

BRIEF REPORT

Parasite Prevalence and Richness in Sympatric Colobines: Effects of Host Density

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Factors that influence proximity and the number and duration of contacts among individuals can influence parasite transmission among hosts, and thus parasite prevalence and species richness are expected to increase with increasing host density. To examine this prediction we took advantage of a unique situation. Following the clearing of a forest fragment that supported red colobus (*Ptilocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*), the animals moved into a neighboring fragment that we had been monitoring for a number of years and for which we had described the primate parasite community. After the animals immigrated into the fragment, the colobus populations more than doubled and colobus density became almost twice that found in Kibale National Park, Uganda. Despite this increase in host density, the richness of the parasite community did not increase. However, in both colobus species the prevalence of *Trichuris* sp., the only commonly occurring gastrointestinal parasite, increased. Over the next 5 years the prevalence and intensity of infection of *Trichuris* sp. in red colobus declined and their population numbers slowly increased. 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. While *Trichuris* sp. infections are typically asymptomatic, we consider it a possibility that they contributed to the decline of the black-and-white colobus, and that the red colobus may be serving as a reservoir for *Trichuris*, thereby increasing the infection risk for black-and-white colobus. Am. J. Primatol. 67:259–266, 2005. © 2005 Wiley-Liss, Inc.

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INTRODUCTION

Factors that influence host proximity and the number and duration of contacts among individuals can influence parasite transmission among hosts [Altizer et al., 2003]. Thus, parasites with no intermediate hosts that can be transmitted by social contacts are expected to be more common in larger groups and in denser populations [Freeland, 1976; Loehle, 1995]. In fact, in host-parasite models involving direct transmission, the probability that parasites will spread though the host population is an increasing function of host density, contact rates, and infectious period [Anderson & May, 1991]. It has been predicted that hosts living at high densities will experience increased transmission and prevalence of any given parasite species, and correspondingly higher numbers of parasite species harbored by the host population [Altizer et al., 2003; Anderson & May, 1991; Roberts et al., 2002]. This theory is supported by the results of meta-analytical studies. For example, Nunn et al. [2003] analyzed a comparative data set of 941 host-parasite combinations, representing 101 anthropoid primate species and 231 parasite taxa, and demonstrated that host population density was consistently associated with total parasite species richness and the diversity of helminths, protozoa, and viruses (examined separately).

Despite such theoretical and meta-analytical research, however, few empirical studies have examined how parasite prevalence or species richness vary as a function of density, group size, or social organization [Altizer et al., 2003]. One factor contributing to this lack of empirical data is the difficulty of obtaining information on parasite communities before and after a significant change in host density occurs. Furthermore, in primates such studies must be of long duration to document changes in either the parasite community or the primate population.

In this study we quantified changes in the gastrointestinal parasite communities of red colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*) following the immigration of new groups into a small forest fragment, which resulted in a dramatic increase in colobus density. This study is part of a long-term project to monitor primate populations in community-owned forest fragments [Chapman et al., in press; Onderdonk & Chapman, 2000]. We have been monitoring primate populations in over 20 forest fragments bordering Kibale National Park, Uganda; however, in this study we focused on the populations that inhabit Crater Lake Nkuruba [Chapman et al., 1998]. Early in 2000 a group of red colobus and two groups of black-and-white colobus immigrated into the small study fragment after the fragments they inhabited were converted to agricultural and grazing lands. Since we had data on the parasites of the colobus before this event occurred, it provided us an opportunity to examine the effect of an increase in host density on the prevalence, abundance, and richness of gastrointestinal parasites.

MATERIALS AND METHODS

The colobus monkeys that inhabited the forest surrounding Crater Lake Nkuruba were studied from 1995 to 2004, and parasite assessments were conducted every year between 1999 and 2004. This 6.4-ha forest borders (3.6 km

Kibale National Park in western Uganda (795 km²; 0 13'–0 41' N and 30 19'–30 32' E). Each summer since 1999 the colobus population size and gastrointestinal parasites have been assessed. To obtain reliable estimates of group size and composition, observers often stayed with each group for up to 12 hr and waited for the group members to make a coordinated movement across a canopy opening.

