



Constraints on Group Size in Red Colobus and Red-tailed Guenons: Examining the Generality of the Ecological Constraints Model

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*The ecological constraints model proposes that an increase in group size will increase intragroup feeding competition and thereby constrain group size. Although this model has received wide acceptance, tests of it are based only on a few studies of species that have similar ecological requirements and social organizations, and there are reasons to question the widespread acceptance of the assumptions underpinning it. Via a 2-year study, we explored determinants of group size in species that feed on markedly different types of foods: the folivorous red colobus (*Procolobus pennantii*) and the frugivorous/insectivorous red-tailed guenon (*Cercopithecus ascanius*). We established 4 study sites approximately 15 km apart in Kibale National Park, Uganda, to examine the relationship between average group size and food availability. In both species, we quantified interdemic variation in diet, density of food trees, rate of travel, and group size. Red colobus at all sites relied heavily on leaf resources (75.5%–86.9%), but fruit (6.4%–13.9%) and flowers (2.0%–13.9%) were important in some populations. In general, red-tailed guenons fed on fruit (35.7%–59.7%), insects (14.5%–17.6%), and young leaves (12.2%–32.8%), but the amount of time allocated to these foods varied among sites. Average monthly density of trees bearing food items ranged among sites from 45 to 79 trees/ha for red colobus and from 19.6 to 67.3 trees/ha for red-tailed guenons. For both species, rate of travel was similar among sites, with one exception for red colobus. Average red colobus group size varied*

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among sites from 14 to 40 (28 groups counted). Red-tailed guenon group size varied among sites from 11 to 24 (16 groups counted). As predicted by the ecological constraints model, group size increased with food tree density across sites for both species.

KEY WORDS: colobus; cercopitheceine; group size; social organization; food abundance; day range; diet; group movement; ecological constraints model.

INTRODUCTION

Identifying ecological factors underlying primate group size and social organization has been a central theme in primate behavioral ecology (Altmann, 1974; Chapman, 1990a,b; Chapman *et al.*, 1995; Struhsaker, 1975; Terborgh, 1983). Determinants of group size have been extensively discussed in terms of their costs and benefits (Altmann, 1974; Bradbury and Vehrencamp, 1976; Chapman, 1989; McDonald, 1979; 1983; Milton, 1984; Waser, 1981), and various authors have suggested that grouping confers such predictable benefits that differences in group size can be explained by the disadvantages (Clutton-Brock and Harvey, 1977; Terborgh and Janson, 1986; Wrangham *et al.*, 1993). The most widely acknowledged cost of group living is intragroup feeding competition, which has clear fitness effects, including increased mortality (Dittus, 1979) and lower female reproductive rates (Whitten, 1983). Intragroup competition can reduce foraging efficiency in two ways: via direct contest over food resources (interference competition; Janson, 1985, 1988; Nicholson, 1954; van Schaik, 1989) or exploitation independent of direct interaction (exploitation competition; Chapman *et al.*, 1995; Janson, 1988; van Schaik and van Noordwijk, 1988; Terborgh, 1983). Unfortunately, competition has proved extremely difficult to detect and quantify because of the difficulty of establishing whether food is limiting for wild primate populations.

Recent reviews of constraints on group size suggest that indices of exploitation competition can predict a large proportion of the variance in animal group size whenever a group has to travel further per day than a solitary forager does to satisfy its food requirements (Chapman *et al.*, 1995; Janson and Goldsmith, 1995; Wrangham *et al.*, 1993). This has led to the development of a general model: the ecological constraints model of group size (Chapman and Chapman, 2000). The foundations of this model have been well-established through studies on a variety of vertebrates (Bradbury and Vehrencamp, 1976; Elgar, 1986; Pulliam and Caraco, 1984). An increase in group size normally increases the distance that must be traveled to find adequate food supplies (Chapman, 1990a,b; Milton, 1984). Thus, individuals

must travel farther and expend more energy if they are in a large group than if they were to forage in a smaller group or alone. With an increase in the time spent traveling, a point is approached in which energy spent in travel exceeds that obtained from the environment, and a smaller group size becomes advantageous. In this way, ecological factors can influence movement patterns and foraging efficiency and thereby constrain group size.

This model rests on one critical assumption: When resource availability is constant, the addition of new members leads to increased intragroup feeding competition, necessitating increased travel. The need for increased travel can result from larger groups depleting patches quickly, necessitating that the group visit many patches. Alternatively, for species that do not deplete the patches in which they feed or that feed on dispersed foods but are unable to increase group spread, individual search fields may increasingly overlap as group size increases. This reduces per-capita encounter rate with food, thereby increasing the area that must be searched to find food. Van Schaik *et al.* (1983) suggested that foraging animals tend to move away when approached by others, presumably to avoid foraging conspecifics that reduce the availability of dispersed food items or to avoid contest competition. They dubbed this behavioral mechanism *pushing forward*. Unfortunately, there are few field data to support these two mechanisms leading to higher travel costs with increasing group size.

It is often assumed that increased intragroup competition associated with increased group size must lead to longer day range for group size to be constrained by ecological conditions (Chapman, 1990a,b; Isbell, 1991; Olupot *et al.*, 1994; Terborgh, 1983; Terborgh and Janson, 1986). However, this need not necessarily be the case. If groups are always attempting to be in the largest group possible, e.g., to decrease predation risk or to increase effectiveness in intergroup competition, then they will always be traveling to the maximum level possible within the constraints of available resources. Thus, one might expect an increase in group size with an increase in food availability, but travel may remain constant because food per individual remains the same regardless of group size. Previous studies showed that food availability, daily travel distance, and group size are interrelated. For example, Struhsaker (1967) documented that two groups of vervets (*Chlorocebus aethiops*) that were roughly the same size had very different day ranges. He attributed this difference to the fact one group lived in a less productive habitat, which forced them to cover a larger area on an average day.

