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Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model

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Abstract The ecological-constraints model proposes that increased group size increases within-group feeding competition, necessitating increased travel and, consequently, constraining group size. Previous studies have supported the model for frugivores, but its applicability to folivores remains untested. This study evaluated the generality of the model by re-examining the relationship between day range and group size for a folivorous species for which published accounts have not found a relationship between these factors. This study differs from earlier studies by accounting for variation in food availability, which may drive changes in day range. We quantified the relationships among food availability, day range, and group size for two red colobus groups at Kibale National Park, Uganda. Mean day range and home range were significantly greater for the group of 48 individuals compared to the group of 24 individuals. The large group traveled more and rested less than the small group. The large group also traveled more rapidly than the small group. Food availability significantly predicted mean day range for the large group, but not for the small group. Analyses of covariance demonstrated that the large and small group responded differently to changes in food availability. These observations suggest that the large red colobus group experiences greater levels of within-group feeding competition than the small group. This study provides added support for the generality of the ecological-constraints model and contributes toward an understanding of the mechanisms controlling feeding competition and social organization in primates.

Keywords Group living · Food availability · Social organization · Folivores · Kibale National Park · Uganda

Introduction

How various ecological factors influence the size and composition of social groups has become a principal focus in behavioral ecology (Eisenberg et al. 1972; Clutton-Brock and Harvey 1977; Terborgh 1983; Janson 1988b; Janson and van Schaik 1988). Consequently, determinants of group size have been extensively discussed in terms of their costs and benefits (Alexander 1974; Bradbury and Vehrencamp 1977; Terborgh and Janson 1986; Boinski 1987, 1989; Dunbar 1997).

Benefits of group living for primates fall into three broad categories: predator avoidance (Hamilton 1971; Chapman and Chapman 1996; Noë and Bshary 1997; Boinski et al. 2000), foraging advantages (Cody 1971; Wrangham 1980; Struhsaker 1981; Garber 1988), and avoidance of conspecific threat (van Schaik and Kappeler 1993; Janson and Goldsmith 1995; Treves and Chapman 1996). Although there is disagreement as to the relative importance of these potential advantages of group living, grouping is viewed to confer such predictable advantages that differences in group size can be explained by the disadvantages (Dunbar 1997; Parrish and Edelman-Kashet 1999). Increased within-group feeding competition is recognized as the major cost of group living among primates (Terborgh and Janson 1986; Wrangham et al. 1993; Janson and Goldsmith 1995).

The ecological-constraints model suggests that exploitation competition, the reduction of resources by competitors without direct conflict, limits group size any time a group must travel further per day than would a solitary forager to meet the energetic requirements of its members (Milton 1984; Janson 1988b; Wrangham et al. 1993; Chapman et al. 1995; Chapman and Chapman 2000b). Two mechanisms are proposed to constrain group size. In the first case, the model assumes that food items occur in discrete depletable patches and it proposes that an in-

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crease in group size will lead to increased day range due to more rapid patch depletion necessitating increased travel between patches. Thus, individuals must travel farther and expend more energy if they are in a large group than if they are in a smaller group or alone (Milton 1984; Chapman 1990). Smaller groups become advantageous when an increase in travel costs is not repaid by an increase in energy gained or some other fitness advantage (Chapman and Chapman 2000b). The model assumes that when resource availability is constant, the addition of new members will lead to increased within-group feeding competition necessitating increased travel (Waser 1977; Wrangham et al. 1993; Chapman et al. 1995). The need for increased travel can result from larger groups depleting patches more quickly, forcing groups to visit more patches.

In the second case, for species that either do not deplete patches within which they feed or that feed on dispersed foods and cannot increase group spread as group size increases, individual search fields may increasingly overlap, reducing per capita encounter rate with food, thereby increasing the area that must be searched to find food (van Schaik and van Hooff 1983; Janson 1988b; Chapman and Chapman 2000c). In this situation, as group size increases, individuals are “pushed forward,” increasing the distance traveled per day (van Schaik and van Hooff 1983).

If groups are always attempting to maximize group size (e.g., to reduce predation or to be more effective in intergroup competition), then they may already be traveling the maximum distance possible. In such a case, an increase in food availability would be expected to result in an increase in group size, while travel remains constant (Wrangham et al. 1993). Thus, the ecological-constraints model predicts a strong relationship among group size, day range, and food availability, but not necessarily between any two variables alone.

Although the theoretical base of the ecological-constraints model was established in reference to stable, cohesive grouping species, it has been tested to a great extent by examining primate species exhibiting a fission-fusion social structure which involves group members foraging in subgroups that frequently change in size and composition (Wrangham et al. 1993; Chapman et al. 1995). The question arises as to the applicability of the model to species living in cohesive social groups.

Moreover, examples from the literature caution against the widespread acceptance of the model across the primate order, especially among folivorous primate species, in which previous studies have found no relationship between group size and day range (Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998). For example, an intrapopulation comparison of two red colobus monkey (*Procolobus badius*) groups found that day range was 8.7% shorter for a group of 65 animals compared to a group of 20 individuals (Isbell 1983). In addition, Janson and Goldsmith's (1995) empirical review reported equivocal results as to the relationship between daily foraging costs and group size for folivores.