Fecal samples were collected, stored individually in vials in a 10% formalin solution, and transported to the University of Florida, where they were examined for helminth eggs and larvae 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 $\mu\pm$ SD with the use of an ocular micrometer fitted to a compound microscope, and representative samples were photographed. Coprocultures were used to match the parasite eggs to larvae for positive identification [Gillespie, 2004; Gillespie et al., in press]. Some necropsies were conducted on animals from Kibale that had died of natural causes, which facilitated matching of the egg to the adult form, as well as species identification.

The parasite infections were described in terms of prevalence, intensity of infection (or abundance), richness, and multiple infections. Comparisons of parasite prevalence are useful for determining whether parasites are impacting host populations (i.e., population declines have been correlated with increased infection prevalence). Prevalence refers to the proportion of individuals in a population that are infected. Since we could not individually recognize each of the animals in the population each year, we attempted to collect samples in a short period of time (e.g., during a single day or two), and we tried to rotate among individuals so as not to repeatedly sample the same individual. However, repeat sampling did occur, and thus the current data should be viewed as an index of prevalence. The frequency of multiple-species infections in individuals can be another useful indicator that parasites may be impacting host populations, since 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]. Consequently, 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 only report data on the average number of *Trichuris* eggs per gram of feces in infected individuals as an indication of environmental contamination (i.e., infection risk) or potential for spillover to individuals of the same and different species.

RESULTS

In 1995 there were five black-and-white colobus inhabiting the forests of Crater Lake Nkuruba. The population apparently remained stable over the next few years, since in 1999 there were still five animals in a single group. Early in 2000 two groups of black-and-white colobus immigrated into the study fragment from neighboring fragments that had been cleared, and the population increased by 400% to 20 animals (Fig. 1). In subsequent years the populations steadily declined, and in 2004 only eight animals remained in the fragment. We do not know whether this decline was caused by the death of individuals or by emigration. Initially all of the groups remained independent, but apparently as the size of some groups became small, group fusion occurred, and in 2004 only one group remained.

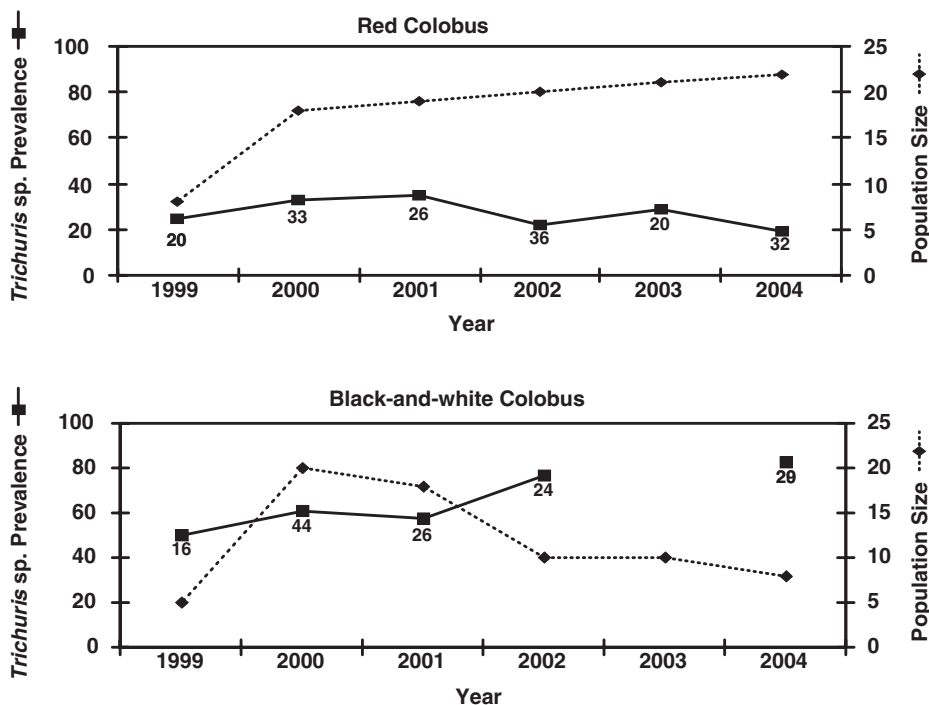


Fig. 1. The prevalence of *Trichuris* sp. in red colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*), and the population sizes of these colobus monkeys in a forest fragment near Kibale National Park, Uganda, between 1999 and 2004. Animals immigrated into this fragment in 2000 following the clearing of neighboring forest fragments. The numbers of fecal samples analyzed each year for each species are indicated in association with prevalence.

