

Red colobus monkeys display alternative behavioral responses to the costs of scramble competition

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Food competition is an expected cost of group living. It is therefore puzzling that there is little evidence for competition among group-living folivorous monkeys, for example, daily travel distance does not seem to increase with group size. It is even more puzzling that folivores do not form larger groups despite this apparent lack of food competition. This has become known as the folivore paradox, and to date, there is no broadly accepted theoretical solution. However, there have been no multigroup studies that have controlled for the potentially confounding effects of variation in habitat quality. We studied 9 groups of red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda, and controlled for spatial and temporal variation in food availability. We found that larger groups occupied larger home ranges than smaller groups and that group size was related to increased foraging effort (longer daily travel distance), increased group spread, and reduced female reproductive success. Our results also suggest that monkeys in larger groups spent more time feeding and less time engaged in social behavior. These results suggest that folivorous red colobus monkeys experience within-group scramble competition and possess a suite of behavioral responses that may mitigate the cost of competition and represent adaptations for group living. The results offer insight into the folivore paradox and the evolutionary ecology of group size. *Key words*: activity budget, exploitation competition, folivore, food availability, group size, habitat quality. [*Behav Ecol*]

Food competition is commonly accepted as an inescapable consequence of group living and is among the primary factors invoked to explain variation in social structure and group size among social mammals (Alexander 1974; Wrangham 1980; Jarman and Southwell 1986; Rubenstein 1986; van Schaik 1989). Within-group scramble, or exploitation, competition is defined as the collective depletion of limited resources and results in reduced foraging efficiency for all group members (Nicholson 1954; Janson and van Schaik 1988). Scramble competition intensifies as groups get larger and imposes a limit on group size because there will be a threshold below which further reductions in foraging efficiency cannot be tolerated. The energetic cost of travel is the presumed mechanism by which scramble limits group size; as groups get larger, food patches are depleted more quickly, individuals obtain less food from a given patch, and must travel further to find sufficient food resources (Milton 1984; Janson 1988; Chapman CA and Chapman LJ 2000b; Wrangham 2000). The predicted outcome is that there will be a positive relationship between group size and day journey length. Group size should also be positively related to home range size because a larger group will need to occupy a larger area that contains enough food for all members.

Two intriguing observations about the social ecology of folivorous monkeys raise questions about our theoretical understanding of food competition. First, field data suggest that large groups of folivores do not travel further in a day than small groups (Clutton-Brock and Harvey 1977; Struhsaker

and Leland 1987; Isbell 1991; Janson and Goldsmith 1995), which is puzzling because it suggests that food competition within groups is inconsequential, which in turn suggests that group size should not be limited by the availability of food. Second, given this apparent lack of feeding competition, it is paradoxical that these monkeys do not typically form larger groups (Janson and Goldsmith 1995; Crockett and Janson 2000; Steenbeek and van Schaik 2001; Koenig and Borries 2002), particularly because larger groups are thought to provide better protection from predators (Alexander 1974). This has been called the folivore paradox, and although social explanations related to infanticide avoidance have been proposed (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001; Koenig and Borries 2002), there is currently no broadly applicable theoretical solution.

We recently reviewed the literature and found evidence to suggest that folivores may experience scramble competition and that it may limit group size (Snaith and Chapman 2007). However, to effectively address the relationship between day range and group size, multigroup, ecologically controlled studies are required.

Controlling for ecological variation in resource availability is critical, as it remains the most likely confounding factor preventing clear interpretation of previous results. Studies that found no relationship between group size and day range (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Isbell 1991; Yeager and Kirkpatrick 1998) are problematic because they generally did not account for ecological variation in food resources, and if group size is adjusted in response to habitat quality, then there may be no need to increase day range (i.e., larger groups can exist in richer habitat without incurring greater scramble costs).

Furthermore, increasing day range may not be the only behavioral indicator of scramble competition (reviewed in Snaith