Challenges to the ecological-constraints model, however, are not limited to folivores. Bronikowski and Altmann (1996) found that baboon (*Papio cynocephalus*) groups traveled farther in years when group size was smaller. Struhsaker and Leland (1988) found that a large (32 individuals) and a small (15 individuals) group of redbellied monkeys (*Cercopithecus ascanius*) had similar day ranges (1,546 vs 1,595 m) despite the twofold difference in group size. Lastly, in a 2-year study of five groups of blue monkeys (*C. mitis*), Butynski (1990) found no relationship between day range and group size.

These findings are unexpected in light of the ecological-constraints model, since we anticipate larger groups to travel farther each day to meet the energetic requirements of group members. However, none of these studies provided data on the overall food availability for the groups studied. Consequently, food availability may have simply been greater for the larger groups, allowing them to maintain large groups without increased travel costs. Such examples illustrate the need to quantify food availability when exploring the relationship between group size and day range.

Previous studies have examined the relationship between group size and day range by focusing on groups with overlapping home ranges (Struhsaker and Leland 1987, 1988; Janson 1988a). It may seem plausible that food availability can be taken to be constant for groups with overlapping ranges. However, even in cases of high spatial overlap among groups, closer inspection sometimes reveals a great deal of heterogeneity in resource availability (Chapman et al., in press a). For example, recall that Struhsaker and Leland (1988) found that a large and a small group of redbellied monkeys with overlapping ranges had similar day ranges despite a twofold difference in group size. Close inspection of the study reveals that food availability may have differed between the groups despite their overlapping ranges. Unlike the larger group, the smaller group's “range was restricted to the north and east by grassland and colonizing bush and appeared to contain areas of suboptimal habitat” (Struhsaker and Leland 1988, p. 370). Hence, even in cases where home ranges overlap, estimates of food availability are essential to understand the interplay among group size, day range, and resource availability.

Few studies have directly quantified relationships among day range, group size, and food availability for primates. Studies that have investigated these issues are limited to a subset of species with analogous ecological requirements and comparable social systems, namely frugivorous species with fission-fusion social structure (Milton 1984; White and Wrangham 1988; Chapman 1988, 1990; Strier 1989). The short-term costs and benefits for a fission-fusion subgroup to change in size and composition may not be comparable to the long-term costs and benefits of a cohesive group changing size through births, deaths, immigration, and emigration. Hence, the formulation and testing of the ecological-constraints model rests on a number of assumptions which lead to questions concerning its widespread applicability, and the model may not apply to animals with stable group composition.

The objective of this study was to re-examine the relationship between day range and group size for a species where published accounts have found no such relationship. This study differs from earlier studies by incorporating detailed estimates of food availability. To meet this objective, we conducted an intrapopulational comparison of two neighboring red colobus groups of very different sizes with overlapping home ranges in Kibale National Park, Uganda. Since group size remained unchanged for each red colobus group for the duration of the study, we hypothesized that declines in food availability would result in increased day ranges for each group. In addition, we hypothesized that the magnitude of increase in day range resulting from changes in food availability would be greater for the large compared to the small group due to increasing intragroup competition with increasing group size. This investigation was designed to examine the generality of the ecological-constraints model by quantifying the relationship between day range, group size, and food availability for a folivorous, non-fission-fusion grouping species.

Methods

Study species and study site

The red colobus monkey (*P. badius*) occurs patchily throughout forested equatorial Africa (Oates et al. 1994). Red colobus are diurnal, arboreal anthropoid primates typically exhibiting a multi-male/multi-female, non-fission-fusion social structure (Struhsaker 1975; Oates 1994). Home range overlap among groups is common, and intergroup interactions range from tolerant to aggressive. Red colobus are selective folivores. Relative proportions of mature leaves (6–44%), young leaves (31–54%), fruits (6–41%), and seeds (1–31%) in the diet are highly variable among sites (Struhsaker 1978b; Oates 1994; Davies et al. 1999).

Kibale National Park is a 766-km² reserve located in western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E) near the base of the Ruwenzori Mountains (Chapman et al. 1997; Struhsaker 1997). Tall, closed-canopy forest accounts for 57% of the park. The remainder forms a mosaic of swamp (4%), grasslands (15%), pine plantations (1%), and colonizing forest (19%) (Butynski 1990; Chapman and Lambert 2000). The study site, Kanyawara, is located at the northern end of the park at an elevation of 1,500 m (Chapman et al. 2000). Kanyawara experiences a bimodal pattern of seasonal rainfall, with peaks occurring in March–May and August–November (Chapman et al. 1997). Mean annual rainfall (1990–1998) is 1,778 mm. Daily temperature maxima and minima averaged 23.7°C and 15.5°C, respectively, from 1990 to 1998. The red colobus groups studied ranged in both mature, relatively undisturbed forest and lightly, selectively logged forest.

