
Prediction of Parasite Infection Dynamics in Primate Metapopulations Based on Attributes of Forest Fragmentation

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Abstract: *Although the effects of forest fragmentation on species and ecological processes have been the focus of considerable research in conservation biology, our capacity to predict how processes will be altered and which taxonomic or functional groups will be most affected by fragmentation is still poor. This problem is exacerbated by inherent temporal and spatial variability in fragment attributes. To improve our understanding of this interplay, we examined how various fragment attributes affect one potentially important ecological process, parasite infection dynamics, and considered how changes in this process affect host metapopulations. From August 1999 to July 2003 we surveyed red colobus (*Piliocolobus tephrosceles*) metapopulations inhabiting nine fragments (1.2 to 8.7 ha) in western Uganda to determine the prevalence and richness of strongyle and rhabditoid nematodes, a group of potentially pathogenic gastrointestinal parasites. We used noninvasive fecal flotation and sedimentation (n = 536) to detect parasite eggs, cysts, and larvae in colobus fecal samples. To obtain an index of infection risk, we determined environmental contamination with *Oesophagostomum* sp., a representative strongyle nematode, in canopy (n = 30) and ground vegetation plots (n = 30). Concurrently, physical (i.e., size, location, and topography) and biological (i.e., tree diversity, tree density, stump density, and colobine density) attributes were quantified for each fragment. Interfragment comparisons of nine potential factors demonstrated that an index of degradation and human presence (tree stump density) strongly influenced the prevalence of parasitic nematodes. Infection risk was also higher in the fragment with the highest stump density than in the fragment with the lowest stump density. These results demonstrate that host-parasite dynamics can be altered in complex ways by forest fragmentation and that intensity of extraction (e.g., stump density) best explains these changes.*

Key Words: anthropogenic pathogens, disturbance ecology, infection risk, Kibale National Park, *Piliocolobus tephrosceles*, Uganda

Predicción de la Dinámica de la Infección Parasitaria en Metapoblaciones de Primates con Base en Atributos de la Fragmentación de Bosques

Resumen: *A pesar de que los efectos de la fragmentación de bosques sobre especies y procesos ecológicos han sido el foco de considerable atención en la biología de la conservación, nuestra capacidad para predecir como se alterarán los procesos y que grupos taxonómicos o funcionales serán mas afectados por la fragmentación aun es pobre. Este problema se agrava por la inherente variabilidad espacial y temporal en los atributos de los fragmentos. Para mejorar nuestro conocimiento de esta interacción, examinamos el efecto de varios atributos de los fragmentos sobre uno de los procesos ecológicos potencialmente importante, la dinámica de la*

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infección parasitaria, y consideramos como pueden afectar a las metapoblaciones de huéspedes los cambios en este proceso. De agosto 1998 a julio 2003, muestreamos metapoblaciones de colobos rojos (*Ptilocolobus tephrosceles*) en nueve fragmentos (1.2–8.7 ha) en Uganda occidental para determinar la prevalencia de parásitos gastrointestinales patógenos. Utilizamos técnicas no invasoras de flotación y sedimentación fecal ($n = 536$) para detectar huevos, quistes y larvas de parásitos en muestras fecales de colobos. Para obtener un índice de riesgo de infección, determinamos la contaminación ambiental con *Oesophagostomum sp.*, un nematodo estrombilo representativo, en parcelas en el dosel ($n = 30$) y sobre el suelo ($n = 30$). Concurrentemente, cuantificamos atributos físicos (i. e., tamaño, localización, topografía) y biológicos (diversidad de árboles, densidad de árboles, densidad de tocones y densidad de colobos) en cada fragmento. La comparación de 9 factores potenciales entre fragmentos demostró que un índice de degradación y de presencia humana (densidad de tocones) influyó significativamente en la prevalencia de nemátodos parásitos. El riesgo de infección también fue mayor en el fragmento con la mayor densidad de tocones en comparación con los fragmentos con la menor densidad de tocones. Estos resultados demuestran que la dinámica hospedero-parásito puede ser alterada por la fragmentación de bosques y que la intensidad de extracción (e.g., densidad de tocones) es la mejor explicación de estos cambios.

