

**21** *Can parasite infections be a selective force influencing primate group size? A test with red colobus*

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### Introduction

Identifying ecological factors underlying group size and social organization is a central focus of primatology (van Schaik, 1983; van Schaik & van Hooff, 1983; Chapman & Chapman, 2000b). Factors that might explain the variation in group size have been extensively evaluated in terms of costs and benefits. Animals that live in a group are thought to increase their fitness by avoiding predation (e.g. benefiting from group defense) or social pressures (e.g. infanticide). These factors favoring group living are countered by the costs of group living, such as competition for food or elevated travel costs as a result of patch depletion. The majority of primate socioecology models have focused on these advantages and disadvantages (Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Sterck *et al.*, 1997; Chapman & Chapman, 2000b; Crockett & Janson, 2000; Chapman & Pavelka, 2005).

In contrast to these mainstream theories are a series of ideas about how parasite infections could be a selective force influencing primate social organization. In a series of intriguing papers published in the 1970s, Freeland proposed that aspects of primate social organization evolved to decrease the impact of parasite infections (Freeland, 1977a, 1976, 1977b, 1979, 1980). One of these predictions centers on the effects of parasitism on group size. Freeland (1976) suggested that as group size increases, there is an increased chance of mortality due to acquiring pathogenic levels of parasites. This could occur as a result of environmental contamination with infectious material caused by a large number of animals concentrated in a small area or because larger groups have more immigrants, which may introduce novel parasites. He documented that for mangabeys (*Lophocebus albigena*) the number of intestinal parasite species per individual was a function of group size (Freeland, 1979). Despite the potential significance for parasites to influence primate social organization, these ideas were generally not further empirically tested (but see recent reviews: Loehle, 1995; Heymann, 1999; Nunn *et al.*, 2000; Nunn & Altizer, 2006). This is illustrated by the fact that in the classic book on primate behavior and ecology by Smuts *et al.* (1987), disease is not listed in the index (Heymann, 1999), nor is parasite.

The objective of this chapter is to test predictions concerning how parasite infection could be a selective force influencing primate group size. We first examine the rationale behind various predictions and the conditions required for these predictions to operate. Subsequently, we discuss counter-strategies that primates could employ to avoid acquiring parasites, while still receiving the benefits associated with living in a group. Finally, we present data to explore the relationship between group size and parasite infection for two groups of

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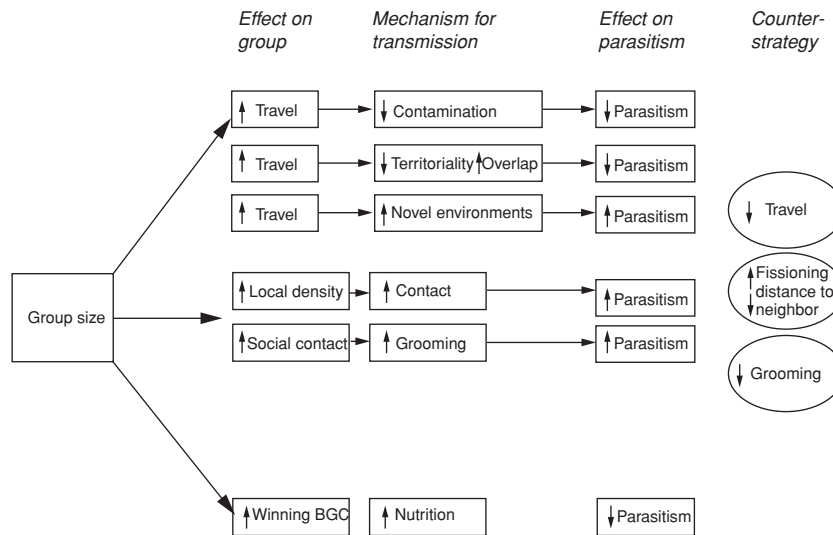


Figure 21.1. A consideration of how group size may affect primate groups, the mechanisms of parasite transmission, and the effect on parasitism. Also considered are possible counter-strategies that primates could use to decrease impacts of parasitism. BGC is between group contest competition. An example of the logic depicted here is that if group size increases social contact, including aggressive interactions, and grooming increases as a means of reconciling those interactions, this may lead to an increase in parasitism. If this does there would be selection for decreased grooming (or another counter-strategy could operate).

red colobus (*Procolobus rufomitratus*) living in Kibale National Park, Uganda that differ markedly in size.

