Mortality Associated With Gastrointestinal Parasites Infecting Red Colobus (*Procolobus Rufomitratus*) and Black-and-White Colobus (*Colobus Guereza*) in Fragmented and Unfragmented Forests at Kibale National Park, Uganda

Taxonomic group	Parasite species	Mode of infection	Potential morbidity/mortality	Sources
Protozoan	*Entamoeba coli*	Cyst or trophozoite ingested	Typically asymptomatic	Beaver et al. [1984]
	Entamoeba histolytica/dispar	Cyst or trophozoite ingested	Hepatic and gastric amoebiasis, death	Loomis [1983]
	Giardia sp.	Cyst ingested	Typically asymptomatic, possibly epizoonotic	Baskin [1993]; Fiennes [1967]
Nematoda	*Oesophagostomum* sp.	Larvae ingested	Severe diarrhoea, weight loss, death	Crestian & Crespeau [1975]; Roperto et al. [1985]
	Strongyloides fulleborni	Larvae ingested, skin penetration	Mucosal inflammation, ulceration, death	McClure & Guilloud [1971]; Pampiglione & Ricciardi [1972]
	Strongyloides stercoralis	Larvae ingested, skin penetration	Mucosal inflammation, ulceration, death	McClure & Guilloud [1971]; Pampiglione & Ricciardi [1972]
	Trichuris sp.	Larvated egg ingested	Typically asymptomatic	Baskin [1993]; Beaver et al. [1984]
	Unknown strongyle	Larvae ingested and/or skin penetration	Mucosal inflammation, ulceration, death	McClure & Guilloud [1971]; Pampiglione & Ricciardi [1972]
	Colobenterobius sp.	Larvated egg ingested	Dysentery, enteritis, ulceration, death	Baskin [1993]; Beaver et al. [1984]
	Ascaris sp.	Larvated egg ingested	Intestinal obstruction, death	Baskin [1993]; Beaver et al. [1984]
Cestoda	*Bertiella* sp.	Mite infected with cysticercoid larvae ingested	Typically asymptomatic	Baskin [1993]; Beaver et al. [1984]

Mortality and morbidity data come primarily from captive studies, so evaluating their impact on wild animals should be made with caution. All of these species are considered generalists and can infect both primates and humans.

TABLE II. Prevalence (%) of Gastrointestinal Parasite Infections in Red Colobus (*Procolobus Rufomitratus*) from Forest Fragments and Unfragmented Forests in Kibale National Park, Uganda

Parasite species	Fragmented ($n = 390$)	Unfragmented ($n = 561$)	Significance*
Ascaris sp.	<1	0	NA
Bertiella sp.	<1	0	NA
Colobenterobius sp.	<1	1	NS
Entamoeba coli	13	3	****
Entamoeba histolytica/dispar	10	3	***
Giardia sp.	6	0	NA
Oesophagostomum sp.	4	2	**
Strongyloides fulleborni	5	4	NS
Strongyloides stercoralis	2	0	NA
Trichuris sp.	50	36	****
Unidentified strongyle	6	0	NA
Overall	50	37	****

*χ^2tests of raw values; **$P<0.05$; ***$P<0.005$; ****$P<0.001$; NS = not significant; $P>0.05$; NA = not applicable; no χ^2 test performed as one forest type had zero prevalence.

TABLE III. Prevalence (%) of Gastrointestinal Parasite Infections in Black-and-White Colobus (*Colobus Guereza*) from Forest Fragments and Unfragmented Forests in Kibale National Park, Uganda

Parasite species	Fragmented ($n = 94$)	Unfragmented ($n = 106$)	Significance*
Ascaris sp.	6	0	NA
Entamoeba coli	6	9	NS
Entamoeba histolytica/dispar	5	9	NS
Oesophagostomum sp.	4	9	NS
Strongyloides fulleborni	7	3	NS
Trichuris sp.	90	84	NS
Unidentified strongyle	5	0	NA
Overall	90	84	NS

*χ^2 tests of raw values; NS = not significant; $P>0.05$; NA = not applicable; no χ^2 test performed as one forest type had zero prevalence.

Chapman, 2006]. For species occurring at low prevalence (Table II), this analysis should be considered preliminary as a larger sample would have been desirable.