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and Chapman 2007). For example, reduced foraging efficiency may be indicated by increasing feeding and/or travel time, and such reductions may be compensated for with decreasing resting and/or social time (Caraco 1979; Altmann 1980; Dunbar RIM and Dunbar P 1988). As trees fill up with competitors, some individuals may have less opportunity to feed in the upper portion of the tree crowns where food quality may be best (nitrogen, and thus protein, availability improves with greater exposure to sunlight [Ellsworth and Reich 1993; Hollinger 1996]). In addition, individuals may increase group spread (occupy more trees) to reduce the effects of communal depletion, which may reduce the need to increase day range (Clutton-Brock and Harvey 1977; Janson and Goldsmith 1995). Alternatively, large groups may adopt a fissioning strategy where subgroups travel and forage independently of each other. Finally, if behavioral responses are insufficient to compensate for increasing foraging costs, the energetic costs of food competition may lead to nutritional stress and compromised reproductive success in larger groups (e.g., reduced fecundity and/or infant survival) (van Schaik 1983; Whitten 1983; Dunbar 1988; Knott 1999). However, this cost may be difficult to observe if large groups have a competitive advantage in between-group contest competition, which may offset the costs of within-group competition (Wrangham 1980; Clark and Mangel 1986; Dunbar 1988; Janson and van Schaik 1988; Janson 1992; Koenig 2000).

To our knowledge, there have been no multigroup, ecologically controlled studies that have measured a range of possible responses to scramble competition in folivorous primates. Here we measure and control for spatial and temporal variation in food availability and examine several alternative behavioral responses to food competition in red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda. If red colobus experience within-group scramble competition, then we predict that larger groups will have longer day ranges and larger home ranges, will spread out more, feed less frequently in the upper canopy, spend more time feeding and traveling and less time resting and/or engaged in social behavior, and will be more likely to fission temporarily into smaller foraging groups. If there is a fitness cost associated

with within-group competition, then reproductive success may be reduced in larger groups. If larger group size confers a competitive advantage, we predict that larger groups will occupy better quality habitat and will displace or be avoided by smaller groups.

MATERIALS AND METHODS

We studied folivorous red colobus monkeys at Kanyawara in Kibale National Park, Uganda (795 km²; 0°13' to 0°41'N and 30°19' to 30°32'E) between May 2005 and August 2006. The research site is described by Chapman et al. (1997) and Struhsaker (1997). Although Kibale forest has 2 wet and dry seasons each year, there is a large degree of variability both within and between years, and there is no strong predictable seasonality in vegetation phenology or food availability (Struhsaker 1997). Red colobus are an ideal subject because they are highly folivorous and show extreme variation in group size (9 to >120 individuals, from Struhsaker 2000b and this study). Red colobus group composition is generally multimale, multifemale with both sexes (but primarily females) dispersing, there is no peak in birth seasonality, and interbirth intervals vary widely with an average of about 23 months (Struhsaker 1975; Struhsaker and Leland 1987). Red colobus are well studied at Kibale (Struhsaker 1975; Chapman CA and Chapman LJ 1999). However, the small-scale ecological correlates of group size and the effects of group size on ranging behavior and fitness are not well understood.

We followed 9 groups of monkeys and controlled for ecological variability in 2 ways. First, we selected groups that occupied overlapping home ranges and followed them simultaneously (5 groups during May and 4 groups during June 2006). Second, we quantified the food available to each group using vegetation transects and phenological data. Data were collected by T.V.S. and 15 field assistants. We conducted an intense training period to standardize data collection techniques and to minimize interobserver error.

We followed 9 groups of monkeys for 215 complete follow days (2586 h of data, 22 980 scan samples; Table 1). Each

Table 1
Nine groups of red colobus monkeys followed in Kibale National Park, Uganda

Group name	Group size	Month	Full contact days	Days discarded ^a	Full-group follows ^b	Days fissioned	Subgroup name ^c	Subgroup size	Subgroup full-day follows
1	70	May	27	5	22				
2	25	May	27	5	22				
3	84	May	29	5	24				
SM	45	May	27	5	22				
LM	127	May/June	33	5	22	7	LM sub 1	27	2
							LM sub 2	Unknown	2
							LM sub 3	Unknown	1
5	51	June	27	5	22				
6	40	June	27	5	22				
10	74	June	27	5	16	6	10 sub 1	39	6
							10 sub 2	32	6
							10 sub 3	43	3
							10 sub 4	32	3
11	71	June	25	5	20				
									Total: 23
									Grand total full-day follows: 215

^a The first 5 days of observation were discarded for every group for habituation.

^b Only full-group, full-day follows ($n = 192$) were included in calculating group-level variables.

^c Subgroups were followed simultaneously when possible, table includes only subgroups for which full-day follows were obtained.

group was followed from 6:30 AM to 7:00 PM for at least 25 consecutive days. Although all groups were well habituated to humans (all groups occupied areas heavily used by researchers and most groups had previously been followed), the first 5 follow days for each group were considered habituation, and the data were discarded.