Palabras Clave: ecología de la perturbación, riesgo de infección, patógenos antropogénicos, *Ptilocolobus tephrosceles*, Parque Nacional Kibale, Uganda

Introduction

For fragmented forests to have conservation value, they must retain sufficient ecological integrity to maintain species and biological processes over the long term. Despite the large scope of research examining forest fragmentation, our capacity to predict how ecological processes will be altered and which taxonomic or functional groups will be most affected by fragmentation is still poor. Such difficulties are well illustrated by primates inhabiting forest fragments. No clear generalizations emerge as to what types of primates are most susceptible to fragmentation or what types of fragments are most likely to support primates, despite a growing body of research (Tutin et al. 1997; Onderdonk & Chapman 2000; Marsh 2003). Our inability to evaluate the potential of forest fragments for primate conservation appears to be driven by several factors. First, most previous work has been conducted in fragments protected from human use (Tutin et al. 1997; Gilbert 2003); typical fragments, however, are not protected and are characterized by open access by private citizens who depend on the fragments for fuelwood, medicinals, or bushmeat (Chapman et al. 2003). Although studies involving protected fragments have provided invaluable insights into how physical attributes such as fragment size, shape, and degree of isolation affect resident wildlife, they may have biased our perception of the value of real-world forest fragments for conservation.

Second, a number of simple logical predictions relating to primates in forest fragments have not proven to be general. For example, home range size was frequently cited as influencing a species' ability to survive in a fragment (Estrada & Coates-Estrada 1996). Onderdonk and Chapman (2000), however, found no relationship between home range size and ability to live in fragments for a community of primates in western Uganda. Similarly, it has

been suggested that a highly frugivorous diet may limit the ability of a species to live in fragments (Estrada & Coates-Estrada 1996). Tutin et al. (1997), however, found that several frugivorous species were at higher or similar densities in forest fragments than in the intact forest of Lopé Reserve, Gabon (see also Tutin 1999; Onderdonk & Chapman 2000).

Lastly, past studies often focused on simple correlates to primate metapopulation viability in forest fragments. Finding single correlative explanations for complex biological phenomena, however, such as determinants of primate abundance in fragments, is unlikely. This problem is exacerbated by inherent temporal and spatial variability in fragment attributes. Researchers have highlighted the importance of physical attributes such as fragment size, shape, and isolation (Laurance & Bierregaard 1997) and biological attributes such as predator, prey, and tree density and diversity on ecological processes and species survival probabilities (Crooks & Soulé 1999; Terborgh et al. 2001; Laurance et al. 2002). How such attributes affect parasites and infectious disease in primate population dynamics in forest fragments remains largely unexplored.

Helminthic and protozoal parasites can affect host survival and reproduction directly through pathological effects and indirectly by reducing host condition (Chandra & Newberne 1977; Boyce 1990; Coop & Holmes 1996). Severe parasitosis can lead to blood loss, tissue damage, spontaneous abortion, congenital malformations, and death (Chandra & Newberne 1977; Despommier et al. 1995). Less severe infections, however, 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; Packer et al. 2003). Through these proximate mechanisms, parasites can potentially regulate host populations (Gregory & Hudson 2000; Hochachka &

Dhondt 2000). For example, based on a 68-month study of howler monkeys (*Alouatta palliata*) and a parasitic bot fly (*Alouattamyia baeri*), Milton (1996) concluded that the annual pattern of howler mortality results from a combination of effects, including age, physical condition, and larval burden of the parasitized individual, which becomes critical when the population experiences dietary stress (see also Milton et al. 1994). Similarly, Gulland (1992) studied the interactions of Soay sheep and nematode parasites and demonstrated that at times of population crashes, sheep were emaciated, had high nematode burdens, and showed signs of protein-energy malnutrition. In the field, sheep treated with antihelminthics had lower mortality rates, whereas experimentally infected sheep with high parasite loads, but fed nutritious diets, showed no sign of malnutrition.