Behavioral observations

From May through August 1998, we intensively studied two habituated groups of red colobus monkeys at Kanyawara, one large group (48 individuals) and one small group (24 individuals). Data were collected on feeding ecology, group size and composition, day range, home range, and food availability.

For each group, data on group movement and behavior were collected on 4 consecutive days every other week, producing 576 h of observation. Groups were followed from first movement in the morning until final movement in the evening (typically 0630 to 1845 hours). Each group had several recognizable individ-

uals, allowing verification of group identity. Every half-hour, point samples were taken on the first ten adult or subadult individuals noted (Struhsaker 1975; Chapman and Chapman 1999). For each point sample, the first activity the individual sustained for at least 5 continuous seconds was recorded. If an individual was feeding, the tree species and part eaten were also recorded. Plant parts were categorized as mature leaves, young leaves, leaf buds, petioles, flowers, unripe fruit, ripe fruit, and bark. The age class (subadult or adult) and sex of each observed animal was noted. Duration of scan samples was variable, but none exceeded 15 min.

We determined day range by marking, on the ground and on a map, the center of mass of visible animals in the group every 15 min, and then summing the distances between successive chronological points for each day. Group spread was measured every half-hour as the distance from the perceived center of mass of the group to a point perpendicular to the direction of group travel at which no additional individuals could be seen multiplied by two. For both day range and group spread, measurements were made by two individuals with a 50-m tape to ensure accurate estimations. Mean rate of travel was determined for each group by dividing the summation of day ranges for the group ($n=24$ days) by the total number of minutes spent traveling during the study. Number of minutes spent traveling was estimated by summing the number of 15-min intervals that included travel and multiplying by 15. Home range was determined for each week by mapping the linear day range for the 4 follow-days and then mapping the location of all trees ≥ 20 cm diameter at breast height (DBH) within the group's spread along the line (see below for justification of 20-cm criteria). All trees were then plotted in the ArcView geographic information system, allowing for detailed estimates of area (ArcView GIS, version 3.1, 1996). Group size estimates were made opportunistically when groups crossed a narrow point forcing them to travel in a single-file line (a minimum of one group count considered to be accurate due to good visibility was obtained per observation week).

Previous studies suggest that factors such as intergroup aggression (Struhsaker 1974) and intensity of rainfall (Isbell 1983) best predict day range length for red colobus. Consequently, periods of rainfall, threats of predation, and intergroup interactions were documented. The duration and intensity (light, average, or heavy) of rainfall was recorded. Actual measures of daily rainfall were measured at Makerere University Biological Field Station located 200 m from the home ranges of the large and small red colobus group. Threats of predation were defined as any time chimpanzees (*Pan troglodytes*) were within 50 m of group members or crowned eagles (*Stephanoaetus coronatus*) flew within 25 m of group members. Intergroup encounters were defined as incidents in which members of another red colobus group were within 50 m of the focal group (Struhsaker 1975).

Food availability assessment

Food availability was assessed each week in the 3 days following the 4-day follow for each group. The location of all trees with a DBH ≥ 20 cm within the area used by the monkeys in the previous 4 days were mapped in relation to the extensive trail system. In the area used by the observed groups, the trails were typically 50 m apart. A 20-cm cutoff was used for tree DBH since red colobus rarely feed in smaller trees. The mean DBH of trees on which red colobus fed was 63.72 ± 54.4 cm, and red colobus feed on trees less than 20 cm DBH only 7.3% of the time ($n=109$ trees; C.A. Chapman and L.J. Chapman, unpublished data).

The small home range used by red colobus monkeys facilitates the mapping of all potential food trees instead of relying on transect or sample plot estimates of overall food species abundance and diversity. This provides a complete catalogue, not just an estimate, of available food resources. During the study, 6,596 trees were mapped and their phenology assessed (mean = 903 ± 165 trees per week for the large group and 197 ± 26 trees per week for the small group). For each tree, DBH was measured, species was identified, and the presence or absence of red colobus food items

was noted. Only trees with red colobus food items present upon examination were included in food availability calculations.

DBH was used as an estimate of food patch size (Chapman 1988; Whitten 1988). A number of studies support the use of DBH as an indicator of plant productivity. Chapman et al. (1992) demonstrated DBH to be the most consistently accurate method for obtaining good estimates of fruit abundance (both biomass and number) for a variety of tree species. In addition, a number of studies from the forestry literature demonstrate that DBH predicts overall estimates of leaf biomass with a standard deviation of less than 15% (Brown 1978; Harrington 1979; Catchpole and Wheeler 1992). The use of DBH as an indicator of leaf biomass is also advocated in the comparative study of primary and successional tropical forests (Uhl and Jordan 1984; Uhl 1987).

Potential food trees for each group during a given week are defined as trees of those species fed upon by the focal group for at least 5% of feeding observations for that week. This criterion was used because red colobus frequently feed in trees of many species for short periods (Struhsaker 1975; Chapman and Chapman 2000a). Consequently, during weeks when food resources were scarce, and trees fed on for short periods were common, estimates of food availability would be erroneously high if all trees were included in food tree analyses (Chapman and Chapman 2000a). Species accounting for at least 5% of the red colobus feeding time account for 65% of feeding time for the large group and 75% of feeding time for the small group.