**Do parasite infections vary as a function of primate group size and can this select for groups of different sizes?**

Parasite infections can influence fitness (Coop & Holmes, 1996; Murray *et al.*, 1998) and if the intensity of infections varies as a function of group size this could lead to selection for groups of different sizes. Parasite infections could be influenced by group size in a number of ways; some of which will produce very diametrically opposed outcomes (Figure 21.1). Here we consider how group size could lead to changes in four non-mutually exclusive factors that could influence the intensity of parasites: local density, social contact, travel, and the outcome of between group contest competition (BGC).

First, factors that influence host proximity and the number and duration of contacts among individuals can affect parasite transmission among hosts (Anderson, 1978; Altizer *et al.*, 2003). In host–parasite models with direct transmission, the probability that parasites will spread through the host population is an increasing function of parasite pathogenicity, host density, and host immune response; new infections depend on host contact rates and per contact probabilities of successful infection (Anderson & May, 1992). As a result, directly transmitted parasites may have increased transmission rates in denser populations (Freeland, 1976; Anderson & May, 1992; Loehle, 1995). Accordingly, corresponding increases in prevalence and a higher number of parasite species with direct transmission may be harbored by the host population (Anderson & May, 1992; Roberts *et al.*, 2000; Altizer *et al.*, 2003). This theory has been supported for primates by meta-analyses and empirical research. 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 positively associated with total parasite species richness. A higher prevalence of intestinal parasites was found in howler monkeys (*Alouatta palliata*) in a dense population than a less dense one (Stuart *et al.*, 1990). Similarly, Chapman *et al.* (2005b) demonstrated that the prevalence of *Trichuris* sp. in two colobine species increased when there was a dramatic increase in population density in a forest fragment associated with groups immigrating to the fragment (but see Stoner, 1996). These mathematical models, meta-analyses, and a handful of empirical studies suggest that high density, which would likely occur at a local scale with larger groups, increases the probability that parasites spread through a group.

Secondly, this expected density effect relies on one of two mechanisms operating: the number of social interactions and partners must increase with group size, or there must be an increase in the probability of contacting contaminated material with increasing group size (considered next). In a comparative analysis of 44 primate species, Dunbar (1991) demonstrated that the frequency of social grooming increased with group size. This increased contact is associated with the potential for increased parasite transmission through contact with infective stages on the fur, contact with other animals' saliva, and/or transfer of respiratory pathogens (Nunn & Altizer, 2006). As a consequence, through more frequent social interaction that involves physical contact, such as grooming, individuals in larger groups may acquire more severe parasite infections than individuals in smaller groups.

Thirdly, the way a group travels through its environment will influence the probability of contacting infected areas or individuals. There are three competing hypotheses concerning the way ranging patterns may be influenced

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by parasitism (Nunn & Dokey, 2006). (a) For parasite species transmitted by the fecal-oral route, transmission can be influenced by the number and duration of contacts with contaminated feces (Freeland, 1979, 1980; Anderson & May, 1992; Ezenwa, 2004; Vitone *et al.*, 2004). Thus, the greater the contact between hosts and infected feces (i.e. repeated use of the same contaminated area), the higher the parasite load and the more species-rich the parasite infection within a host. Accordingly, there is a greater potential for severe symptoms (Altizer *et al.*, 2003; Chapman *et al.*, 2005b). Freeland (1976) proposed that the need to avoid acquiring diseases could influence ranging behavior. In a test of the effect of movement patterns on infection risk, he noted that 40% of defecations hit branches that are used for mangabey locomotion before reaching the forest floor (Freeland, 1980). He also noted that the mangabeys remained in areas longer in the rainy season than in the dry season, and speculated that infection risk was lower in the rainy season due to the fact that rain washes infective stage parasites to the forest floor, reducing contamination levels in the treetops (but see Olupot *et al.*, 1997 for opposing data) (b) When intensive ranging is associated with territoriality, this could decrease home range overlap and reduce exposure to new parasites (Nunn & Dokey, 2006) (c) Alternatively, since the probability of contacting infected items may increase as groups travel further and larger groups tend to travel further than smaller groups (Isbell, 1991; Snaith & Chapman, 2007), there may be an increase in infections with group size. Furthermore, if large groups range further and encounter more novel habitats, the richness of their parasites may increase as a function of group size (Freeland, 1979; Loehle, 1995; Nunn & Altizer, 2006). This would particularly apply to species that have large degrees of home range overlap with conspecifics or with sympatric species capable of hosting the same parasites (but see Gasser *et al.*, Chapter 3, this volume for the difficulty in determining if interspecific transmission has occurred).