Similarly, the red colobus population in the fragment was relatively stable between 1995 ($n=6$) and 1999 ($n=8$), but it more than doubled in size to 18 animals in 2000 when a group immigrated into the area. Unlike the black-and-white colobus, the size of the red colobus populations steadily increased over the next 4 years, reaching 22 animals in 2004. By 2002 the groups had fused to become a single cohesive group.

We have seen no indication that solitary individuals move among fragments, even though we have spent a considerable amount of time at Crater Lake Nkuruba working on the colobus (~ 770 hr of observations) and other projects (at least 2 days a month since 1995), and have repeatedly surveyed a number of other forest fragments. Nevertheless, it is quite possible that a low level of immigration occurs among the fragments. Such events could bring animals with novel infections into the Crater Lake Nkuruba population.

We collected 335 fecal samples from the colobus monkeys of Lake Nkuruba between 1999 and 2004 (196 from red colobus, and 139 from black-and-white colobus; Fig. 1). The most prevalent parasite was *Trichuris* sp. It was identified based on both egg size and its distinctive morphology (i.e., with bipolar plugs), and the identity was verified by necropsies. The prevalence of *Trichuris* sp. increased in both colobus species following the immigration of the new groups. For the black-and-white colobus, prevalence continued to increase over time and was significantly correlated with year (Spearman rank correlation=0.900, $P=0.037$). In contrast, there was no correlation between year and *Trichuris* sp.

prevalence for red colobus (Spearman rank correlation = -0.486 , $P=0.329$), and in the final year of the study its prevalence was lower than before the immigration of the new animals and the increase in colobus density. *Trichuris* sp. was significantly more prevalent in black-and-white colobus than in red colobus ($t=6.203$, $P<0.001$).

Although we have identified a number of other parasite species in fecal samples from colobus in Kibale National Park and other neighboring forest fragments [Gillespie, 2004; Gillespie et al., in press], we found only two other species in our examinations of the Lake Nkuruba fecal samples. *Oesophagostomum* sp. was found in one red colobus sample in 2003, which was identified on the basis of egg size and morphology, and verified by cultured larvae and adults obtained by necropsy from animals in Kibale. In 2004 *Strongyloides fulleborni* was identified in a black-and-white colobus sample on the basis of egg size and morphology, and verified by cultured rhabditiform larvae. The low frequency of finding parasites other than *Trichuris* sp. suggests that the increase in colobus density did not lead to an increase in species richness or the proportion of the population with multiple infections.

The intensity of *Trichuris* sp. infection decreased over time for red colobus and was negatively correlated with year (Spearman rank correlation = -0.820 , $P=0.046$), whereas it increased over time for black-and-white colobus (Spearman rank correlation = 0.909 , $P=0.033$; Fig. 2). Since these relationships were opposite to each other, the overall intensity of colobus infection was not correlated with year (Spearman rank correlation = 0.700 , $P=0.188$) even though it was positive.