Food availability was assessed using two indices, density of food trees and cumulative DBH per hectare of food trees. Food tree density was calculated by summing the number of food trees bearing food items within a group's area of use for each 4-day observational period and was expressed as food trees per hectare. SPSS statistical software (SPSS, version 10, 1999) was used to run linear regressions attempting to predict day range for the large and small group from the two indices of food availability. Analyses of covariance were run to determine whether the large and small group reacted in the same manner to changes in food availability.

Results

Red colobus were observed for 576 h from May to August 1998 (282 h for the small group and 294 h for the large group) and 9,166 point samples were collected (4,433 for the small group and 4,733 for the large group). The size of the two groups remained stable throughout the study (24 individuals for the small group and 48 individuals for the large group). Group composition changed slightly for each group over the length of the study due to reclassification of infants and juveniles to older age classes. Over the total study, the large group rested significantly less ($n=24$ days, $U=175$, $P=0.02$) and traveled significantly more ($n=24$, $U=178$, $P=0.02$) than the small group. The percentage of the activity budget spent feeding did not differ between the groups ($n=24$, $U=205$, $P=0.09$). In addition to traveling more, the large group also traveled more rapidly than the small group (1.24 m per minute compared to 0.91 m per minute). Group spread was significantly larger for the large group (66.14 ± 13.0 m) compared to the small group (51.67 ± 10.0 m) ($n=24$, $t=-4.31$, $P \leq 0.001$, $df=46$).

Day range length was significantly longer for the large group compared to the small group (577 ± 184 m vs 309 ± 110 m, respectively; $n=24$ days per group, $t=-6.125$, $P \leq 0.001$). In fact, the small group's maximum day range did not even meet the minimum day range of the large group. Mean day range for the small group varied from 183 to

Table 1 Mean day range and home range of the large and small groups of red colobus for each week of behavioral observations at Kibale National Park, Uganda

Group	Week	Mean day range (m)	Weekly home range (ha)
Large	1	770.0	2.3
	2	606.0	9.3
	3	497.5	12.9
	4	585.0	8.3
	5	535.0	12.6
	6	468.8	8.0
Mean		577.0	8.9
Small	1	463.8	3.1
	2	358.8	1.8
	3	310.8	1.6
	4	183.0	1.8
	5	250.0	1.9
	6	290.0	1.8
Mean		257.6	1.7

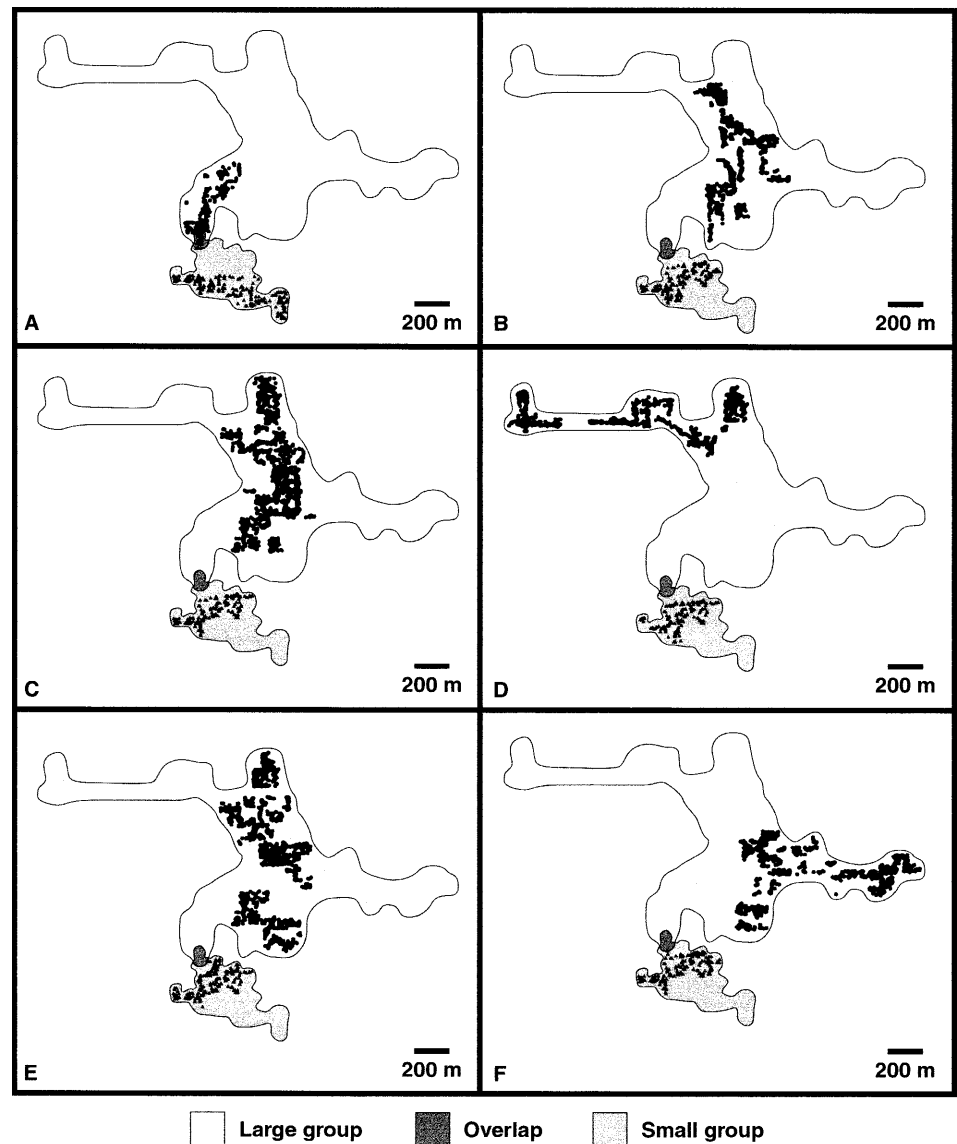
464 m, while mean day range for the large group varied from 469 to 770 m (Table 1).