Although the ecological constraints model has received widespread acceptance, tests of the model with primates are based on relatively few studies that were limited to species that have similar ecological requirements and social organization (*Ateles*: Chapman, 1988a, 1990a,b; Chapman *et al.*,

1995; Symington, 1987, 1988a,b; 1990; *Brachyteles arachnoides*: Milton, 1984; Strier, 1989; *Alouatta palliata*: Chapman, 1990a; *Pan*: Chapman *et al.*, 1994, 1995; White and Wrangham, 1988). For species with stable grouping patterns, testing the model is difficult because one must relate changes in group size to a set of ecological conditions and both ecological conditions, e.g., phenological states, and group size—births, deaths, immigration, and emigration—typically change slowly. As a result, researchers have often examined fission–fusion societies (Chapman, 1990a,b; Chapman *et al.*, 1995; Milton, 1984). In these societies, animals from a single community forage in subgroups that frequently change size and composition. Because subgroup size is flexible, animals can respond to ecological changes that occur over short temporal and spatial scales, and one can relate ecological change to change in subgroup size.

Despite supporting evidence for the ecological constraints model from studies of fission–fusion societies, there is reason to question its widespread acceptance throughout the primate order. Isbell (1991) pointed out that there is no relationship between group size and daily travel distance for some folivorous and frugivorous/insectivorous primate species. For example, a red colobus (*Procolobus pennantii*) group of 9 individuals had a day range length of 578 m, whereas a group of 68 red colobus had a day range length of 593 m (Isbell, 1983, 1991; Struhsaker and Leland, 1987). Similarly, Struhsaker and Leland (1988) documented that after a red-tailed guenon (*Cercopithecus ascanius*) group divided, the daily distance traveled by the smaller of the two groups (15 members; $1595 + 312$, $n = 10$ days) was similar to the daily distance traveled by the large group (30–35 members; $1546 + 287$, $n = 9$ days). Similarly, Butynski (1990) found no relationship between group size and day range for 5 groups of blue monkeys (*Cercopithecus mitis*). Such examples appear to violate an assumption of the model because an increase in group size does not correspond to an increase in travel distance, assuming resource availability is similar between groups.

If species rely on dispersed foods, the addition of extragroup members would not increase the rate of patch depletion. For such species, additional group members may result in increased overlap of search fields resulting in increased travel (van Schaik *et al.*, 1983), but such a process has not been broadly examined. For species such as red-tailed guenons and patas monkeys (*Erythrocebus patas*), which spend a great deal of time searching for and feeding on small dispersed foods, travel distance would not have to increase with larger group sizes and search field overlap would not increase as long as the group could spread out (Chism and Rowell, 1988; Isbell, 1991; Isbell *et al.*, 1998).

Such observations raise the intriguing question of what controls group size in folivorous species or in ones that feed on dispersed food items, e.g.,

frugivore/insectivores for which no relationship between group size and day range has been documented. For red-tailed guenons, Isbell (1991) suggested that the harassment of females by males may constrain group size. This hypothesis is based on observations by Struhsaker and Leland (1988) on a group of red-tailed guenons that split. They found that the smaller group increased their reproductive rate relative to the larger group, despite the fact that the food resource base did not appear to differ between them. They attributed the difference in the reproductive rates to higher levels of aggression and greater male harassment of females in the larger group. The idea is that male harassment can constrain group size because as group size increases, the number of females in the group increases, more males are attracted to the group, male tenure in the group will decrease, and this increases the level of male harassment. What remains unclear from Struhsaker and Leland's (1988) description is why males are more frequently taking over large groups, when they would have higher reproductive success if they took over small groups which they could have longer tenure. Possibly, small groups are more difficult to overtake. Also, it is unclear whether the increased level of aggression associated with large groups is a result of increased male harassment versus aggression associated with increased feeding competition, as the ecological constraints model would predict, or simply an effect of having more animals in close proximity (T. T. Struhsaker, pers. comm.).

In a 2-year study, we explored determinants of group size with primate species that feed on markedly different foods. We focus on red colobus and red-tailed guenons, species for which there are reasons to question the applicability of the ecological constraints model. Red colobus are supposed to use nondepleting patches, and it has been documented that an increase in red colobus group size does not correspond to an increase in day-range length (Isbell, 1983, 1991; Struhsaker and Leland, 1987). Red-tailed guenons rely on dispersed food resources, and an increase in their group size did not correspond to an increase in day-range length (Isbell 1991; Struhsaker and Leland 1988). We established 4 study sites approximately 15 km apart along a north-south axis in Kibale National Park, Uganda, to examine the relationship between average group size and food density.