Group size and composition were determined by taking frequent counts of all individuals and identifying their age/sex class (adult female with infant, adult female no infant, adult male, subadult, juvenile, infant, and unknown). Group counts were conducted opportunistically whenever conditions were favorable (e.g., crossing openings), but at least once a day. Reported group size and composition data were derived from a compilation of these counts, taking into consideration the visibility and context of each count.

Subgroups were defined as a portion of the group that was separated by more than 300 m from the rest of the group, with no group members scattered in between. Whenever possible, we followed all subgroups simultaneously. Subgroup data and subgroup counts were collected in the same manner as for whole groups but are considered separately in analyses.

Behavior and ranging

Behavioral data were collected using scan sampling. The behavior of 5 adult or subadult individuals was recorded every 30 min from 7:00 AM to 6:30 PM or later if the group had not settled for the night. At the beginning of each scan, the first monkey seen was used, but we waited 5 s before recording its behavior to avoid biasing our data in favor of eye-catching behaviors. We then moved to the next monkey to the right of the first, until the behavior of 5 monkeys was recorded. Data recorded were age/sex class; activity (feed, rest, travel, social); feeding height (upper, middle, or lower third of tree crown); food tree species; plant part; and diameter at breast height (DBH).

Diet was determined from these scan data. Staple tree species were defined as any tree consumed for >1% of the feeding observations of any group (following Rothman et al. 2007). Similarly, staple foods were defined as any species–plant part combination consumed for >1% of feeding observations of any group; plant parts included mature leaves, young leaves, petioles, leaf buds, fruits, flowers, bark, and seeds.

Intergroup encounters were recorded whenever observed. When possible, we recorded the size and identity of all groups involved and measured the closest intergroup distance achieved. Interactions were classified as mutual avoidance, directional avoidance, or aggressive displacement involving fights and/or chases.

Ranging behavior was recorded by marking the location of the center of the group at 30-min intervals on a detailed map showing the trail network and a grid of 10 × 10 m cells. The distance traveled in each half hour was recorded, along with group spread (calculated as the area of an ellipse defined by the distance between the most distantly separated monkeys along 2 perpendicular axes) and the number of trees occupied by the group. Day range was calculated by summing all half-hourly distances. Previous research on this species suggests that 20 days are sufficient to obtain stable average day range estimates (Gillespie T, Chapman CA, unpublished data, after 20 days of data collection, cumulative average day range estimates stabilized). Home range was estimated by plotting all day ranges onto a map of the study area with a 100-m grid and including all grid cells entered. This coarse-scale short-term estimate of home range will relatively overestimate the size of smaller home ranges and should not be taken to represent year-round red colobus home range size in comparative studies.

Habitat quality

To estimate variation in habitat quality, we developed an index that incorporated spatial variation in staple food tree availability (total leaf biomass of all trees eaten >1% in the diet of any group), temporal variation (phenology of food items), and food quality (based on a preference index).

Available habitat was quantified from vegetation transects sampled between May 2005 and August 2006. A grid of 100 × 100 m cells was overlain on a 496-ha area that captured the observed home ranges of all groups. A 100-m transect was placed within each grid cell, normally starting from a trail intersection near the edge of the cell, and all trees >10 cm DBH within 5 m of either side of the transect were identified and measured. The 10-cm threshold was selected because red colobus rarely feed in smaller trees (Gillespie and Chapman 2001).

Food availability is often calculated using stem density or the cumulative DBH or basal area of food species. However, stem density does not account for the size of each tree, and the sum of dbh or basal area will not scale in the same manner as the sum of crown volume or leaf biomass. We thus calculated an index of leaf biomass based on studies of tree allometry and resource allocation, which have demonstrated that leaf biomass scales as $M^{3/4}$ and DBH scales as $M^{3/8}$, where M = total mass of the tree (Enquist et al. 1998; Enquist and Niklas 2001). Enquist et al. found both theoretical and empirical support for these relationships and found them to be robust across tree species and ecosystems. We transformed the equations provided by Enquist et al. to find leaf biomass = DBH^2 . We validated this index for 6 of the most common red colobus food trees in Kibale. We selected these tree species based on 4 years of independent red colobus feeding data from Kibale (Chapman CA, unpublished data). We measured the DBH and crown volume of 10 individuals of each species (we use crown volume as an index of leaf biomass). Crown volume was calculated from the estimated height and width of the crown, assuming cylindrical crown shape. We found that the relationship between DBH^2 and crown volume was significant for all trees combined and was significant for all but one species individually, and for that species, a positive trend was demonstrated (all trees, $r = 0.697$, $P = 0.001$, $n = 60$; *Celtis africana* $r = 0.811$, $P = 0.004$, $n = 10$; *Celtis durandii* $r = 0.839$, $P = 0.002$; *Funtumia africana* $r = 0.940$, $P < 0.001$; *Markhamia lutea* $r = 0.858$, $P = 0.001$; *Prunus africana* $r = 0.766$, $P = 0.010$; *Strombosia scheffleri* $r = 0.555$, $P = 0.096$). Based on these scaling relationships, we use DBH^2 as an index of the leaf biomass of an individual tree and summed across trees to obtain the cumulative leaf biomass for each species in an area.