Overall home range for the large group was more than seven times that of the small group (36.90 ha for the large group compared to 5.04 ha for the small group). The weekly home range was significantly larger for the large compared to the small group ($n=6$ weeks, $U=1$, $P \leq 0.004$). The weekly home range for the small group varied from 1.61 to 3.13 ha, while that for the large group varied from 2.27 to 12.92 ha (Table 1). The small group commonly foraged in the same area from observation week to observation week (Fig. 1). In contrast, the large group demonstrated minimal overlap in areas foraged between weeks of observation (Fig. 1).

Three thousand and twenty-one feeding observations were made (1,314 for small group, 1,707 for the large group). During the entire study period, the small group fed on 75 food items from 30 species. The large group fed on 100 food items from 41 species. Three of the seven species accounting for 5% or more of the overall diet in each group were the same: *Prunus africana*, *Strombosia scheffleri*, and *Funtumia latifolia*. However, the large group commonly fed on trees of the same species in succession (28% of movement between focal feeding trees, i.e., trees that account for >50% of feeding observations for two consecutive scans, $n=175$), while the small group fed on trees of the same species in succession to a much lesser extent (10% of movements between focal trees, $n=145$).

Overall food availability for the duration of the study, expressed as cumulative DBH per hectare of food trees, was 73% greater for the small compared to the large group (1,737 cm/ha for the large group and 3,012 cm/ha for the small group). Cumulative DBH per hectare of food trees for the large group varied among weeks from 1,070 to 2,098 cm/ha, while for the small group, it varied among weeks from 1,033 to 3,766 cm/ha. Overall food availability for the duration of the study, expressed as density of food species, was 25% greater for the small

Fig. 1A–F Weekly home ranges and food tree availability of a large and a small red colobus group at Kibale National Park, Uganda. *Dots* represent all trees greater than 20 cm diameter at breast height (DBH) in the weekly home range of each group. **A** Week 1. **B** Week 2. **C** Week 3. **D** Week 4. **E** Week 5. **F** Week 6



compared to the large group (40 trees per hectare for the large group compared to 50 trees per hectare for the small group). Food tree density for the large group varied among weeks from 24 to 45 trees per hectare, while for the small group, it varied among weeks from 18 to 63 trees per hectare.

Mann-Whitney *U*-tests were performed to determine if days with or without rainfall, threats of predation, or intergroup encounters affected day range for each group and for both groups combined. Rainfall within the magnitude that fell during this study (0–57.8 mm per day, daily mean=2.4 mm) had no effect on day range for either group or both groups combined (small group: $n=24$, $U=45.5$, $P=0.89$; large group: $n=24$, $U=33.5$, $P=0.63$; combined: $n=48$, $U=172.0$, $P=0.94$). Threats of predation by crowned eagles and chimpanzees had no apparent effect on day range for either group or both groups combined (small group: $n=24$, $U=36.5$, $P=0.79$; large group: $n=24$, $U=31.5$, $P=0.53$; combined: $n=48$, $U=154.0$,

$P=0.88$). Encounters with other red colobus groups had no apparent effect on day range for either group or both groups combined (small group: $n=24$, $U=23.5$, $P=0.21$; large group: $n=24$, $U=58.0$, $P=0.95$; combined: $n=48$, $U=48.0$, $P=0.731$).