METHODS

Study Sites

Kibale National Park (766 km²) is located in western Uganda (0°13' 0°41'N, 30°19' 30°32'E) near the foothills of the Ruwenzori Mountains

(Chapman *et al.*, 1997; Skorupa, 1988; Struhsaker, 1975, 1997). Mean annual rainfall in the region (measured at Makerere University Biological Field Station, Kanyawara) is 1778 mm (1990–1998); the mean daily minimum temperature is 15.5°C; and the mean daily maximum temperature is 23.7°C (1990–1998, Chapman and Chapman, unpublished data). We conducted the study at four sites distributed throughout the park (Sebatoli, Kanyawara K-30, Dura River, and Mainaro; Fig. 1). Within Kibale, there is an elevational gradient from north to south that corresponds to a north-to-south increase in temperature and decrease in rainfall (Howard, 1991; Struhsaker,

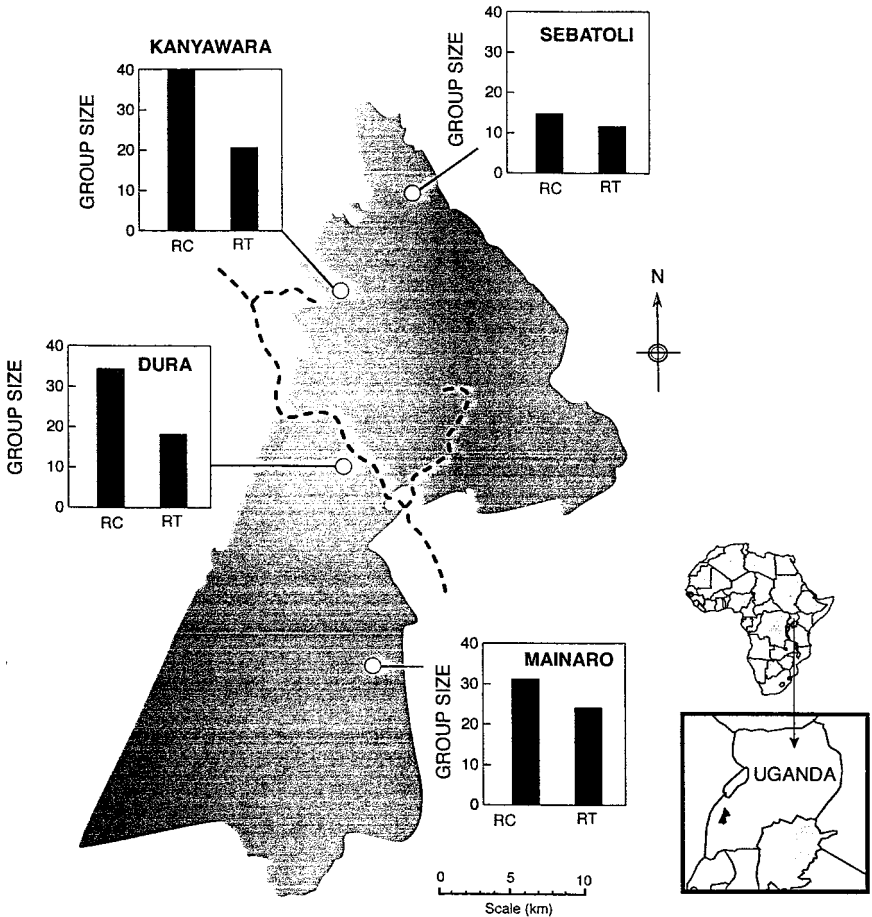


Fig. 1. Map of Kibale National Park, Uganda, showing the location of the 4 study sites and the average group size of red colobus and red-tailed guenons at each site.

1997). The most northern site, Sebatoli (elevation 1500 m, 1997 rainfall 1491 mm) is considered *Parinari* forest by foresters because the spreading crown of *Parinari excelsa* can be distinguished on aerial photographs. The canopy is dominated by trees such as *Parinari excelsa*, *Carapa grandiflora*, *Olea welwitschii*, *Aningeria altissima*, *Strombosia scheffleri*, and *Newtonia buchanani* (Osmaston, 1959). Kibale forest received National Park status in 1993. Before 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (Chapman and Chapman, 1997; Osmaston, 1959; Struhsaker, 1997). As a result, the forest near Sebatoli was commercially logged in the late 1960s. We were unable to obtain information on the level of extraction. However, detailed quantification of stand structure suggests that the level of extraction was similar to or slightly lower than an area just to the south, K-15 forestry compartment (Chapman and Chapman, unpublished data), in which the harvest averaged 21 m³/ha or approximately 7.4 stems/ha (Skorupa, 1988; Struhsaker, 1997). Incidental damage in the K-15 forestry compartment was much higher: approximately 50% of all trees probably were destroyed by logging and incidental damage (Chapman and Chapman, 1997; Skorupa, 1988).

Kanyawara (K-30 Forestry Compartment, elevation = 1500 m, 1997 rainfall = 1976 mm) is a 282-ha area that has not been commercially harvested. However, before 1970, a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997).

At the Dura River (elevation = 1250 m, 1997 rainfall = 1500 mm), the forest is no longer considered a *Parinari* forest, as *P. excelsa* and the tree species associated with it are relatively rare and *Pterygota mildbraedii*, *Cola gigantea*, *Pipadeniastrum africanum*, and *Chrysophyllum albidum* are the dominant canopy species (Kingston, 1967).

Further south at Mainaro (elevation = 1200 m, 1997 rainfall = 1394), the forest is dominated by *Cynometra alexandri* and affiliated species (Kingston, 1967). At both the Dura River and Mainaro sites, a few timber trees have been extracted by pitsawyers (approximately 0.1 trees/ha), but this activity has had little impact on the forest. Detailed enumeration of the tree communities in these areas is provided by Chapman *et al.* (1997).