To improve our capacity to evaluate the conservation value of forest fragments, we examined how various fragment attributes affect one ecological process, parasite infection dynamics, and consider how changes in this process may affect host metapopulations of red colobus (*Piliocolobus tephrosceles*, Oates 1994) inhabiting a series of forest fragments in western Uganda.

Methods

Study Species and Site

Colobinae is a large subfamily of leaf-eating Old World monkeys represented in Africa by species of three genera: *Colobus*, *Procolobus*, and *Piliocolobus* (Grubb et al. 2002). These monkeys live in groups of highly variable size (5–300 individuals), often form mixed-species associations with other primates, and have a complex digestive tract that allows them to digest leaves (Struhsaker 1981; Oates 1994; Chapman & Chapman 2000). African colobines are forest dependent and, consequently, 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 distur-

bance (WRI 1998), and forest cover continues to decline at 0.7% annually (FAO 1999). Largely because of this habitat loss, 50% of African colobine species are endangered, and an additional 20% are rare (Grubb et al. 2002; IUCN 2004 Red List). *P. tephrosceles* is one of the most endangered of the colobines, with a patchy distribution across central Africa. We surveyed nine forest fragments supporting this red colobus species that lie within the agricultural landscape adjacent to the western boundary of Kibale National Park and in the foothills of the Ruwenzori Mountains in Uganda. Elevation in the region averages 1500 m, mean annual rainfall in the region is 1741 mm (1990–2003), and mean daily minimum and maximum temperatures are 14.9° C and 20.2° C (1990–2001) (Chapman et al. 2002). Rainfall is bimodal, with two rainy seasons generally occurring from March to May and September to November.

Before agricultural expansion, midelevation, moist, evergreen forest dominated the region (Naughton-Treves 1997). 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 (Chapman et al. 2003). Fragments range from 1.2 to 8.7 ha and occur in areas largely unsuitable for agriculture (i.e., forested, swampy valley bottoms, steep forested rims of crater lakes; Table 1). These fragments are used by local villagers to varying degrees and are surrounded by small-scale agriculture or tea plantations (Table 1).

Fecal Sampling and Analysis

From August 1999 to July 2003 we collected 536 fecal samples from red colobus in forest fragments to determine the prevalence of infection with strongyle and rhabditoid nematodes, a group of potentially pathogenic parasites. Samples were collected from habituated and semihabituated adult and subadult males and females. We made every attempt to sample as widely as possible within

Table 1. Prevalence (%) of strongyle and rhabditoid nematode infections in red colobus monkeys (*Piliocolobus tephrosceles*) in forest fragments near Kibale National Park, Uganda.

Fragment	<i>n</i>	Oesophagostomum <i>sp.</i>	Unidentified <i>strongyle</i>	Strongyloides fulleborni	Strongyloides stercoralis	All
Bugembe	31	3	16	6	0	25
CK	66	2	2	0	0	4
Kifuruka	53	2	0	4	0	6
Kiko 1	45	5	9	11	9	34
Kiko 2	40	7	0	9	0	16
Kiko 3	25	24	28	16	12	68
Kiko 4	44	3	9	5	0	17
Nkuruba	179	<1	0	0	0	<1
Rutoma	53	0	6	0	0	6
Average		5	8	6	2	20

each metapopulation. Individual recognition was not always possible, so some individuals may have been sampled more than once. All samples were collected immediately after defecation to avoid contamination and examined macroscopically for adult nematodes. Samples were stored individually in 5.0-mL sterile vials in a 10% formalin solution. Preserved samples were transported to the University of Florida where they were examined for nematode eggs and larvae after concentration by sodium nitrate flotation and fecal sedimentation (Sloss et al. 1994). Nematodes were counted and identified on the basis of egg or larvae color, shape, contents, and size (Gillespie 2004). We took measurements to the nearest $0.1 \mu\text{m} \pm \text{SD}$ with an ocular micrometer fitted to a compound microscope. Unknown parasites were photographed for later identification. Coprocultures ($n = 10$) and opportunistic necropsies ($n = 2$) (MAFF 1979; Gillespie 2006) facilitated positive identification of nematode eggs to larvae and adult worms. Because taxonomic accounts of the gastrointestinal parasites of red colobus remain unavailable, we often identified parasites only to the genus or family level.