Fourthly, when assessing any proposed selective force influencing group size, it is assumed that the factor has a biologically meaningful effect relative to the advantages of larger groups (i.e. the benefits do not outweigh the costs). In cases where large group size increases the likelihood of winning between group contests for food (Koenig, 2002; Chapman unpublished data), the nutritional gains from a larger group size may be substantial and may compensate for the costs of increased parasite infections associated with larger groups. How costly a parasitic infection will be parasite- and situation-dependent. For example, helminth and protozoan parasites can impact host survival and reproduction directly through pathological effects and indirectly by reducing host condition (Coop & Holmes, 1996; Murray *et al.*, 1998) and even up-regulation of host immunity can reduce breeding success (Ilmonen *et al.*, 2000). However, parasites do not necessarily induce negative health effects if hosts have adequate

energy reserves or nutrient supplies (Munger & Karasov, 1989; Gulland, 1992; Milton, 1996), suggesting that the outcome of host–parasite associations may be contingent on host nutritional status, as well as on the severity of infection (Chapman *et al.*, 2006).

### **Counter-strategies that primates may employ to avoid parasite infections**

Theory supports the idea that parasites with direct (oral-fecal) transmission strategies are more common in large groups relative to small groups because large groups have more social contacts and contact with contaminated items (Anderson & May, 1992). However, the concurrent increased probability of pathogenic effects on hosts is also expected to result in selection for host strategies to minimize the impact of parasite infections (Freeland, 1976). For example, if the level of parasite infection found in large groups has a fitness cost it can limit group size. If counter-strategies exist, we would expect individuals in larger groups to have mechanisms to decrease the amount of social contact or decrease the chances of contact with contaminated items. To decrease social contact, large social groups could fission into subgroups, they could increase group spread (increasing nearest-neighbor distance), or they could groom less. To avoid contact with contaminated items, large groups could travel further than smaller groups, they could revisit the same feeding or sleeping site less frequently, or again they could fission into subgroups.

Let us consider just two counter-strategies in more detail: fissioning of a large group into smaller subgroups, and an increase in travel during the day (day range). Chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles* sp.), and gelada baboons (*Theropithecus gelada*) routinely fission into smaller units and reunite at later times (i.e. from days to weeks) (Stammbach, 1987; Chapman, 1990a; Mitani *et al.*, 2002) and this is considered a central part of their social organization. However, many species which are considered to have cohesive groups also occasionally divide for extended periods before reuniting, including long-tailed macaques (*Macaca fascicularis*) (van Schaik & van Noordwijk, 1988), red colobus (Chapman & Chapman, 2000a), and howler monkeys (Aureli *et al.*, submitted; Chapman, 1990b). Dividing a group into small subgroups would both decrease social contact and decrease the distance they would need to travel to acquire adequate food resources, which may decrease disease transmission. The fact that many species form subgroups suggests that fissioning could be a widespread strategy.

Similarly, for a number of species, increases in day range have been documented to occur with increases in group size (reviewed by Isbell, 1991).

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Again, by being in a small group animals would both decrease social contact and decrease the distance they would need to travel, thus decreasing disease transmission.