Behavioral Observations

We observed behavior of red colobus from July 1996 to June 1997 at all four sites, producing 832 hours of observation. Rebel activity prevented

us from sampling at Mainaro in January, February, and April, 1997. We observed red-tailed guenons from July 1997 to June 1998 at all four sites, producing 587 hours of observations. We used an observational method that approximates methods employed in previous studies in Kibale (Butynski, 1990; Struhsaker, 1975; Waser 1974). In each half hour that the observer was with the group, he or she took 5-point samples of different individuals that were in clear view. For each observation, we noted the first activity the individual sustained for ≥ 5 continuous seconds. If the subject was feeding, we recorded the species and the plant part, e.g., fruit, young leaf, and leaf petiole. We estimated distance traveled every half hour as the straight-line distance between the apparent center of mass of the group in the previous 30-min sample to the current center of mass (Waser 1974; Olupot *et al.* 1994). Distance estimations were assisted by the fact that we plotted travel routes on detailed trail maps.

When possible, we conducted observations at each location during 2 consecutive days each month. On the first day, we attempted to locate the study group early in the morning and to follow it until late afternoon. This assisted in locating the same group early the next morning. Observations generally began at $\sim 8:30$ h and ended at $\sim 16:00$ h; however, the time that observations started varied because of difficulties in traveling to sites or because the study group could not be readily located. To address this potential bias, we adjusted behavioral samples from different sites so that the same proportion of observations were from each hour of the day by randomly removing observations from the datasets of sites with the greater number of observation hours during a particular hour of the day. This approach produced a sample that can be compared among sites and time periods; however, caution must be used when comparing the results of this study to research conducted using different methods.

Group Counts

Obtaining reliable counts of forest-dwelling primate groups is extremely difficult because inactive subjects are often hard to locate and when groups travel they often take different pathways. Accordingly, we endeavored to count groups in each area. Each month between July 1996 and May 1998 (22 months), two observers spent 2 days at each site simply following groups and attempting to get counts. We rarely attempted counts when a group was stationary; the best counts were obtained when a group crossed a gap, such as the river (Dura, Sebatoli, and Mainaro) or a road (Kanyawara and Dura). We repeated counts of the same group to ensure accuracy. We identified groups either by seeing recognizable individuals

or by matching the group count to previous ones from the same area. In addition, we counted opportunistically while collecting behavioral or phenological data and the subjects crossed a road or river. Skorupa (1988) found that red colobus groups in a logged area in Kibale divided into independent subgroups that could be separated by several hundred meters on 33% of the days ($N = 74$ days over 15 months). We observed similar patterns with a red colobus group in an unlogged area (K-30). As a result, we were concerned that counts of particular populations could be biased by considering subgroups to be groups. However, we did not observe group fissioning in any population other than the K-30 one, and we were able to determine that fissioning had occurred by noting recognizable individuals in the separate subgroups. Furthermore, the average maximum difference of counts of groups with recognizable individuals is small (mean difference among populations = 2.48, range = 1.0 to 4.3, excluding the group known to fission).

Ecological Assessment/Phenology

The ecological constraints model predicts that group size will be a function of food availability. We examined the applicability of this model by determining if average monthly food-tree density corresponded to average group size of red colobus and red-tailed guenons at each of the four sites. To obtain an index of habitat-wide food availability, we constructed vegetation transects (200 m \times 10 m) at each site: 6 transects at Kanyawara and 4 at Dura River, Mainaro, and Sebatoli. In Kanyawara, we selected transect locations at random from within existing trail systems (Chapman and Chapman, 1997, 2000). At the Mainaro, Dura River, and Sebatoli sites there were no preexisting trails, so we established transects perpendicular to each other at 50- to 100-m intervals. This regime produced a sampling area of 3.6 ha (1.2 ha at Kanyawara and 0.8 ha at Dura River, Mainaro, and Sebatoli). We marked each tree >10 cm diameter at breast height (DBH) within 5 m of each side of the trail with a numbered aluminum tag and measured its DBH. This produced a sample of 1543 trees: 590 at Kanyawara, 338 at Dura River, 293 at Mainaro, and 322, at Sebatoli).

We recorded phenological information monthly between January 1990 and July 1998 at Kanyawara ($n = 103$ months), July 1995 and July 1998 at Mainaro and Dura River ($n = 36$ months), and July 1996 and July 1998 at Sebatoli ($n = 24$ months). We documented the stage of leaf development—(leaf bud, young leaves, mature leaves; visually assessed through binoculars)—and noted the presence or absence of flowers and ripe and unripe fruit for all trees. We used phenology data to correct for the proportion

of individual trees of a given species that were actually producing the relevant plant part, e.g., young leaves, ripe fruit, in a given month.

When relating mean group size for a site to food density, we used the behavioral observations to determine which species to consider food trees. We calculated the density of food trees for a particular month as the density of trees containing food items eaten for >10% of a species' foraging time. We only considered foods that were eaten for >10% of their foraging time because both red colobus and red-tailed guenons often eat for short periods in trees of several species (Struhsaker, 1975, 1980). When food resources were relatively scarce and the trees fed upon for only short periods happen to be common, the estimate of food availability would be erroneously high. Foods that were eaten for >10% of foraging time represent an average of 82.1% of the red colobus total foraging effort (Sebatoli 90.6, Dura River 83.6, K-30 83.0%, Mainaro 71.3%) and an average of 76.8% of red-tailed guenon noninsect foraging time (Sebatoli 65.5%, K-30 74.1%, Dura River 80.4%, Mainaro 87.3%). This method assumes that trees of the same species produce similar crops of food items at the different sites. We indexed overall food availability at a site as the average of the monthly estimates of the density of trees bearing food items.