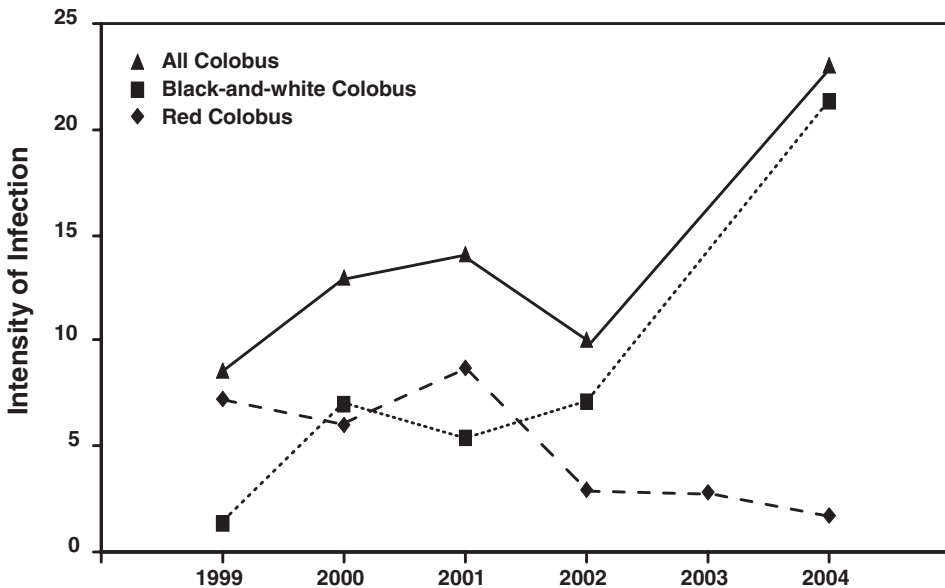


Fig. 2. The intensity of infection (eggs/g in infected individuals) for red colobus (*Piliocolobus tephrosceles*), black-and-white colobus (*Colobus guereza*), and all colobus living in a forest fragment near Kibale National Park, Uganda, between 1999 and 2004. Animals immigrated into this fragment in 2000 following the clearing of neighboring forest fragments. The numbers of fecal samples analyzed each year for each species are presented in Figure 1.

DISCUSSION

As a result of immigration of animals into the fragment, the colobus populations more than doubled, and the density of the animals increased to almost twice that found in Kibale National Park (Kibale: 358 colobus/km² [Chapman et al., 1999]; Crater Lake Nkuruba: 657 colobus/km²). Despite this increase, and counter to what was expected [Altizer et al., 2003; Anderson & May, 1991; Roberts et al., 2002], there was little evidence to suggest that with an increase in density there was also an increase in the richness of the parasite community or in the proportion of the population with multiple infections. *Oesophagostomum* sp. and *Strongyloides fulleborni* were each found only on one occasion. Both of these species have direct life cycles in which the larvae are ingested [Huffman et al., 1997], and species with such simple life cycles are those most likely to increase with host density. The prevalence of *Oesophagostomum* sp. in the colobus of the unlogged forest of Kibale was 5.50% (average between the two species [Gillespie et al., in press]), while its prevalence in the Crater Lake Nkuruba population was only 0.26%. However, in ground vegetation plots where eggs and larvae were isolated, *Oesophagostomum* sp. L3 larvae were more abundant in Crater Lake Nkuruba (0.82 larvae/m³) than in the unlogged forest of Kibale (0.14 larvae/m³ [Gillespie et al., in press]). Why *Oesophagostomum* sp. and *Strongyloides fulleborni* are not more prevalent in the colobus is an unanswered question that will be explored in future studies.

Factors that influence host proximity and the number and duration of contacts can influence parasite transmission among hosts, and it is expected that hosts living at high densities will have an increased prevalence of any given parasite species. Let us first consider the patterns of change in *Trichuris* sp. prevalence following the dramatic increase in host density, and then evaluate three explanations for the pattern: stress associated with immigration, nutritional stress, and the possibility that the two colobus are differentially affected by *Trichuris* sp.