However, both the formation of subgroups and day range–group size relationships have been argued to be a function of feeding competition since with large groups the nutritional needs of all group members cannot be easily met as patches are depleted more rapidly. Consequently, the group is forced to travel longer distances or form subgroups (Chapman & Chapman, 2000b). Thus, investigating these possible counterstrategies will require finding instances where groups divide when food resources would not require it, or it will necessitate a multivariate approach where the variance can be partitioned between factors related to the density and distribution of food patches and to parasite infection risk. Furthermore, Freeland (1976) points out that if large groups increase distance traveled each day they may enter new habitats which could harbor novel parasites. An increase in parasite richness could result in greater 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 variety of parasites demonstrate greatly elevated pathogenic effects in the presence of HIV (Kaplan *et al.*, 1996).

In closing, in a discussion concerning counter-strategies it is important to stress that if elaborate defenses have evolved to reduce parasite transmission or its impact on hosts then expected correlations between parasitism and group size may not be found (i.e. the “ghost of parasitism past”; Nunn & Altizer, 2006). As a result, we might expect to find that some populations or species might live in large groups, but have low parasite levels because they have evolved counter-strategies.

**Case study: Red colobus of Kibale**

We examined the effect of group size on gastrointestinal helminth (nematode) infections of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. The existence of two neighboring red colobus groups that differ strikingly in size (i.e. ~36 versus 132 individuals) allowed us to evaluate the hypothesis that larger social groups have higher levels of parasite infection and more diverse parasitic faunas than smaller social groups. We examined fecal samples to determine indices of gastrointestinal parasite infections in these two groups over 23 months, and collected behavioral data on both groups to determine whether animals in the large group are employing counterstrategies to reduce the risk of infection. We contrasted the parasite infections of the large and small group of red colobus, and collected behavioral data to test

five predictions concerning possible counter-strategies that could be employed to decrease parasite infection risk. Firstly, we examined whether the large group traveled more than the small group, with the expectation that the large group would travel further in search of non-contaminated areas. Secondly, we determined the home range size of both groups with the expectation that the large group would have a bigger home range than the small group and thus could more easily find non-contaminated areas. Thirdly, we expected the large group to fission into smaller subgroups more frequently than the small group, which would effectively decrease social contact and the likelihood of encountering contaminated material (but see potential conflicting factors discussed above). Fourth, we expected members of the large group to engage in grooming less than members of the small group to decrease social contact and reduce the chances of disease transmission. Finally, we predicted that the large group would increase group spread (indexed by an increasing nearest neighbor distance) relative to the small group and reduce the chances of disease transmission.

### Methods

Fecal samples ( $n = 1033$ ) were collected from two red colobus groups in the Kanyawara study area of Kibale between July 2004 and May 2006. Kibale ( $795 \text{ km}^2$ ;  $0^\circ 13' - 0^\circ 41' \text{N}$  and  $30^\circ 19' - 30^\circ 32' \text{E}$ ) is a moist, mid-altitude ( $920 - 1590 \text{ m}$ ) evergreen forest intermixed with swamps, secondary forests, and grasslands (Struhsaker, 1997; Chapman & Lambert, 2000). Two groups were selected based on their size: the smaller group consisted of 36 individuals and the large group consisted of 132 individuals.

In total, 628 fecal samples were collected from the larger group (average per month = 30.0, range 17–76), and 405 samples were collected from the smaller group (average per month = 19.8, range 14–43). Fecal samples were collected directly after defecation, stored in 10% formalin solution, processed using sodium nitrate flotation (Sloss *et al.*, 1994), and examined using a Leica DM 2500 microscope with PL Fluotar objectives. Eggs and larvae of parasites were counted and identified on the basis of egg color, shape, contents, and size. Digital images were taken with an Infinity 1 (1.3 megapixel) camera of representative samples of each parasite or for parasites where identification was questionable, and measurements were made to the nearest  $0.1 \text{ micron} \pm \text{SD}$ . These images were sent to taxonomic experts to verify identification. Coprocultures and necropsies were used to match parasite eggs to larvae for positive identification (Gillespie *et al.*, 2005a, 2005b, Chapman *et al.* unpublished data). The parasite infections were described in terms of prevalence of infection, species richness, load (eggs/g), and multiple infections. Prevalence