RESULTS

Interdemic Variation in Diet, Density of Food Trees, Rate of Travel, and Group Size

For both red-tailed guenons and red colobus, we quantified interdemic variation among the four sites in diet, density of food trees, rate of travel, and group size. As expected, red colobus at all sites relied heavily on leaf resources (range among populations in percentage of foraging effort spent eating leaves = 75.5–86.9%); however, the leaf part selected varied among locations (Table I). For example, the Kanyawara population relied heavily on leaf petioles (14.2% of their foraging time), whereas the Mainaro population did not (1.8%). Similarly, the extent to which red colobus populations relied on fruit (range 6.4–13.9%) or flowers (2.0–13.9%) varied among populations. Interdemic variation in red-tailed guenon diet is also evident. In general, they fed on fruit, leaves, and insects, but the amount of time spent eating each of these different food items varied among sites (Table I). For example, the amount of time devoted to eating young leaves varied between 32.8% at Sebatoli and 12.2% at the *Cynometra*-dominated forest of Mainaro.

There is considerable intersite variance in the foraging effort devoted

Table I. Description of the diet in terms of plant parts and insects for four populations of red colobus and red-tailed guenons at four sites in Kibale National Park, Uganda

Species	Food item	Sebatoli	K-30	Dura River	Mainaro
Red-tailed guenons	Young leaves	32.8	26.7	15.0	12.2
	Mature leaves	0	0.4	0.4	0.7
	Leaf petiole/buds	1.9	1.1	0	0
	Fruit	44.6	35.7	55.6	59.7
	Flowers	2.7	3.7	8.19	11.6
	Insects	17.6	31.2	20.6	14.5
	Other	.5	1.24	0.4	1.36
Red colobus	Young leaves	72.4	57.6	65.1	57.5
	Mature leaves	7.4	9.9	4.6	16.2
	Leaf petiole/buds	7.1	14.2	8.7	1.8
	Fruit	6.4	6.7	13.9	10.8
	Flowers	3.3	2.0	6.2	7.2
	Insects	0.0	0	0	0
	Other	3.4	9.6	1.5	6.5

to specific species (Table II). In many cases, it can be attributed to differences in the relative abundance of tree species among different sites; however, in some cases this is not the case. For example, red-tailed guenons at Kanyawara fed extensively on the fruits of *Mimusops bagshawei* (1.2% of their foraging time), but they did not eat them at Sebatoli, despite the fact that the tree is almost twice as abundant at Sebatoli than at Kanyawara. As might be expected, the use of particular plants varied over time. Much of the variation is likely due to changes in the availability of food items, which corresponds to the phenology of the plant species being eaten or to the availability of other preferred items (Chapman *et al.*, 1999).

For red-tailed guenons the average monthly density of trees bearing food items ranged among sites from 19.6 to 67.3 trees/ha (average = 48.1 trees/ha). The logged site (Sebatoli) had a significantly lower density of food trees than all the other sites ($F = 7.81$, $P < 0.001$, Scheffe $P < 0.01$ for Dura River and Kanyawara, and $P < 0.10$ for Mainaro). For red colobus, the range in average monthly density of food trees is not as extreme as that of red-tailed guenons (45–79 trees/ha, average 66.6 tree/ha); however, Sebatoli again had a lower density of food trees than that of Kanyawara ($F = 3.62$, $P = 0.019$, Scheffe $P < 0.05$).

The average rate of travel for red-tailed guenons is was 32 m per hour, and there was little intersite variation, with the exception that they traveled marginally less at Dura River than at Kanyawara ($F = 2.83$, $P = 0.051$, Scheffe $P = 0.079$). The average rate of travel for red colobus was 41 m per hour, at Mainaro they traveled more than at either Dura River or

Table II. Percentage of time that red colobus and red-tailed guenons spent eating from different species of trees and their density at four sites in Kibale National Park, Uganda^a