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 a fragment with high stump density (Kiko 3) and one with low stump density (Nkuruba). From January to August 2002 we sampled 30 1-m^3 vegetation plots (15 from each fragment) at a height of 12 m within canopy trees used within the previous 2 hours by red colobus. We used the single rope-climbing technique to access the canopy plots (Laman 1995; Houle et al. 2004). We sampled 30 1-m^3 ground vegetation plots below all trees sampled for canopy plots. We sampled soil plots (0.05 m^3 surface scratches) within randomly selected ground vegetation plots, 10 from Kiko 3 and 10 from Nkuruba. 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). We examined samples with dissecting and compound microscopes and counted infective-stage individuals of the most prevalent strongyle nematode, *Oesophagostomum* sp. (L3 larvae).

Fragment Characteristics

Forest fragment attributes quantified were forest fragment size and type, distance from fragment to Kibale and to the next nearest fragment, and number of trees per hectare, tree species per hectare, tree stumps per hectare, red colobus per hectare, and total colobines per hectare. We measured the size of each fragment, taking GPS readings at locations along fragment edges or measuring fragment perimeters with a 50-m tape measure. We classified

fragments as crater lake, hillside, or valley bottom. Crater lake and hillside fragments ($n = 4$) were forests on steep hills or sides of volcanic explosion craters; for analyses, they were considered together. Valley-bottom fragments ($n = 5$) had swamp vegetation at their lowest levels. Consequently valley-bottom fragments may retain greater humidity, potentially providing a better environment for the development of nematodes during their free-living stage.

Distance to Kibale National Park and nearest fragment were straight-line distances measured from topographic maps. The behavioral ecology and dispersal patterns of red colobus in forest fragments are largely unknown, so the degree of isolation of colobus populations is also unknown. We selected 50 m as an arbitrary cutoff for minimal distance between fragments because it provides an order of magnitude of variation in regards to isolation (50 m for Kiko 1 to 500 m for Bugembe).

At each fragment we identified and measured all trees >10 cm dbh (diameter at breast height; Chapman et al. 2003). Sizes of trees on very steep craters were visually estimated (error in visual estimation = $\pm 3.7\%$, $n = 46$). Because colobus rarely feed in small trees (Gillespie & Chapman 2001), this represents a nearly complete inventory of all colobus potential food sources. We also counted all tree stumps remaining after harvest by local people. To do this, we carefully searched through vine tangles and dense herbaceous vegetation for hidden stumps. For most tree species, the stump will remain for several years. Because stump density shows a strong positive relationship with the frequency of extractive endeavors (i.e., charcoal production, brick manufacture, pit sawing, beer brewing, and alcohol distillation; Chapman et al. 2003), we used this tree-stump inventory as an index of habitat degradation.

Because parasite dynamics can be influenced by host density, we conducted sweep censuses (Chapman et al. 2000) to determine the density of red colobus and black-and-white colobus (*Colobus guereza*). We included total colobine density as well as red colobus density in the biological attributes we examined because black-and-white colobus may serve as a reservoir host for red colobus infection with shared parasites (Gillespie et al. 2005b).

Results

Mean fragment size of the nine fragments surveyed was 5.11 ha (range 1.20–8.70 ha). Five of the fragments were classified as valley bottom and four as crater lake or hillside. Mean distance to Kibale National Park was 2.4 km (range 0.2–6.5 km) and to the nearest fragment was 142 m (range 50 [the criteria for an isolated fragment] to 500 m). Mean tree density was 133 trees/ha (range 27–445 trees/ha). There was a mean of 15.9 tree species/ha (range 4–73 species/ha). The level of degradation of the fragments

was highly variable, and stump density average was 69.2 stumps/ha (range 0.16–221.76 stumps/ha). Red colobus density averaged 3.70 red colobus/ha (range 0.55–8.33 colobus/ha). Mean colobine density (red colobus and black-and-white colobus) was 5.52 colobines/ha (range 1.66–9.41 colobines/ha).