For black-and-white colobus, the prevalence of infection with *Trichuris* sp., *Oesophagostomum* sp., *E. coli*, *E. histolytica/dispar*, and *S. fulleborni* did not differ between animals in forest fragments and unfragmented forest (Table III). Only black-and-white colobus from forest fragments were infected with *Ascaris* sp. and the unknown strongyle nematode (Table III). There were no species of parasite found only in unfragmented forest. The number of parasite species infecting individual black-and-white colobus did not differ between forest fragments and unfragmented forest ($t = -0.219$, $P = 0.827$, fragmented forest mean = 1.03, unfragmented forest mean = 0.97). As was demonstrated for the red colobus, again there were no relationships between prevalence, load (eggs per gram), or richness of parasite infections in the red colobus and the size of the fragment, density of red colobus, or density of all colobus (red+black-and-white colobus; $P>0.16$ in all cases), with the exception of the prevalence of *Trichuris* sp., which was marginally related to the size of the fragment ($r = -0.468$, $P = 0.079$).

Many of these parasites are considered generalists and thus can occur in many hosts (Table I). If this is the case, one would expect that infections in one colobus species might promote infections in the second species (i.e., the first species acts as a reservoir). However, correlating the prevalence or load of each parasite in one colobus monkey species to the prevalence or load in the other colobus was nonsignificant in all cases ($P>0.30$). Similarly, the richness of infection in one colobus species was not correlated to the richness in the second species ($r = 0.460$, $P = 0.299$). The lack of a relationship with richness might be a reflection that the richness of infections was relatively low (zero to four species in any one individual) and that prevalence of some rare parasites was low.

Infection Risk

Trichuris sp. eggs were more abundant in canopy plots (fragmented mean = 1.36 ± 0.35 SD, unfragmented mean = 0.47 ± 0.25, $t = -2.43$, $P = 0.022$) and ground vegetation plots (fragmented mean = 1.87 ± 0.48, unfragmented mean = 0.43 ± 0.26, $t = -2.40$, $P = 0.026$) from fragmented compared with unfragmented forest. *Oesophagostomum* sp. L3 larvae were more abundant in ground vegetation plots from fragmented compared with unfragmented forest (fragmented mean = 3.33 ± 0.64, unfragmented mean = 0.14 ± 0.11, $t = -4.95$, $P<0.001$), but were not found in canopy plots. No infective-stage primate parasites were identified from the soil plots in either the fragmented or unfragmented forest.

Colobus Population Size

Of the forest fragments censused, 10 had red colobus and persisted for the duration of the study

(i.e., were not cleared). In these fragments, red colobus declined from 163 individuals in 2000 to 131 individuals in 2003, a 20% reduction. Of the forest fragments censused, 12 had black-and-white colobus and were not cleared over the duration of the study. In these fragments, black-and-white colobus increased from 97 individuals in 2000 to 101 individuals in 2003, a 4% increase.

Results of our censuses of red colobus and black-and-white colobus over the past three decades in the K-30 compartment of the Kibale National Park demonstrate that the densities of both colobus species are stable [Chapman et al., 2000].

DISCUSSION

Red colobus in forest fragments had a higher prevalence of four of five gastrointestinal parasites recorded for colobines in both fragmented and unfragmented forests, and harbored five additional parasites that occur only in fragment colobines. In contrast, none of these parameters differed between fragmented and unfragmented forest populations of black-and-white colobus, despite infection risk with two generalist parasites being higher for both colobines in forest fragments. These results support our hypothesis that forest fragmentation can be associated with changes in an important ecological association, host–parasite systems. Furthermore, the nature of red colobus infections were promoted by fragmentation, whereas black-and-white infections were not, and for those fragments that were not cleared, the red colobus populations had declined, whereas the black-and-white populations had not.