Species	Kanyawara K-30			Sebatoli			Mainaro			Dura River		
	Time	Density	Selectivity	Time	Density	Selectivity	Time	Density	Selectivity	Time	Density	Selectivity
Red Colobus												
<i>Celtis durandii</i>	14.1	47.1	299	5.4	2.5	214.3	6.0	33.8	17.7	27.2	63.8	42.6
<i>Cynometra</i>	0.0	0.0		0.0	0.0		40.7	63.8	63.8	0.0	0.0	
<i>Funtumia latifolia</i>	7.2	33.8	21.2	5.4	25.0	21.4	3.0	2.5	119.8	12.8	43.8	29.3
<i>Aningeria altissima</i>	0.8	1.7	48.1	8.7	23.8	36.4	0.0	0.0		14.9	2.5	594.9
<i>Strombosia scheffleri</i>	9.2	12.5	73.4	11.0	36.3	30.2	0.0	0.0		2.6	2.5	102.6
<i>Albizia grandbracteata</i>	8.4	1.3	642.9	1.0	0.0		1.8	0.0		10.8	1.3	828.4
<i>Pygeum africanum</i>	13.0	0.0		5.9	2.5	234.7	2.4	0.0		0.0	0.0	
<i>Celtis africana</i>	9.9	4.2	236.0	4.3	0.0		0.0	0.0		1.5	0.0	
<i>Chrysophyllum</i>	1.6	2.6	62.9	4.6	8.8	52.2	2.4	0.0		6.2	47.2	13.0
<i>Markhamia platycalyx</i>	9.2	50.0	18.4	3.1	38.8	7.9	0.0	1.3		1.0	8.8	11.7
<i>Bosqueia phoberos</i>	0.8	0.0	1.6	3.1	0.0		5.4	21.2	25.4	3.1	22.5	13.7
<i>Newtonia buchananii</i>	0.0	0.0		11.2	26.3	42.7	0.0	1.3	0.0	0.0	0.0	
<i>Mimusops bagshawei</i>	0.4	3.3	12.0	0.8	6.3	12.1	5.4	0.0		4.6	0.0	
<i>Parinari excelsa</i>	3.9	2.9	133.6	5.1	0.0		0.0	0.0		0.0	0.0	
<i>Celtis zenkeri</i>	0.0	0.0		1.8	1.3	137.4	5.4	1.3	414.6	0.0	0.0	
<i>Macaranga</i>	1.3	0.0		4.8	0.0		0.6	0.0		0.0	0.0	
<i>Croton</i> sp.	0.0	0.8	0.0	4.8	41.3	11.7	0.6	1.3	46.1	0.0	0.0	81.4
<i>Cola gigantea</i>	0.0	0.0		0.0	0.0		0.0	0.0		5.1	6.3	0.0
<i>Milletia dura</i>	2.0	8.0	25.4	2.6	3.8	67.1	0.0	0.0		0.0	1.3	0.0
<i>Ficus sansibarica</i>	0.9	1.7	55.8	3.3	0.0		0.0	0.0		0.0	0.0	0.0
<i>Ficus mucoso</i>	0.0	0.0		0.0	0.0		4.2	11.3	37.2	0.0	1.3	0.0
<i>Diospyros abyssinica</i>	0.1	40.0	0.2	0.5	2.5	20.4	3.0	1.3	230.3	0.0	1.3	0.0
<i>Donbeya mukole</i>	3.5	9.2	38.4	0.0	0.0		0.0	0.0		0.0	0.0	0.0
<i>Ficus exasperata</i>	0.3	3.8	6.9	2.6	2.5	102.0	2.4	0.0	0.0	0.0	3.8	0.0
<i>Pseudospondias microcarpa</i>	0.0	1.7	0.0	0.0	0.0		1.2	0.0		0.5	3.8	13.5
<i>Chaetacme aristata</i>	0.6	17.1	3.4	0.0	0.0		0.0	0.0		2.1	0.0	
<i>Trema guineensis</i>	0.0	0.0		0.0	0.0		0.0	0.0		2.1	0.0	3.6
<i>Bequertiodendron</i>	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
<i>Sapium</i>	0.1	0.0		1.3	2.5	51.0	0.6	0.0		0.0	0.0	
<i>Ficus natalensis</i>	0.5	0.4	131.8	1.3	0.0		0.0	0.0		0.0	0.0	
<i>Strychnos mitis</i>	0.0	7.5	0.0	0.0	0.0		1.8	0.0		0.0	0.0	
<i>Celtis mildbraedii</i>	0.0	0.0		1.8	0.0		0.0	0.0	0.0	0.0	0.0	
<i>Bridelia</i>	1.6	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
<i>Premna angolensis</i>	0.0	4.6	0.6	0.0	0.0		1.2	1.3	92.1	0.0	2.5	0.0
<i>Fagaropsis angolensis</i>	0.0	2.5	0.0	0.0	6.3	0.0	1.2	0.0		0.0	0.0	