Three kilometers of phenology trails were established in 1998 to track 309 trees of 37 species (Chapman et al. 2004). Since that time, each tree has been surveyed each month to determine phenophase. Following Struhsaker (1975), the proportional abundance of each plant part was scored using a scale of 0–4 (where 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% crown). An index of monthly availability was obtained by calculating an average score for each species–plant part combination each month (following Peres 1994). We used a paired t -test (with the May and June scores of a single tree as the pair) to determine whether there were temporal differences in food availability between months. We control for differences across months by including a phenology term in our habitat quality equation below.

Preferred foods are eaten more frequently than would be expected on the basis of their relative availability in the environment, and a variety of indices exist for calculating food preferences on this basis (Lechowicz 1982; Krebs 1989). We used Manly's α for constant prey populations (Manly et al. 1972; Chesson 1978; Krebs 1989), calculated for all staple trees as

$$\alpha_i = (r_i/p_i) / \sum_i^n (r_i/p_i),$$

where α_i represents the preference index of food type i , r_i represents its proportion in the diet, p_i represents its proportional availability in the environment (proportion of total leaf biomass), and n represents all staple trees. Because Johnson (1980) demonstrated that calculations of preference are strongly affected by the inclusion of common but rarely eaten foods, we included only those foods that represented 1% or more of the diet (staple foods). We pooled feeding data from all groups to obtain r_i and used the entire area used by all groups to obtain p_i . Manly's α is normalized so that the sum of all α values is 1. Food types with $\alpha > 1/n$ are preferred and $\alpha < 1/n$ are avoided. Foods with greater α values are assumed to be of higher quality to red colobus than those with lower values. Pooling data in this way may lead to biases if a very high-quality species is very rare or patchy and only available to one or a few groups, in which case its preference index may be too low.

We combined these data sets to calculate an index of habitat quality as

$$HQ = \sum_i^n (s_i t_i \alpha_i),$$

where HQ represents the relative quality of the home range of a group, s_i represents the spatial availability (cumulative leaf biomass) of staple food species i , t_i represents its temporal availability (phenology score for the most eaten plant part of species i for the appropriate month), α_i represents its preference index, and n represents all staple trees. Because phenology data were not available for all species, we substituted the mean value of the appropriate plant part (i.e., if there were no phenology data for species x and the most eaten part of this species was young leaves, then the average young leaf score of all species was used). The habitat quality index is reported as an overall value reflecting all available food in the home range of each group and on a per hectare basis to normalize for differences in home range size.

Group size effects

We examined whether group size was related to day range length, home range size and quality, group spread, number of trees occupied, feeding height, feeding tree size, and activity budget using nonparametric partial correlation tests that controlled for the effect of habitat quality per hectare (r_k is the partial correlation coefficient for ranked data). All groupwise tests were conducted using mean group values of behavioral and habitat measures ($n = 9$). Because we ran multiple comparisons, we reduced α from 0.05 using the Benjamini and Yekutieli modified false discovery rate method, which has been shown to be a meaningful experimentwise correction for multiple pairwise tests that reduce Type I error while maintaining statistical power (Narum 2006). For 12 pairwise tests, the appropriate critical value is 0.016 (Narum 2006). Because directional predictions were made, these tests were 1 tailed. Subgroup size effects were measured for group 10 by comparing subgroup size to day range length and group spread using Spearman correlation tests (r_s). For these comparisons, $n = 5$ (4 subgroups with 3 or more follow days plus the whole group) and $\alpha = 0.033$ for 2 pairwise tests, 1 tailed.

We used the number of offspring (infants + juveniles) relative to the number of adult females in a group as an index of female reproductive success. Because we do not know the reproductive history of the females in each group, this ratio was determined using group count data. We used a Spearman cor-

relation to compare the ratio of offspring/female to the number of adult females in a group, which is an appropriate test because the number of offspring and the number of females in a group are necessarily nonindependent and nonrandom (Jungers et al. 1995; Smith 2005).