Host density is considered to be of central importance to infection rates in directly transmitted parasites [Anderson & May, 1992] and within-species studies have shown that host density correlates positively with parasite prevalence and diversity [Morand & Poulin, 1998; Packer et al., 1999]. There were considerable differences in colobus density between the fragmented and unfragmented forests as well as among fragments; however, patterns of colobus density did not correlate with infection prevalence. Consequently, the patterns of parasitism observed in colobines in forest fragments do not seem to be the result of density-dependent factors. However, we have shown previously that when colobus density rose suddenly as the result of the immigration of animals into a fragment because of the complete deforestation of neighboring fragments that the prevalence of *Trichuris* sp. increased in both colobus species. Over the next 5 years, the prevalence and intensity of infection of *Trichuris* sp. in red colobus declined and their population numbers increased slowly. In contrast, the prevalence and intensity of infection of *Trichuris* sp. increased in black-and-white colobus and remained high following the immigration and their population size declined [Chapman et al., 2005]. The differences between these studies in the role of density may reflect that in the later case, the sudden immigration pushed the population well above carrying capacity and thus the animals were stressed nutritionally. We have shown previously a synergy between nutritional status, parasite infection levels, and populations change [Chapman et al., in press-b; Chapman et al., 2006]. Thus, density per se may not be important in this system, possibly because the colobus are already at very high densities, and density may only seem to be important because it is associated with an increased probability of animals being stressed nutritionally.

Our results present conflicting evidence with regard to whether humans and livestock are exposing colobus in forest fragments to novel pathogens. Four species infecting red colobus, *S. stercoralis*, *Ascaris* sp., *Giardia* sp., and an unknown strongyle, and two species infecting black-and-white colobus, *Ascaris* sp., and the unknown strongyle nematode are possibly of human or domestic animal origin. We make this statement because these generalist parasites occur at high frequency in the human populations in the region [NEMA, 1997], but are absent from colobus within Kibale National Park, where the people and primates interact at a greatly reduced frequency [Gillespie et al., 2005a,b]. This suggests that humans and livestock may act as reservoirs, maintaining a high infection risk for parasites that are detrimental to red colobus, even as red colobus densities decline toward extinction in fragments [Holt et al., 2003; McCallum & Dobson, 2002]. However, we found no evidence of a positive association between the nature of the infections in the two colobines, suggesting that transmission among these species is not occurring. These conflicting results indicate that further investigations are needed to determine if transmission is occurring among species. This suggestion is supported by recent molecular studies of *Oesophagostomum bifurcum*. Although early molecular studies using relatively simple approaches for genetic differentiation suggested that the *Oesophagostomum* from humans and Mona monkeys (*Cercopithecus mona*) were of the same population [Gasser et al., 1999], more recent studies using high resolution DNA fingerprinting clearly show clear genetic groupings with humans being separate from nonhuman primates [Gruijter et al., 2005]. Similarly, morphological studies of adults using light and scanning electron microscopy of parasites identified as *Trichuris trichiura* show morphological differences between specimens collected from nonprimates and those from humans [Ooi et al., 1993]. The use of such tools would be extremely useful in determining if transmission of parasites among human, nonhuman primates, and

livestock is occurring in this system of forest fragments.

Our understanding of how anthropogenic habitat change alters the quality of a habitat for wildlife is in its infancy and this is especially true for how it alters disease dynamics. It is unlikely that there will be reliable and broadly applicable single-factor explanations for complex biological phenomena such as population density and long-term studies have highlighted the importance of multifactor explanations [Chapman et al., in press-b; Milton, 1996]. The colobines in the forest fragment are experiencing differences in nutrition [Chapman et al., 2004] and likely predation associated with fragmentation. However, this study indicated that patterns of parasitism may play a significant role in determining the ability of specific species to survive in forest fragments. A greater understanding of the role of parasitism and how it is influenced by factors such as host nutrition will greatly improve the ability of conservationists to make rational decisions about the risks and benefits of extraction and management activities.

ACKNOWLEDGMENTS

Permission to conduct this research was granted by the Uganda Wildlife Authority, the Ugandan National Council of Science and Technology, and the Office of the President of Uganda. This research complied with animal care regulations and applicable laws for Uganda and the United States. We thank Evelina Jagminaite, Dennis Sebugwawo, and members of the Kibale Fish and Monkey Project for field assistance; Ellis Greiner for assistance in identifying unknown parasites; and Sara Hawkins, Joseph Mahoney, and Jennifer Zipser for laboratory assistance. Sue Boinski, Lauren Chapman, Ellis Greiner, Robert Holt, and Michael Huffman provided helpful comments on this manuscript.

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