Four types of strongyle or rhabditoid nematodes were found in red colobus inhabiting forest fragments: *Oesophagostomum* sp., *Strongyloides fulleborni*, *S. stercoralis*, and an unidentified strongyle (Table 1). Mean prevalence among fragments of *Oesophagostomum* sp. was 5%, but the range was 0 to 24%. *S. fulleborni* prevalence averaged 6% among fragments and ranged from 0 to 16%. The prevalence of *S. stercoralis* was the lowest of all nematodes examined averaging 2% among fragments, but it ranged from 0 to 12%. Mean prevalence of the unidentified strongyle was 8% (range 0–28%). In general, the average prevalence of strongyles collectively was 20% (range < 1–8%).

Fragment size correlated negatively with red colobus density ($r = -0.749$, $p = 0.020$), total colobus density ($r = -0.705$, $p = 0.034$), and stump density ($r = -0.811$, $p = 0.008$). Tree density correlated positively with the number of tree species per hectare ($r = 0.906$, $p = 0.001$). Red colobus density correlated positively with total colobus density ($r = 0.792$, $p = 0.011$). Individually and collectively, the prevalence of all strongyles and rhabditoids correlated positively with stump density (Table 2). With the exception of *Oesophagostomum* sp., prevalence of all strongyles and rhabditoids, individually and collectively, correlated negatively with fragment size (Table 2). *S. stercoralis* prevalence correlated positively with red colobus and total colobine density (Table 2).

When predicting strongyle and rhabditoid prevalence with a step-wise multiple regression that included stump density, fragment size, and colobus density, stump density explained 85% of the variance ($F = 38.84$, $R^2 = 0.847$, $p < 0.001$). Fragment size and colobus density did not account for a significant proportion of the variance when considered in relation to stump density. The trend was

the same when examining each nematode species individually, with stump density accounting for 61% of the variance in *Oesophagostomum* prevalence ($F = 13.41$, $R^2 = 0.608$, $p = 0.008$), 76% of the variance in *S. fulleborni* prevalence ($F = 21.64$, $R^2 = 0.756$, $p = 0.002$), 91% of the variance in *S. stercoralis* prevalence ($F = 71.66$, $R^2 = 0.911$, $p < 0.001$), and 59% of the variance in prevalence of the unidentified strongyle ($F = 9.93$, $R^2 = 0.587$, $p = 0.016$). In each of these comparisons, fragment size and colobus density did not account for a significant proportion of the variance when considered in relation to stump density.

Oesophagostomum sp. L3 larvae were more abundant in ground vegetation plots from Kiko 3, the fragment with high stump density, compared with Nkuruba, which had low stump density (Kiko 3 mean = 3.33 ± 0.64 larvae/m³, Nkuruba mean = 0.82 ± 0.98 larvae/m³, $t = -2.87$, $p = 0.005$). *Oesophagostomum* sp. L3 larvae were not found, however, in canopy or soil plots.

Discussion

Our results demonstrate that an index of habitat degradation—stump density—best explained the prevalence of red colobus strongyle and rhabditoid nematode infections in forest fragments in western Uganda. We also found a greater risk of infection with nematodes in the fragment with the highest stump density than in the fragment with the lowest stump density. In some cases, fragment size and colobine density were also related to prevalence, but these variables did not explain a significant amount of variation that was independent of stump density. These results establish that host-parasite dynamics can be altered in complex ways by forest fragmentation and that intensity of extraction (e.g., stump density) best explains these changes in western Uganda.