RESULTS

Behavior and ranging

Group size varied from 25 to 127 individuals. Average day range length varied among groups from 418 to 953 m. Home range size varied from 23 to 66 ha and home ranges overlapped extensively among groups. Average group spread varied from 298 to 10 746 m² overall, and the average number of trees occupied varied from 4 to 35 trees.

All groups spent the greatest proportion of their time feeding (mean 40–51% across groups), followed by resting (25–30%), then traveling (16–29%), and engaged in social activities (5–10%). Individuals in all groups spent more time feeding in the upper tree crowns (mean 42–84% of feeding observations) than the lower crowns (1–8%).

Red colobus ate 268 identifiable food items (species–plant part combination) from 95 tree species. Young leaves made up the largest portion of the diet (77.2% of feeding observations), followed by petioles (11.6%), fruit (3.4%), mature leaves (2.7%), seeds (1.9%), and flowers (1.4%). Bark, dead wood, soil, and insects were eaten infrequently. Diet composition varied widely from group to group. Fifty-six items from 40 species were eaten for >1% of the feeding observations of any group. These were defined as staple foods and were used to calculate Manly's α and HQ.

We observed 42 intergroup interactions between groups of known relative size (study groups and groups for which we obtained a count sufficient to determine whether it was larger or smaller than the focal group). Of the interactions, 13 were mutual avoidances, 20 were directional avoidances, and 9 were aggressive displacements. Eleven of 20 directional avoidances occurred at more than 50 m.

Habitat quality

We identified and measured 17 381 trees along 496 vegetation transects. We thus sampled 49.6 ha to characterize an area of 496 ha that captured all areas used by the study groups. The phenology data set included data for 309 trees of 33 species. The only significant temporal change in plant part availability was that young leaves were more available during May than during June ($n = 309$ trees, May average score 1.54, June average score 1.24, paired $t = 4.689$, $P < 0.001$), making the phenology term in the calculation of HQ important. We calculated Manly's α for all staple food species; 12 of the 40 staple food trees were preferred. Several of the most eaten foods were not preferred because they were abundant. Habitat quality varied from 20 375 to 61 596 or 453/ha to 1100/ha, across groups.

Group size effects

When statistically controlling for habitat quality per hectare, group size was positively related to home range size ($r_k = 0.851$, $P = 0.004$), day range length ($r_k = 0.854$, $P = 0.004$; Figure 1), group spread ($r_k = 0.885$, $P = 0.002$), and the number of trees occupied ($r_k = 0.939$, $P < 0.001$; Table 2). There was no significant relationship between group size and time spent feeding in the upper crown ($r_s = -0.612$, $P = 0.053$). There were no significant relationships between group size and time budget variables when habitat quality was

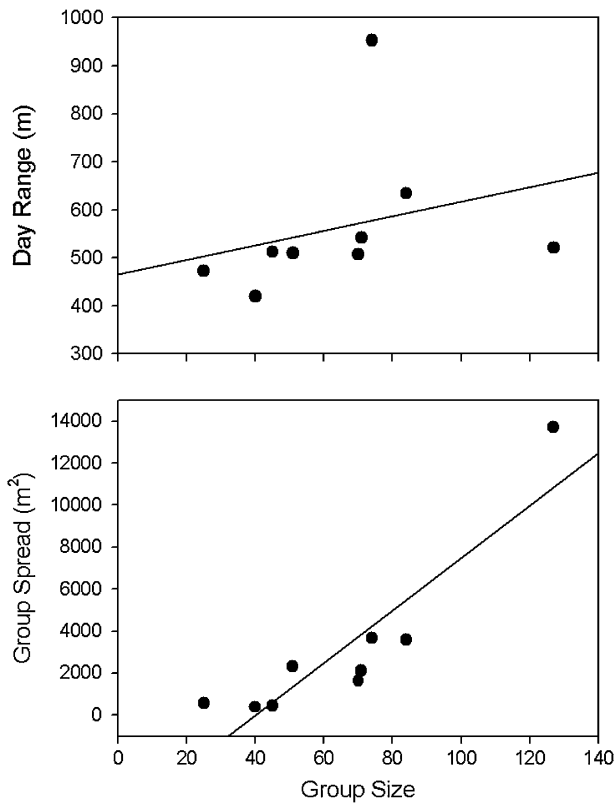


Figure 1
Group size effects on day range and group spread across 9 groups of red colobus monkeys.