Red-tailed Guenons

<i>Celtis durandii</i>	14.8	47.1	31.5	4.8	2.5	192.8	29.4	33.8	86.9	29.8	63.8	46.7
<i>Chrysophyllum</i>	0.5	2.6	18.1	12.5	8.8	142.4	15.8	21.2	74.7	5.1	47.5	10.6
<i>Celtis africana</i>	7.7	4.2	182.3	4.3	0.0		1.7	1.3	126.9	0.0	0.0	0.0
<i>Bosqueia phoberos</i>	3.9	50.0		1.9	0.0		0.0	0.0		5.9	22.5	26.3
<i>Teclaea nobilis</i>	7.1	17.1	41.3	1.9	0.0		1.3	0.0		2.3	0.0	
<i>Diospyros abyssinica</i>	7.4	40.0	18.6	1.9	2.5	77.1	1.0	1.3	76.2	0.0	0.0	
<i>Pygeum africanum</i>	2.5	0.0		7.2	2.5	289.2		0.0		0.5	0.0	
<i>Warburgia stuhlmannii</i>	0.0	0.0		0.0	0.0		7.9	0.0		0.0	0.0	
<i>Croton</i>	0.0	0.8	0.0	8.2	41.3	19.8	0.0	1.3	0.0	0.0	0.0	4.6
<i>Uvariopsis congensis</i>	1.1	60.4	1.8	6.0	0.0		4.0	43.8	9.0	2.8	60.0	
<i>Maesa lanofolata</i>	1.6	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
<i>Albizzia grandbractea</i>	0.9	1.3	72.5	4.6	0.0		0.0	0.0		1.0	1.3	80.4
<i>Bequeritodendron</i>	1.2	3.3	35.7	0.0	6.3	0.0	0.0	0.0		6.3	57.5	10.9
<i>Mimusops baqshawei</i>	1.6	3.8	43.4	2.2	2.5	86.7	0.3	0.0		4.5	0.0	
<i>Ficus exasperata</i>	0.0	0.0		0.0	0.0		4.3	63.8	152.3	0.0	0.0	
<i>Cynometra</i>	0.0	0.0		0.0	0.0		4.3	32.5	6.7	0.0	0.0	
<i>Celtis mildbraedii</i>	0.0	0.0		0.0	0.0		4.3	0.0	13.2	0.0	0.0	
<i>Ficus natalensis</i>	0.0	0.4	0.0	0.0	0.0			0.0		3.8	0.0	
<i>Linociera johnsonii</i>	0.0	5.4	0.0	1.0	8.8	11.0	2.6	0.0		0.0	0.0	
<i>Markhamia platycalyx</i>	0.6	50.0	1.2	1.4	38.8	3.7	0.0	1.3	0.0	1.0	8.8	11.9
<i>Strychnos mitis</i>	0.8	7.5	11.0	0.5	0.0		1.3	0.0		0.0	0.0	
<i>Olea welwitschii</i>	2.0	3.3	60.7	0.0	0.0		0.0	0.0		0.3	1.3	26.8
<i>Bridellia</i>	0.8	0.0		1.4	0.0		0.0	0.0		0.0	0.0	
<i>Funtumia latifolia</i>	0.1	33.8	0.3	0.7	2.5	28.9	0.0	2.5	0.0	1.4	43.8	3.2
<i>Ficus sansibarica</i>	1.1	0.0		0.7	0.0		0.0	0.0		0.0	0.0	
<i>Monoclora myristica</i>	0.0	0.4	0.0	0.0	0.0		0.0	0.0		1.7	3.8	45.8
<i>Fagara angolensis</i>	0.0	0.0		1.7	0.0		0.0	0.0		0.0	0.0	
<i>Pseudospondias microcarpa</i>	0.1	1.7	6.9	0.5	0.0		0.0	0.0		1.0	3.8	27.5
<i>Lovoa swynnertonii</i>	0.0	0.8	0.0	0.0	3.8	0.0	0.0	0.0		1.6	3.8	41.3
<i>Balanites wilsoniana</i>	0.0	1.7	0.0	1.2	0.0		0.3	0.0		0.0	1.3	0.0
<i>Newtonia buchananii</i>	0.0	0.0		1.4	26.3	5.5	0.0	0.0		0.0	3.8	0.0
<i>Chaetacme aristata</i>	0.4	17.1	2.1	0.0	0.0		0.0	0.0		1.0	3.8	27.5
<i>Casearia</i> sp.	0.0	1.3	0.0	0.0	0.0		0.0	0.0		1.4	0.0	
<i>Spathodea campanulata</i>	0.0	0.8	0.0	0.0	0.0		0.0	0.0		1.2	0.0	
<i>Dombeya mukole</i>	1.2	9.2	12.8	0.0	0.0		0.0	0.0		0.0	1.3	0.0

^aTree density is in individuals >10 cm DBH per ha. Time is the percentage of the total foraging time spent eating items from that tree species. Selectivity percentage of time feeding on a species divided by its density times 100.

Sebatoli ($F = 3.80$, $P = 0.021$, Scheffe $P < 0.05$). At Mainaro, when red colobus were not feeding on *Cynometra alexandri*, they had to travel long distances among feeding sites because food trees were widely dispersed within the monodominant stand of *Cynometra*.

Across the four sites, we counted 28 red colobus groups and 16 red-tailed groups. The number of groups that could be accurately counted at each site depended on the density of the monkeys and the ease of counting them. For red colobus, the average group size varied from 14 at Sebatoli to 40 at Kanyawara. For red-tailed guenons group size varied among sites from 11 at Sebatoli to 24 at Mainaro.

Relationship between Group Size and Density of Food Trees

For species with stable grouping patterns a major problem when testing the ecological constraints model is the difficulty of relating changes in group size to changes in ecological conditions because of the long time frame involved. We attempted to circumvent this problem by conducting a 2-year study at four locations and exploiting interdemographic variation. However, we are still limited in the strength of the test we can employ because we only have a sample size of four populations.

With this limitation in mind, for both red colobus and red-tailed guenons there seems to be a general tendency for group size to increase as the density of potential food resources increases in an area (Fig. 2). There is no evidence of a relationship in either species between group size and average travel distance (Fig. 3).

DISCUSSION

For both red-tailed guenons and red colobus we documented considerable variation in diet, density of food trees, rate of travel, and average group size over short distances (<15 km). This variation was of the magnitude found among populations separated by hundreds or thousands of kilometers. This high degree of variation permitted us to make a preliminary test of the ecological constraints model on species that differ markedly in diet. Comparisons over such small spatial scales offer a number of potential benefits. (1) Studies can be conducted by the same observer using the same methodology. This eliminates the possibility that differences found among populations are simply the result of differences in the methods used by different observers. (2) We can control for phylogeny since contrasts can be made within a species and among subpopulations for which there is

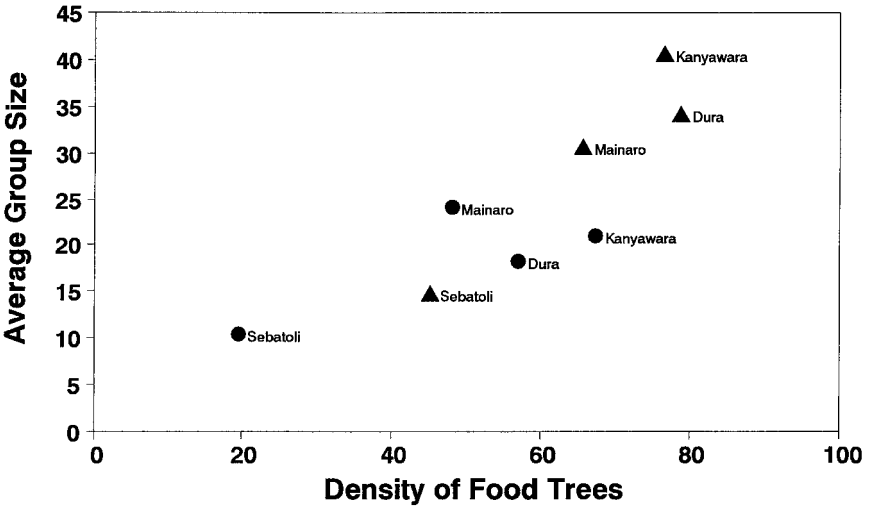


Fig. 2. The relationship between density of food trees and average red-tailed guenon (circles) and red colobus (triangles) group size for 4 populations in Kibale National Park, Uganda.