The linear regressions attempting to predict weekly day range from two indices of weekly food availability demonstrated that food availability was a significant predictor of mean day range length for the large group ($r^2=0.89$, $P=0.003$ for cumulative DBH of food trees; $r^2=0.79$, $P=0.011$ for food tree density; Figs. 2, 3), but not for the small group ($r^2=0.380$, $P=0.192$ for cumulative DBH per hectare of food trees; $r^2=0.399$, $P=0.178$ for food tree density; Figs. 2, 3). Each regression was performed a second time after dropping the most extreme point. These modified regressions demonstrated the same relationships seen in the original regressions with one exception. After removing the most extreme point from the regression predicting day range from food

Fig. 2 Relationship between mean day range and cumulative DBH of food trees per hectare for a large and a small red colobus group at Kibale National Park, Uganda

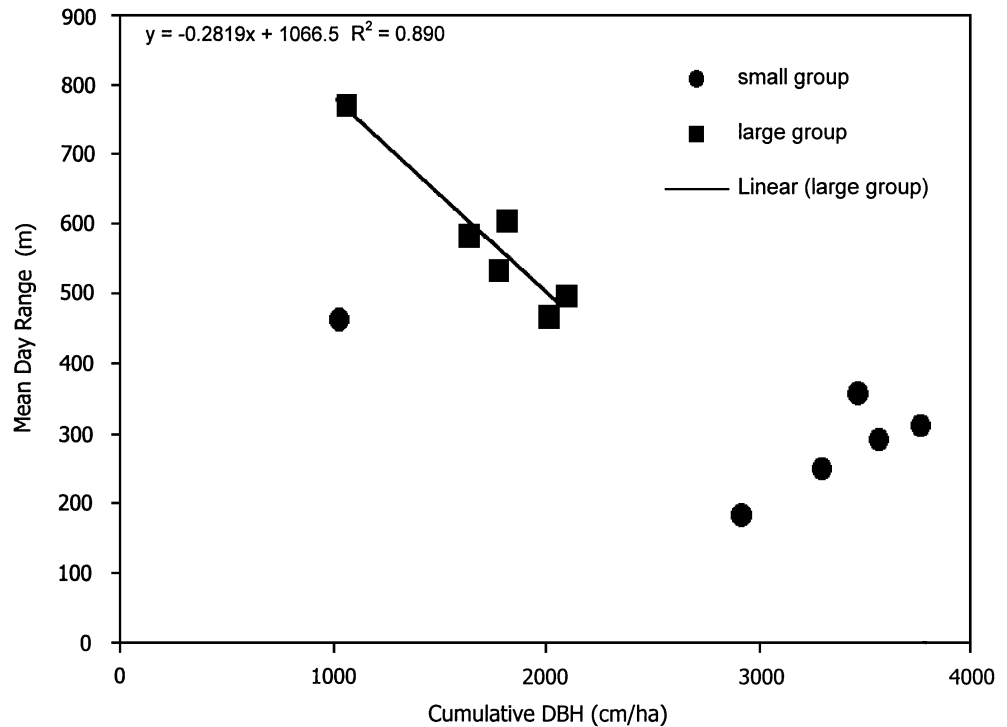
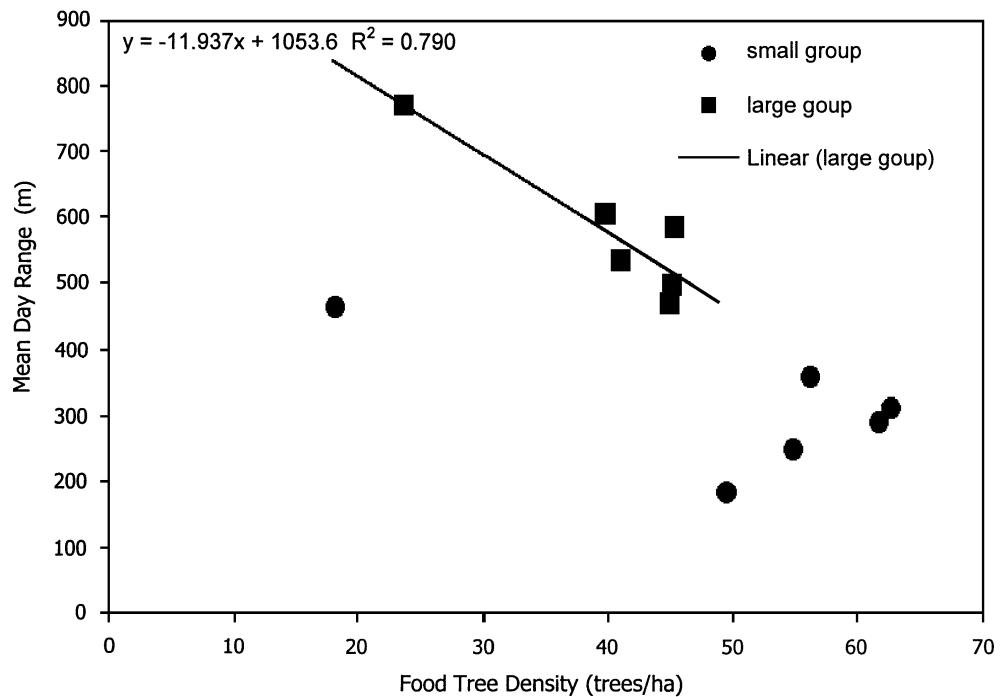


Fig. 3 Relationship between mean day range and food tree density for a large and a small red colobus group at Kibale National Park, Uganda



tree density for the large group, weekly food tree density no longer predicted weekly day range.