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is the proportion of individuals sampled that are infected with a particular parasite. Comparisons of parasite prevalence can be a useful indicator of parasites that may be impacting host populations (i.e. population declines have been correlated to increased infection prevalence). Since we could not individually recognize each animal in the study groups, repeat samples likely occurred and thus this should be viewed as an index of prevalence. 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, Tanzania versus 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. This is because multiple sampling from the same individual may be required to detect an infection. The frequency of multiple-species infections (i.e. the proportion of a population with more than 1 species of parasite) can be another useful index, as multiple-species infections are associated with a greater potential for morbidity and mortality (Kaplan *et al.*, 1996; Parraga *et al.*, 1996). Parasite egg production, or load (egg/g), is highly variable and some researchers suggest that it may not be indicative of actual infection intensity. However, with *Trichuris* sp. from infected red colobus, we typically obtained <10 eggs/g, but during certain times, individuals in certain groups consistently had much higher loads (i.e. over 300 egg/g; all individuals in a group for an extended time; Chapman *et al.* unpublished data). This suggests that load might be a useful index of parasite infection since high levels are temporally and spatially specific; however, we recommend that the results concerning load be viewed critically and only be considered of interest if in concordance with other indices of parasite infection.

Each group was observed for 6 days a month, with observations starting just after sunrise and ending around the time that the group became inactive for the day. During a 15-min block, five point samples were made of different individuals to determine their activity (e.g. grooming, traveling, feeding, resting). During each point sample the nearest neighbor was identified and its distance from the subject was visually estimated. The location of what was perceived to be the center of the group was plotted on detailed trail maps every 15 minutes. For the purpose of determining when a group subdivided, a group was only considered to be divided if two distinct units were separated by more than 100 m, and typically when the group did divide they were separated by more than 500 m.

For the purposes of determining the home range size of the two groups, a detailed map of the Kanyawara study area was divided into 1 ha grid cells by superimposing a 100 × 100 m grid over the trail system. The ranging patterns of the two groups were extracted from follows made between July 2004 and

May 2006. We used these maps to determine which grid cells were entered each day, and to establish the spatial extent of the group's home range during the study (considered to be all grid cells entered plus any cells that fell inside a minimum polygon formed by the outermost entered cells; Snaith & Chapman, unpublished manuscript).

Both two-tailed paired-sample t-tests (paired by month to eliminate seasonal variation in infections, e.g. average amount of time spent grooming each month) were used to determine if there were any differences between the small and large red colobus groups with respect to the following: (1) parasite prevalence; (2) species richness, (3) eggs/g, and (4) multiple infections. The paired t-test assumes that months are independent and none of the indices showed a correlation between successive months ( $P > 0.1$  in all instances). Paired t-tests were used to evaluate behavioural differences between the two groups.

## Results and discussion

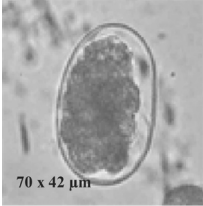
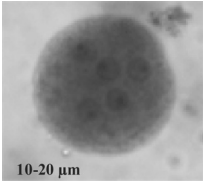
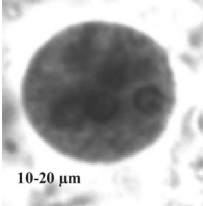
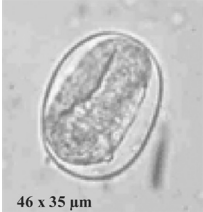

### *Differences in parasite infections between large and small groups*

The helminth parasite community described from the samples collected from both groups included the following nematodes: *Trichuris* sp. (Superfamily Trichuroidea), *Oesophagostomum* sp., an unidentified strongyle nematode (Superfamily Strongyloidea), *Strongyloides fulleborni* (Superfamily Rhabditoidea), and *Colobenterobius* sp. (Superfamily Oxyuroidea; Table 21.1). We also identified two protozoans, likely *Entamoeba coli* and *E. histolytica/dispar*. However, because of the small sample size for *Colobenterobius* sp., the unidentified strongyle nematode, and *Strongyloides fulleborni* these parasites are not considered individually except in the analysis of richness and multiple infections. Further, *E. histolytica* and *E. 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, while *E. dispar* is not. Thus, we do not consider the *E. histolytica/dispar* complex further with the exception of analyses of multiple infections and the richness of the parasite community, where they are considered as one species. The large and small group had the same community of parasites.