We were surprised to find such a strong relationship between infection prevalence and a single attribute because all the attributes examined were selected as likely

Table 2. Correlation matrix of strongyle and rhabditoid nematode prevalence in red colobus monkeys (*Ptilocolobus tephrosceles*) and attributes of the forest fragments they inhabit near Kibale National Park, Uganda.*

	<i>Oesophagostomum</i> sp. (p)	<i>Strongyloides</i> fulleborni (p)	<i>Strongyloides</i> stercoralis (p)	<i>Unidentified</i> strongyle (p)	All (p)
Fragment size	-0.581 (0.101)	-0.777 (0.014)	-0.835 (0.005)	-0.730 (0.025)	-0.811 (0.008)
Fragment type	-0.220 (0.570)	0.049 (0.901)	-0.014 (0.971)	-0.409 (0.274)	-0.185 (0.634)
Distance to Kibale	-0.336 (0.377)	-0.328 (0.389)	-0.401 (0.285)	-0.393 (0.296)	-0.417 (0.264)
Nearest fragment	-0.204 (0.598)	-0.121 (0.757)	-0.291 (0.448)	0.285 (0.458)	-0.019 (0.962)
Trees/ha	0.201 (0.605)	0.142 (0.715)	0.422 (0.258)	0.109 (0.780)	0.199 (0.608)
Tree spp./ha	-0.128 (0.744)	-0.226 (0.560)	0.012 (0.976)	-0.199 (0.607)	-0.184 (0.635)
Red colobus/ha	0.239 (0.536)	0.442 (0.234)	0.672 (0.047)	0.010 (0.980)	0.437 (0.240)
Colobines/ha	0.459 (0.214)	0.367 (0.331)	0.691 (0.039)	0.267 (0.487)	0.511 (0.160)
Stumps/ha	0.811 (0.008)	0.869 (0.002)	0.954 (<0.001)	0.766 (0.016)	0.920 (<0.001)

*The $n = 9$ for all comparisons, Pearson correlation, and corresponding p value provided.

to be influencing primate-parasite dynamics. Many studies of forest fragmentation and its effects on wildlife populations have focused on how fragment size, distance to core/mainland habitat, and distance to the nearest fragment relate to species viability in fragments (Laurance & Bierregaard 1997; Bender et al. 1998). Consequently, we considered it important to examine whether these factors influence host-parasite dynamics. Although these attributes failed to predict patterns of parasite prevalence in red colobus in the series of small (1–10 ha) and proximate (<6.5 km apart) fragments investigated, it would be interesting to examine this relationship further across broader scales of size and distance.

We selected fragment type (hillside/crater lake or valley bottom) as a critical attribute in our analysis because the divergent topography of these fragment types may influence host-parasite dynamics. Valley-bottom fragments include areas dominated by swamp and are characterized by high humidity, whereas hillside and crater lake fragments lack swamp and are characterized by good drainage. Consequently, microclimatic features of valley-bottom fragments may provide a better environment for the development of nematodes during their free-living stage, whereas microclimatic features of hillside and crater lake fragments may lead to rapid desiccation of nematodes during their free-living stage. If that were the case, it could obviously affect host-parasite dynamics; our results, however, suggest this type of fragment does not influence prevalence of parasite infections in red colobus.

We examined tree density and tree species per hectare as fragment attributes in our study because these measures provide an index of colobus food stress, a factor expected to influence colobus susceptibility to infection. Red colobus typically have a highly diverse diet (>42 species), and their density can be predicted from the abundance of important food trees (Struhsaker 1975; Onderdonk & Chapman 2000). Such broad dietary requirements might predispose red colobus to food stress in forest fragments, where the necessary diversity of plant species and parts may not be available (Chapman et al. 2003). Our indices of food availability (tree density and tree species/ha) are admittedly simple measures. Because red colobus have a diverse diet and rarely feed in small trees (Gillespie & Chapman 2001), however, our sampling represents a nearly complete inventory of red colobus potential food sources. Perhaps a more refined index, including nutritional value, phytochemistry, and seasonal availability of colobus food items, would elucidate a relationship between food stress and parasite prevalence.

We examined red colobus and total colobus density as critical fragment attributes in our study because host density is of central importance to infection rates in directly transmitted parasites (Poulin 1998), and within-species studies have demonstrated that host density positively correlates with parasite prevalence and diversity (Morand & Poulin 1998; Packer et al. 1999). There were

considerable differences in colobus density among the fragments; with the exception of one parasite species, however, patterns of colobus density did not correlate with infection prevalence. Consequently, the patterns of parasitism observed in red colobus in forest fragments do not appear to be the result of host density-dependent factors. Redtail guenons (*Cercopithecus ascanius*), however, a species known to harbor many of the parasites infecting red colobus (Gillespie et al. 2004), also inhabit some of the forest fragments we examined. Hence future research examining primate-parasite dynamics in these fragments should focus on these guenons as well as the colobines to improve our understanding of this relationship.