As expected, the prevalence of *Trichuris* sp. increased in both species following the immigration of new animals and the resulting increase in colobus density. However, the long-term responses of the two species differed. While red colobus density increased each year of the study, the prevalence of *Trichuris* sp. declined over time, and at the end of the study was lower than before the rise in colobus density. In contrast, the prevalence of *Trichuris* sp. in black-and-white colobus was not only much higher than in red colobus, it also increased over time. The black-and-white colobus population declined following the immigration of the animals, and in the last year of the study their numbers were only slightly higher than they were at the beginning of the study. *Trichuris* has a direct life cycle, and it is estimated that a single female may lay as many as 1,000–46,000 eggs a day [Cheng, 1973]. Eggs develop in damp soil or more likely in damp parts of the tree (e.g., tree boles and suitable bark), and the larvae are completely formed in approximately 3 weeks [Schmidt & Roberts, 1977]. The fact that we have seen black-and-white colobus routinely come to the ground to eat charcoal, and both colobus species to eat terrestrial vegetation and soil, may indicate that they have an increased risk of infection compared to primates that do not come to the ground. *Trichuris* can be shared among all of the primates in these fragments. The chimpanzees (*Pan troglodytes*) and redbellied monkeys (*Cercopithecus ascanius*) that move among fragments have *Trichuris* sp. infections and may be the source of some infections in the colobines. In addition, while domestic animal use of this fragment is discouraged by a community conservation project, pigs and goats are

occasionally allowed into the fragment and there is a risk of transmission from this source, as well as from humans [Boes & Helwich, 2000].

The initial increase in the prevalence of *Trichuris* sp. following the immigration of the new groups may have resulted because the animals that immigrated were stressed, and their immune system may have been compromised. These animals came from fragments where people had harvested almost every tree over a short period of time, they were forced to move over 3 km through agricultural land, and they had to become accepted by the resident colobus groups in Crater Lake Nkuruba. If the prevalence of *Trichuris* sp. was very high in the immigrants, its prevalence in the population as a whole would be elevated, and thus the initial increase may have been due to the increased susceptibility of stressed animals rather than to increased density. While this alternative hypothesis may explain the initial change in prevalence, it is not clear why the two colobus species responded differently once the stress of movement was removed.

The initial increase in the prevalence of *Trichuris* sp. may also have been due to nutritional stress caused by increased competition over food resources. Again, while this alternative hypothesis may explain the initial change in prevalence, it is not clear why the two colobus species responded differently over time. It is likely not the result of the red colobus being competitively superior to the black-and-white colobus, because in these fragments the dietary overlap of the two colobines is only 17.5%, while within Kibale it can be as high as 43.2%. It is possible that the black-and-white colobus are excluded from particularly critical resources, and thus the dietary stress would be maintained overtime and increase as the red colobus numbers increase. However, we found no behavioral evidence to support this.

While *Trichuris* sp. infections are typically asymptomatic, it is possible that the two colobus species are differentially affected by *Trichuris* sp., and that these infections contributed to the black-and-white colobus population decline. In such an infection the anterior ends of the nematodes burrow into the mucosa of the intestine, where the worms consume blood cells. Trauma to the intestinal epithelium can cause chronic hemorrhaging and anemia. Furthermore, secondary bacterial infection coupled with allergic responses result in colitis, proctitis, and in extreme cases prolapse of the rectum [Schmidt & Roberts, 1977]. Loomis and Wright [1986] described the condition of four black-and-white colobus (*Colobus guereza kikuyuensis*) whose feces contained large numbers of *Trichuris* sp. One of these animals subsequently died and the cause of death was attributed to septicemia caused by the trichurid infection. Furthermore, a number of zoos have reported chronic problems with *Trichuris* sp. in black-and-white colobus that in some cases resulted in death (E. Greiner, personal communications). The lack of similar evidence for red colobus may simply reflect the fact that black-and-white colobus are more common in zoos. However, since certain dogs have been shown to develop immunity to *Trichuris vulpis* while others do not [Miller, 1941], it is possible that red colobus are not as severely affected by *Trichuris* sp. infections as black-and-white colobus. If this is the case, it may explain why red colobus are often the only colobus found in fragments even though they have been described as being more susceptible to disturbance than black-and-white colobus [Struhsaker, 1997]. Since it is likely that the same species of *Trichuris* infects both of these colobus species, the red colobus may be serving as a reservoir for *Trichuris* sp., and thus increasing the infection risk for black-and-white colobus and contributing to their decline in some fragments [Chapman et al., in press]. While these speculations provide a plausible explanation, further study is required to

substantiate them. However, if they prove to be true, such interactions should be considered in the conservation and management of these two species.

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