The paired t-test revealed no differences between the large and small group with respect to *Trichuris* eggs per gram of all samples (paired t-test  $t = 0.262$ ,  $P = 0.796$ ), *Trichuris* eggs per gram in infected individuals ( $t = 0.754$ ,  $P = 0.459$ ), *Oesophagostomum* eggs per gram of all samples (paired t-test  $t = 1.000$ ,  $P = 0.329$ ), *Oesophagostomum* eggs per gram in infected individuals ( $t = 0.439$ ,  $P = 0.666$ ), *Oesophagostomum* prevalence ( $t = -0.963$ ,

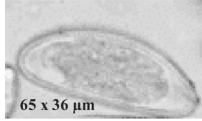
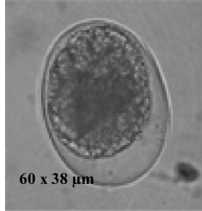
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Table 21.1. A description of the parasites found in the large and small group of red colobus (*Procolobus rufomitratus*) in Kibale National Park, Uganda

Parasite species	Mode of infection	Morbidity/mortality	Image
<i>Oesophagostomum</i> spp.	Larvae ingested	Severe diarrhea, weight loss, death	 70 x 42 μm
<i>Entamoeba coli</i>	Cyst or trophozoite ingested	Typically asymptomatic	 10-20 μm
<i>Entamoeba histolytica</i>	Cyst or trophozoite ingested	Hepatic and gastric amoebiasis, dysentery, death	 10-20 μm
<i>Entamoeba dispar</i>	Cyst or trophozoite ingested	Asymptomatic	Same as <i>E. histolytica</i>
<i>Strongyloides fulleborni</i>	Larvae ingested, skin penetration	Mucosal inflammation, ulceration, death	 46 x 35 μm
<i>Trichuris</i> sp.	Larvated egg ingested	Heavy infections cause abdominal pain and distension, bloody diarrhea, weight loss, nutritional deficiency, rectal prolapse, and reduced growth in human children	 57 x 27 μm

(cont).

Table 21.1 (cont.)

Parasite species	Mode of infection	Morbidity/mortality	Image
<i>Colobenterobius</i> sp.	Ingestion of eggs	Unknown	
Strongyle (unidentified)	Larvae ingested	Unknown	

$P = 0.347$ ), multi-species infections ( $t = 0.899$ ,  $P = 0.380$ ), and species richness ( $t = 1.420$ ,  $P = 0.171$ ). However, the prevalence of *Trichuris* was found to be lower in the large group (mean monthly prevalence = 47.3%) when compared with the small group (57.0%), which is counter to what was predicted ( $t = 2.394$ ,  $P = 0.027$ ). If the logic behind the expectation that the large group would have greater parasite infections than the small group is correct, the fact that we do not find differences in parasite infections would suggest that behavioral strategies may be operating to decrease infections in the large group.

***Counter-strategies and behavioral differences between large and small groups***

Firstly, as predicted, the large group spent more of its time traveling (average percent time spent traveling a month = 3.31,  $SD = 0.835$ ) than the small group (average = 1.32,  $SD = 0.241$ ; paired  $t$ -test = 2.468,  $P = 0.022$ ). Secondly, the home range size of the large group (125 ha) was larger than that of the small group (52 ha). Both groups moved extensively through their home range and entered most regions of the home range every 3–4 months.

Third, as predicted, if the subgroup was employing counter-strategies to decrease parasite transmission, the larger group frequently divided into subgroups, while the smaller group did not. It was difficult to determine when the large group divided because it was difficult to obtain an accurate count of the subgroup that was being followed, or locate two or more subgroups of the large group that contained recognizable individuals. Consequently, our

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estimate of the rate of subgroup formation is likely an underestimate. The large group divided into subgroups on at least 37% of observation days ( $n = 132$  days), while the small group never divided ( $n = 107$  days). It may be more appropriate to consider each month as an independent unit for analysis. At this level of analysis the large group formed subgroups in 75% of the observation blocks, while the small group never formed subgroups.