We examined stump density as a fragment attribute in our analysis because this factor showed a strong positive relationship with the frequency of extractive endeavors (Chapman et al. 2003). Stump density is an index that represents a complex of factors that are likely to contribute to the effect on host-parasite dynamics observed. Red colobus inhabiting fragments with high stump density are likely to experience a higher probability of human contact (novel pathogens, chronic stress), reduced food availability, and restricted ranging (more intensive use of fewer arboreal pathways, more frequent use of ground). Any or all of these factors may contribute to the strong relationship observed between stump density and host-parasite dynamics. Parallel investigations in previously logged forest that is now protected from use suggest that human contact may play a more important role in this equation than reduced colobine food availability (Gillespie et al. 2005a). Future studies will be needed, however, to more systematically distinguish these effects.

In addition to improving our understanding of how forest fragmentation affects host-parasite dynamics, our results also provide insights into the observed decline in red colobus in the forest fragments of western Uganda. Surveys in 2000 and 2003 show that red colobus in forest fragments declined 20% (Gillespie 2004). Altered parasite dynamics may play a role in these declines. Although parasite infections are common in nature and low-intensity infections are often asymptomatic (Anderson & May 1979; May & Anderson 1979), anthropogenic change may result in altered transmission rates, parasite host range, and parasite virulence (Daszak et al. 2000; Patz et al. 2000). Resultant changes in host susceptibility may result in elevated morbidity and mortality and, ultimately, population declines.

The strongyle or rhabditoid nematodes that infect red colobus have the capacity to cause substantial pathology and death in primates. Heavy infections of *Oesophagostomum* sp. and *Strongyloides* spp. have been associated with mucosal inflammation, ulceration, dysentery, weight loss, and death in primates (McClure & Guilloud 1971; DePaoli & Johnsen 1978; Holmes et al. 1980; Harper et al. 1982). Even moderate intensities of *Oesophagostomum*

sp. have proven important in stressed or captive primates (Crestian & Crespaeu 1975; Soulsby 1982). For example, nearly 30% of 70 guenons (*Cercopithecus aethiops*) imported to Italy from Senegal died soon after arrival from severe oesophogostomiasis (Roperto et al. 1985). Secondary bacterial infections of mucosal lesions resulting in ulceration and fatal septicemia are frequent complications of oesophogostomiasis (Soulsby 1982). Even more troubling are *S. stercoralis* and unidentified strongyle infections, which are most likely anthrozoönotic in origin. These parasites occur at high frequency in the human populations in the region but are absent from colobus within Kibale National Park, where the people and primates interact at a reduced frequency (Gillespie 2004; Gillespie et al. 2005a). Because *S. stercoralis* parasitic females live in the superficial tissues of the small intestine and can be present in high numbers because of autoinfection, they can cause significant pathology in humans (Pappas et al. 1999) and potentially in other primates as well. Hence, altered colobus-parasite dynamics may contribute to the red colobus decline observed in the forest fragments of western Uganda.

Our results provide evidence that an easily measured index (stump density) can be used to predict the degree to which a fundamental ecological process (host-parasite dynamics) has been altered by anthropogenic disturbance. Our understanding of how anthropogenic habitat change alters host-parasite dynamics and wildlife-disease dynamics is in its infancy. Considering the central role parasites play on their hosts' ecology (Hudson et al. 1998; Hochachka & Dhondt 2000) and on community biodiversity (Hudson et al. 2002), future research is needed to test the generality of our findings and to investigate linkages between such changes and the performance of host populations in forest fragments. Our results illustrate a pattern that is likely to be common in disturbed systems and may represent an unrecognized threat for the conservation and management of many taxa. Applications of this knowledge will improve evaluation of ecosystem health and wildlife conservation in relation to the risks and benefits of various extractive and management activities.

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