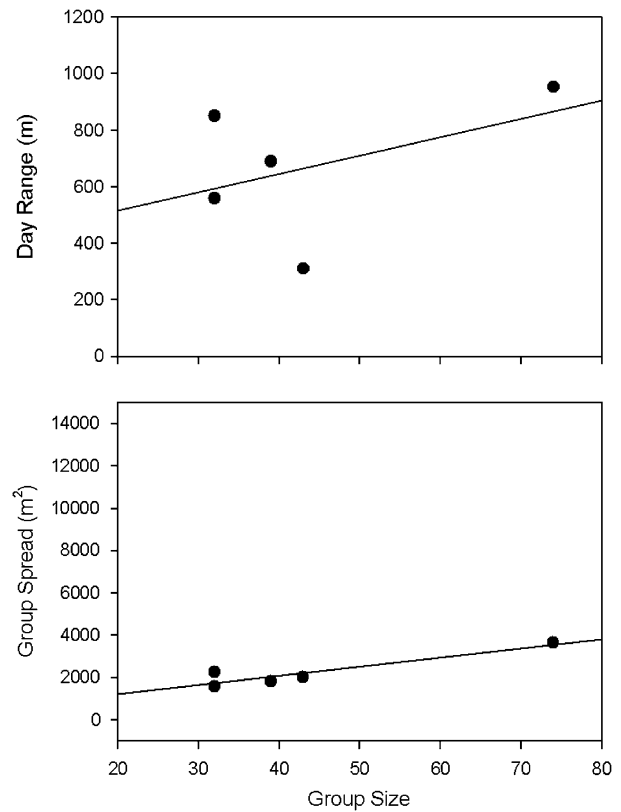


Figure 2
Group size effects on day range and group spread across subgroups of group 10.

controlled. However, there were nonsignificant trends suggesting that feeding time increased ($r_k = 0.584$, $P = 0.044$) and social time decreased ($r_k = -0.680$, $P = 0.032$) in larger groups. The P values do not meet our conservatively corrected

Table 2
Summary of groupwise comparisons

	r_k	P
Behavioral responses to scramble competition in larger groups		
Day range increases	0.854	0.004
Home range size increases	0.851	0.004
Group spread increases	0.885	0.002
# Trees occupied increases	0.939	<0.001
Feeding time increases	<i>0.584</i>	<i>0.044</i>
Travel time increases	-0.198	0.319
Resting time decreases	-0.270	0.259
Social time decreases	<i>-0.680</i>	<i>0.032</i>
Feed less in upper tree crown	-0.612	0.053
Fitness cost of scramble competition in larger groups		
Fewer offspring/female	-0.900	<0.001
Group size habitat covariation		
Overall habitat quality increases with group size	<i>0.617</i>	<i>0.038</i>
Habitat quality per hectare increases with group size	0.150	0.350

For all tests, $n = 9$ groups, r_k is the nonparametric partial correlation coefficient when habitat quality/hectare is controlled, and $\alpha = 0.016$ (experimentwise error correction for 12 tests), 1 tailed. Significant results are bolded and trends (>0.05) are italicized.

critical value of 0.016, but as they are less than 0.05, we believe that the trends are noteworthy and that we simply may not have had sufficient power to detect significant relationships. There was a similar trend suggesting that group size was positively related to overall habitat quality ($r_s = 0.617$, $P = 0.038$), but not to habitat quality/hectare ($r_s = 0.150$, $P = 0.350$).

Two of the largest groups occasionally fissioned into subgroups. Group 10 (74 members) frequently fissioned into 2 or more subgroups, which varied in size from 30 to 54 individuals. Subgroups remained separate for periods lasting from 5 h to 3 days. Although group 10 displayed the longest average day range on days when the whole group was together (953 m for whole group vs. 311, 560, 691, and 852 for subgroups followed for at least 3 full days each), there was no significant relationship between subgroup size and day range ($r_s = 0.205$, $P = 0.370$) or group spread ($r_s = 0.564$, $P = 0.161$; Figure 2). Group LM (127 members) fissioned near the end of the study, but we did not obtain reliable subgroup counts or enough full-day follows of subgroups to characterize their behavior.

The number of offspring per adult female varied across groups from 0.55 to 1.31. The offspring/female ratio was negatively related to the number of adult females in a group ($r_s = -0.900$, $P < 0.001$, $n = 9$), suggesting that this index of reproductive success declined with increasing group size.

Group size seemed to be an important factor determining the outcome of intergroup interactions. We observed 29 directional intergroup encounters, 24 of which (83%) were won by the largest group involved. Of the 20 directional avoidances, smaller groups avoided larger groups in 16 cases. All 9 decided interactions involving fights or chases were won by the larger group and resulted in the smaller group retreating.