Fourth, the prediction that individuals in large groups would decrease the likelihood of parasite transmission by decreasing the rate of grooming was not supported. The large group spent  $5.77 \pm 0.46\%$  of the time grooming, while the small group spent  $5.14 \pm 0.43\%$  of the time grooming (paired t-test,  $t = 1.179$ ,  $P = 0.251$ ,  $n = 23$  months). It may be that the need to maintain social cohesion in large groups by social grooming (Dunbar, 1991) outweighs any benefits to reduce the potential of parasite transmission.

Finally, as predicted, nearest neighbor distances were greater in the large group (average distance per month = 3.05 m,  $SD = 0.466$ ,  $n = 23$  months) than the small group (average = 2.73,  $SD = 0.568$ ; paired t-test = 3.08,  $P = 0.006$ ,  $n = 23$  months). Whether this distance is biologically relevant with regards to disease transmission depends on the disease and its mode of transmission; however, an average difference of only 32 cm is likely too short to have an effect.

### **Conclusions and future directions**

There was no evidence that the large group of red colobus had more severe parasite infections than the small group. However, behavioral differences were found between the groups that suggest that the large group may be engaging in strategies to decrease the rate of transmission of parasites. Unfortunately, decisively concluding that the observed behavioral differences are a counter-strategy evolved to decrease parasite infections is not possible. This is an unfortunate reality for two reasons. First, for the notion that these behaviors act to decrease disease transmission to be accepted, researchers will have to demonstrate that ecological arguments that have been substantially empirically tested are inadequate in explaining the observation. For example, the tendency for the large group to fission may be a strategy to reduce travel costs that are associated with its size. The large group will deplete patches faster, which will necessitate greater travel. Forming smaller subgroups during periods of food scarcity may reduce the costs of travel. This argument follows logic presented in the ecological constraints model (Milton, 1984; Chapman & Chapman, 2000b), which has already received support for red colobus (Chapman & Chapman, 2000a). The second reason to be skeptical concerning claims that these behaviors represent

counter-strategies to decrease parasite infection is that many of the predictions have multiple outcomes. For example, fissioning could reduce the local density and decrease the chance of coming into contact with contaminated material and thus decrease transmission. Alternatively, it could place group members in new habitats where they could encounter novel parasites which they could acquire and subsequently transmit back to other group members.

What will be required in the future are studies that are carefully designed to distinguish between alternative hypotheses. For example, Nunn & Dokey (2006) used a meta-analysis of helminth richness of 119 primate species to distinguish between two competing hypotheses concerning how ranging behavior influences parasitism. They demonstrated that helminth richness increased with an index of territoriality, thus the physical separation of groups associated with territoriality did not lead to declines in measures of parasitism, rather parasitism increased as would be expected if the more intensive use of a home range increased exposure to parasites.

Future studies should attempt to determine which of the mechanisms that propose that parasites influence group size are potentially operating. For example, it should be possible to determine if species benefit nutritionally from winning between-group competition and whether this is of the magnitude to compensate for any elevation in any indices of parasitism. Ideal subjects for such a study would be black-and-white and red colobus. In black-and-white colobus it is the small groups that tend to win in between-group contest (Harris, 2005), while in red colobus it is the larger group that wins (Chapman unpublished data). Thus, one would predict that the difference in infection levels between large and small black-and-white colobus groups would be much greater than between large and small red colobus groups, since a large black-and-white colobus group is doubly disadvantaged as they do not have a nutritional gain from winning contests over food and they have an elevated risk of parasite infection.

In conclusion, it is an exciting time for studies of primate disease ecology and it is a time where we can re-examine some of the ideas that were proposed in the past. Today, we not only have accumulating data sets of primates from around the globe (Nunn & Altizer, 2005), we have information on how anthropogenic disturbance influences parasite–host relationships (Chapman *et al.*, 2005a), we can use new computational and modeling tools (see Nunn, Chapter 5, and Hasegawa, Chapter 25 this volume), and we have a rebirth of interest from researchers from a variety of fields as demonstrated in this volume.

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