Analysis of covariance demonstrated that the large and small group reacted differently to variation in food availability. When cumulative DBH per hectare was used as the index of food availability, the slopes for the two groups differed significantly ($F=6.929$, $P=0.030$, Fig. 2). When food tree density was used as the index of food availability, the slopes of the two groups were not differ-

ent ($F=3.988$, $P=0.081$, Fig. 3). Since the slopes were found to differ, no further analyses were performed.

Discussion

The ecological-constraints model predicts that day range and home range will be greater for larger than for smaller groups, since larger groups must travel over larger areas to

obtain enough food for all group members (Milton 1984; Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995; Chapman and Chapman 2000b). Results from this study support this prediction. In fact, mean day range values for each week did not overlap between the two groups. Furthermore, the overall home range for the large group was seven times that of the small group.

We suggest these observed differences are the result of higher levels of feeding competition in the large group. If competition for food is greater in larger groups, then time spent traveling should be positively correlated with group size (Isbell and Young 1993). In addition, if competition for food is greater in larger groups, then larger groups may travel at a faster rate to visit more food trees in a given day. The activity budgets of the large and small group in this study differed significantly, and demonstrated that the large group traveled more and rested less than the small group. Moreover, the large group traveled 36% more rapidly than the small group. Thus, several findings of this study support the generality of the ecological-constraints model of group size.

These results differ from those of earlier studies that suggested that day range in the red colobus is not dependent upon group size (Struhsaker 1974, 1978a; Isbell 1983; Struhsaker and Leland 1987). These earlier studies suggested that factors such as intergroup aggression (Struhsaker 1974) and intensity of rainfall (Isbell 1983) best predict day range for the red colobus. In the current study, neither intergroup encounters, nor rainfall were found to be a significant predictor of day range for the red colobus. Admittedly, the current study is short-term in comparison to the previous studies, and these factors might have been shown to have an impact over the long-term (e.g., greater variance in the amount of rain falling in a day). However, the short-term nature of this study does not negate the importance of the patterns documented between day range, group size, and food availability, since travel decisions are made on a short time scale (e.g., conditions and events occurring in a daily or weekly time frame). Food availability is a critical component for day range and group size that has often been ignored. Thus, in studies where no relationship was found between day range and group size, variation in overall food availability may have accounted for the differences in day range. Food availability may have simply been greater for the larger groups, allowing them to maintain large group size without higher travel costs.

Why was the mean day range for the large group two and a quarter times and the home range more than seven times greater than that of the small group? The critical factor appears to be food availability. We would expect the large group's day and home ranges to be double those of the small group only if food availability was equivalent for the two groups. The food resources available to and used by the large and small groups differed. Food availability was much greater for the small group. Thus, the differences seen in mean day range and home range for the two groups are probably the result of both higher levels of food competition and lower food availability

for the large group. The small group possibly had a restricted home range due to intergroup aggression. Large groups have a competitive advantage in contests over disputed resources and may supplant smaller groups. However, in the current study, intergroup aggressive encounters involving the small group were extremely rare (three during the study) and did not appear to influence movement patterns. Consequently, it appears that lower levels of food competition and higher food availability, not intergroup aggression, best explain the smaller home range of the small compared to the large group.

Food availability was a significant predictor of mean day range for the large group, but not for the small group. ANCOVA demonstrated that the large and small group reacted differently to variation in food availability. The variation observed in day range for the small group possibly did not exert high costs on group members due to the interaction of high food availability and small group size. One might expect that a substantial increase in group size or a substantial reduction in food availability for the small group would result in an increase in day range as seen in the large group. The apparently high reproductive output of the small group (88% of females with infants vs 50% of females with infants in the large group) provides additional evidence that the small group may not be experiencing the strong costs normally associated with group living. However, the large number of infants in the small group could also be the result of lower rates of predation or illness compared to the large group.

If groups are always attempting to maximize group size (e.g., to reduce predation risk), then we would expect large groups to be found in areas of highest food availability. In addition, large groups would be expected to be able to supplant smaller groups from the highest-quality areas, pushing them into the areas of lower food availability (Struhsaker 1974, 1978a). In the current study, the small group used the same small area of high food availability week after week, whereas the large group ranged over a much larger area and used areas with lower food availability. Why was the small group in this study living in an area of high food availability and the large group in areas of lower food availability? The area of high food availability used by the small group may have been too small to sustain the long-term needs of the large group. Another possibility is that the area used by the small group was considered more dangerous due to a perceived threat of predation (the area borders an open field where many frequently used field station facilities are found).

Mechanisms of the ecological-constraints model

The ecological-constraints model proposes two mechanisms that can constrain group size. The first assumes that food items occur in discrete depletable patches and that an increase in group size will lead to increased day range due to more rapid patch depletion necessitating increased travel between patches. The second mechanism deals with species that either do not deplete patches or which feed on

dispersed foods and cannot increase group spread as group size increases. The latter mechanism proposes that as group size increases, individual search fields increasingly overlap, reducing per capita encounter rate with food, thereby increasing the area that must be searched to find food. The fact that group spread was significantly greater for the large compared to the small group in this study suggests that red colobus can spread out to mitigate increased search field overlap. However, group spread does not appear to increase with group size to the extent needed for all search field overlap to be avoided. Hence, aspects of both mechanisms of group size constraint appear to be at play in the case of the red colobus.