DISCUSSION

Many previous studies found that there was no relationship between group size and day range or travel costs in folivorous monkeys (Clutton-Brock and Harvey 1977; Isbell 1991; Janson and Goldsmith 1995; Yeager and Kirkpatrick 1998; Yeager and Kool 2000; Isbell and Young 2002). Specifically, early work on red colobus monkeys at Kibale suggested that despite considerable variation in group size (9–68), there was little variation in day journey length (Struhsaker and Leland 1987). The absence of a group size effect on day range, in combination with the assumption that folivores rely on evenly distributed foods, led to the assumption that folivores experience little to no within-group scramble competition (reviewed in Snaith and Chapman 2007). However, these early studies made comparisons between groups during different time periods, in different areas, and even across species without controlling for ecological variation, which is expected to affect both group size and day range length. Recent work has indeed begun to suggest that red colobus may experience scramble competition. For example, a large group had longer day ranges than a smaller group (Gillespie and Chapman 2001), the day range of one group increased when food was less available (Gillespie and Chapman 2001), group sizes were larger in richer habitats (Chapman CA and Chapman LJ 2000a; Struhsaker 2000a; Struhsaker et al. 2004), and larger groups depleted food patches more quickly than smaller groups (a necessary condition for food competition to impose an ecological constraint on group size) (Snaith and Chapman 2005). This evidence suggests that folivores experience scramble competition and that it may limit group size.

Here we present the results of the first multigroup study that measures several behavioral indicators of scramble competition in folivorous primates while systematically controlling for spatial and temporal variation in food availability. Our results suggest that red colobus display many of the predicted behavioral responses to scramble competition. As group size increased, groups traveled farther each day, spread out more, occupied more trees, and were likely to fission into smaller foraging groups. We also found trends indicating that individuals in larger groups may have spent more time feeding and less time engaged in social behavior.

The 3 largest groups appeared to have adopted remarkably different ranging strategies. Group 3 ranged in a manner consistent with the general pattern across groups (relatively long day range length as expected for their large group size). Group 10 used a fissioning strategy; they traveled very long distances when the whole group ranged together, but when they fissioned, the subgroups did not travel as far. In contrast, LM remained cohesive most of the time, and while their day range was surprisingly short, their group spread was dramatically larger than any other group.

Our results suggest that red colobus possess a suite of possible behavioral responses to within-group scramble competition, which may complement or mitigate the typical day range response. These behavioral changes may represent mechanisms by which scramble competition imposes fitness costs. The observed changes suggest increased foraging effort, which may be associated with nutritional stress, which in turn is known to affect fecundity and infant survival in some species (van Schaik 1983; Whitten 1983; Harcourt 1987; Dunbar 1988; Ellison 1990; Knott 1999). Our finding that females in larger groups had fewer offspring supports the suggestion that female fitness was compromised with increasing group size, possibly as a consequence of increasing food competition.

Habitat quality is expected to covary with group size, home range size, and day range length and should interact with the group size-related costs of scramble. Larger groups occupied

larger home ranges than smaller groups, which were of higher quality overall, but not per hectare, which suggests that group size and/or home range size may be adjusted in response to habitat quality. The differences in habitat quality per hectare in this study were minor because we purposely reduced intergroup variation in habitat quality by simultaneously following groups in overlapping areas. For this reason, ecological differences were not sufficient to offset the need to increase day range in response to within-group competition. Furthermore, the role of habitat quality in mediating the relationships between group size and behavioral responses to food competition was minor: many of the relationships (e.g., group size vs. day range, group spread, and trees occupied) were significant without controlling for habitat quality, but the predictive relationships were better when habitat was accounted for. Our experimental controls for habitat quality (simultaneous follows, overlapping ranges) were likely sufficient, and the quantitative measurement and statistical control was perhaps unnecessary. When comparing across study sites or groups, there is a much greater risk that unmeasured ecological variation will confound group size effects on day range and activity budgets. Thus, measuring and controlling spatial and temporal variation in habitat quality will be even more important in uncovering such relationships.