Since red colobus group size appears to be explained by the mechanisms outlined by the ecological-constraints model, the question then arises: do red colobus deplete the food patches in which they feed? Theoretically, a food patch is depleted when feeding by individuals has led to the disappearance of all food items (Chapman 1988). However, as food items become rare within a tree, they become progressively harder to obtain. Thus a patch is functionally depleted before all food items are eaten (Chapman 1988). From this perspective, patches can be considered depleted when the rate of food intake drops to a level equal to the average intake in the environment (Charnov 1976).

Results from this study support the idea that the large group of red colobus depleted food patches. This group commonly fed on trees of the same species in succession and rarely revisited the same trees on the same day. In addition, the large group rarely foraged in the same area during successive weeks of observation and often avoided foraged areas for several weeks after they had been used. Lastly, the large group traveled more and rested less than the small group. In contrast, results from this study suggest that the small red colobus group rarely depleted food patches. This group foraged in the same area, day after day, and week after week. In addition, the small group did not commonly feed in trees of the same species in succession. Consequently, the large group appears to deplete food patches, while the small group does not.

Food limitation among colobines

Competition for food has been suggested to result in strong female dominance hierarchies within groups (van Schaik 1989; Isbell 1991). For some folivorous species, a lack of strong female dominance hierarchies within groups, as well as reports that day ranges do not increase as a function of group size, have led to the suggestion that food resources are not limiting in these populations (Isbell 1991; Yeager and Kirkpatrick 1998).

The results of a number of studies are inconsistent with respect to whether or not folivorous primate populations are food limited. McKey (1978) proposed that availability of digestible mature leaves, a resource used by colobus monkeys when more preferred foods are unavailable, limits the size of colobine populations. Milton (1979)

formalized this hypothesis and presented a functional explanation as to why it should operate. Several subsequent studies found significant positive correlations between Asian and African colobine biomass and an index of leaf quality, the ratio of protein to fiber (Waterman et al. 1988; Oates et al. 1990; Davies 1994). A similar correlation exists between leaf quality and the biomass of folivorous lemurs (Ganzhorn 1992). Recent findings demonstrate that this correlation between colobine biomass and protein to fiber ratio of mature leaves is significant between sites within Kibale National Park, the site of the current study (Chapman et al., in press b). These results suggest that folivorous primates are food limited. The current study reinforces these findings. The mechanism by which this food limitation occurs remains uncertain. Folivores may be limited by the physical depletion, nutritional content, or toxin content of resources. Future studies that examine how food limitation is manifested in folivorous primates will add greatly to our current understanding of these species and may provide valuable information for their conservation and management.

Implications for social structure

For folivorous species, the observed lack of strong female dominance hierarchies within groups may not result from the absence of food competition. The female social relationships of these folivores, and of all primates, are best explained as strategies for responding to a continuum of strong to weak contest and exploitation competition. The strength of the contest component of competition within groups largely determines social relationships between females (van Schaik 1989; Isbell 1991; Sterck et al. 1997). In this scenario, strong female dominance hierarchies are found in primate species that experience high levels of contest competition. The potential for strong contest competition is greatest when food resources can be usurped. This is commonly the case with clumped resources of intermediate size such as fruit or flower patches (Janson 1988b; Chapman 1988). Egalitarian social systems are found in those species with weak contest competition (Sterck et al. 1997).

There are two potential ideas as to why egalitarian social systems are the norm among folivorous primates. First, there is little potential for contest competition when food resources are found at high density in small dispersed patches of similar quality, or when patches are large enough to accommodate all group members (i.e., leaves and non-social insects). Second, folivorous primates, due to their ecological strategy of consuming low-quality resources and reducing energy expenditure through decreased travel, may be energetically constrained from fighting over food resources (Milton 1980). One exception to the pattern of low contest competition for folivores is a population of *hanuman langurs* (*Presbytis entellus*) in southern Nepal (Koenig et al. 1998). In this population, females demonstrate a dominance hierarchy suggesting high contest competition.

This population of langurs relies on only three key resources that are found at low density with a clumped distribution (Koenig et al. 1998). The unique distribution of food resources for this folivorous population is proposed to explain the unusually high level of contest competition (Koenig et al. 1998). The case of the hanuman langurs suggests that food distribution, not energetic constraints, best explain why egalitarian social systems are the norm for folivorous primates.

Previous studies of non-folivores have demonstrated that the density and size of food resources together with group size are effective predictors of day range, an index of exploitation competition (Chapman 1988; Chapman et al. 1995). The current study demonstrates that this same relationship can also exist for at least some folivores.

Conclusions

1. The results of this study suggest that for the red colobus monkey, there is a strong relationship among group size, day range, and food availability, but not necessarily between any two variables alone.
2. The implications of this study are that red colobus populations can be food limited and are capable of depleting food patches.
3. This study provides added support for the generality of the ecological-constraints model in explaining primate grouping and ranging behavior. It contributes toward a better understanding of the mechanisms controlling feeding competition and social organization in primates.

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