There may be a fitness advantage available to larger groups if they are more successful in between-group competition, which may partially compensate for the costs of within-group competition. We found some evidence that increasing group size conferred a competitive advantage; more than 80% of decided interactions were in favor of the larger group. Although we can draw no conclusions about whether intergroup competition was food related, these interactions suggest that there may be some benefits associated with larger group size. The finding that larger groups may occupy better quality habitat may or may not support this hypothesis because further work is required to test the direction of this relationship (i.e., do larger groups monopolize better areas or do better areas simply support larger groups?). Furthermore, because we found that female reproductive success declined as the number of females in a group increased, we have no evidence that competitive advantages gained in larger groups translate into fitness gains. The subtle nature of these interactions (only 31% involved highly visible chases or fights; the rest were quiet avoidances) and the distances over which avoidances occurred (most at more than 50 m and several at as far as 200 m) suggest that between-group competition is subtle and difficult to observe in red colobus.

Dunbar (1996) suggested that ecological constraints on group size could be understood in terms of the need to balance the time budget; resting time should be reallocated when foraging demands increase, and group size will be limited by the point at which all spare resting time has been used. However, there has been considerable debate in the literature regarding the flexibility of social and resting time and which of the 2 will be compromised (Altmann 1980; Foley 1987; Dunbar RIM and Dunbar P 1988; Dunbar 1992, 1996; Bronikowski and Altmann 1996). Our results suggest that with increasing group size, feeding time increased, resting time remained unchanged, and social time decreased. However, the statistical relationships were not strong, and more data are required to determine whether these changes in time budget are real.

This response may be related to the digestive constraints of a folivorous strategy that requires considerable time for digestion (van Schaik 1983; Milton 1984; DaSilva 1992; Janson and Goldsmith 1995), which may prevent resting time from being compromised. It may also be related to the concurrent increase in group spread that we observed in larger groups.

In baboons, seasonal reductions in social time have been attributed to increased group spread and reduced social contacts due to seasonally high within-group competition for scarce food resources (Alberts et al. 2005). Our findings may provide an analogous situation, whereby an increasing number of conspecifics results, perhaps counterintuitively, in reduced social behavior.

The observed relationships between group size, home range size, and habitat quality should be considered in light of population distribution theory. If group size varies simply as a result of habitat quality and individuals are free to select the most ideal group, then group choice by individuals may be considered analogous to habitat selection in an ideal free distribution (Fretwell 1972). However, if home range size and quality vary as a function of group size and dominance, then group size dynamics may be analogous to the ideal despotic distribution (Fretwell 1972). We found that although group size was related to increased habitat quality and a between-group competitive advantage, it was also related to increased foraging effort and reduced female reproductive success. This muddies the suggestion of an ideal free and/or ideal despotic distribution because according to theory, all individuals in an ideal free distribution should achieve equal fitness, whereas in an ideal despotic distribution, individuals able to occupy richer habitat (in this case, larger groups) should achieve greater reproductive success (Fretwell 1972).

That there were reproductive costs associated with increasing group size raises the question of why red colobus females, who disperse and can theoretically select groups of appropriate size (Struhsaker 1975), would accept a fitness cost in large groups. Many components of fitness vary with group size, for example, the social and safety benefits of grouping are generally well accepted (Alexander 1974; van Schaik and van Hooff 1983). However, it has been shown that predation risk does not influence group size in red colobus (Struhsaker 2000a) and predation on red colobus at this research site is infrequent (Struhsaker and Leakey 1990). Thus, there seems to be little apparent safety benefit of increasing group size, and the potential social and safety benefits of grouping require further examination.

An optimal group size should theoretically exist, and above and below this optimal size, individuals will experience reduced fitness (Pulliam and Caraco 1984). However, even when optimal group size is exceeded, individuals may still benefit from joining (vs. remaining alone) and thus observed group size for many species exceeds the predicted optimal and there can be no single group size that is optimal for all individuals (Pulliam and Caraco 1984). In this context, it is perhaps not surprising that red colobus experience increasing fitness costs as group size increases. This leads to the question of why very large groups do not permanently fission into smaller groups if they have exceeded the optimal size and fitness is reduced. Further study is required to examine whether there are longer term benefits that may be accrued in large groups, particularly with respect to survival and lifetime reproductive success.

Our study has several limitations. First, because our focus was primarily limited to within-group scramble competition, we have only addressed a subset of possible modes of competition; the relationships we documented here may be influenced by between-group and between-species scramble competition. Second, we only followed 9 groups. Although this is a large number for a study of wild primates, it is still fairly small, and statistical power would be improved with a larger sample size. Third, by designing our research to control ecological variation, we may have reduced our ability to detect the role of such variation in determining primate group size and behavior. Fourth, our habitat quality index is limited because the density of leaf biomass and the relationship between dbh and leaf bio-

mass may vary across tree species, which may affect relative food availability. Despite these limitations, we found clear evidence that red colobus experience food competition and that its costs increased with group size.

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