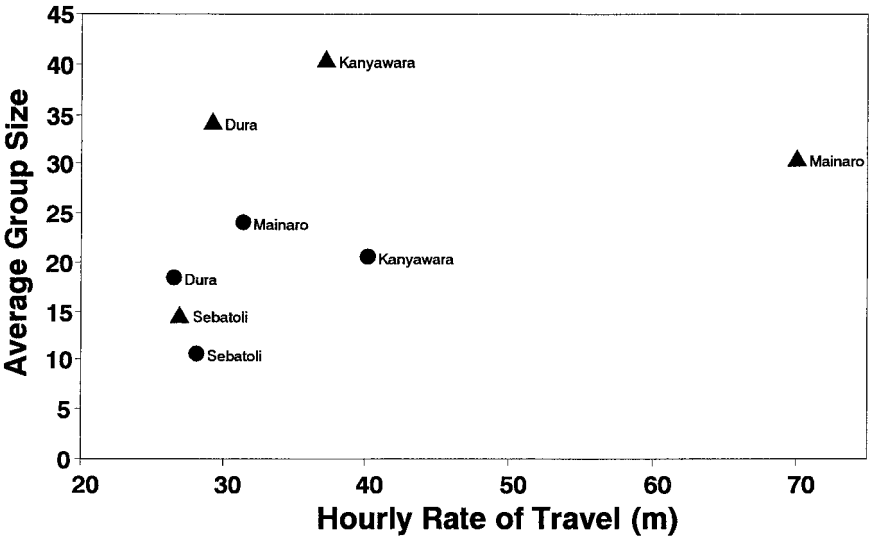


Fig. 3. The relationship between travel rate (m/hr) and average red-tailed guenon (circles) and red colobus (triangles) group size for 4 populations in Kibale National Park, Uganda.

potentially a high degree of genetic exchange. (3) Unmeasured ecological parameters, e.g., composition of the predator community, are less likely to differ among neighboring populations than would be the case if contrasts were made among widely separated populations.

Areas with a high density of potential food resources tended to have larger groups than areas where food resources were less abundant. However, there is no evidence that group size and travel distance covaried. This suggests that individuals of the two species are attempting to be in the largest group possible, e.g., to decrease predation risk or to increase effectiveness in intergroup competition. To do this they travel to the maximum level possible within the constraints of available resources. Accordingly, group size increases with an increase in food availability, but travel may remain constant because food per individual remains the same regardless of group size, i.e., groups are already travelling to the maximum level possible. Future studies may benefit from a multiple regression approach that tests the interactive effects of food density and travel costs. A question of interest is whether some species alter daily distance traveled, rather than group size, in response to changing food density.

Ours is only a preliminary examination of the applicability of the ecological constraints model for the two species; however, it suggests that the mechanisms by which this model operates are functioning on folivores, such as red colobus, and frugivores/insectivore, such as red-tailed guenons. If further investigations suggest that the model can predict folivore and frugivore/insectivore group sizes, then we must consider how the constraints are operating. The ecological constraints model assumes that the addition of new members will lead to increased intragroup feeding competition. The factor leading to increased intragroup feeding competition can vary between species, either animals deplete the patches in which they feed or for species that cannot increase group spread 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. For red colobus, it seems unlikely that individual search fields will increasingly overlap as group size increases. However, red colobus may deplete food patches. Theoretically, a patch, or food tree, may be considered depleted when the feeding activity of the consumer has led to the disappearance of all food items. However, as food items become rare within a tree, they become progressively harder to obtain. Thus, a patch will be functionally depleted when the rate of food intake drops to a level equal to the average intake in the environment (Charnov, 1976; Stephens and Krebs, 1986).

To date, the strongest evidence that red colobus do not deplete the food patches is that previous studies in Kibale (Isbell 1983; Struhsaker and Leland 1987) indicate no relationship between group size and day range.

It is possible that the large groups could have occupied home ranges where food resources were more plentiful than those of smaller groups. However, some of the groups studied previously had overlapping home ranges, suggesting that the availability of food resources would be similar (T. T. Struhsaker, pers. comm.). In addition, the distance traveled daily by one group for which there were long-term observations did not change when the size of the group changed (T. T. Struhsaker, pers. comm.), and food tree densities were similar for the groups studied by Isbell (1983) and by Struhsaker (1975) despite differences in group size and little difference in the daily distance they traveled (Isbell, pers. comm.). In contrast, a 3-month study in 1998 demonstrated that a group of 48 traveled significantly further each day than a group of 24 (Gillespie, unpublished data). These conflicting results illustrate the need for further investigation that quantifies group size, travel distance, and food availability and examines indirect measures and possible social constraints of group size (Isbell, 1991; Isbell *et al.*, 1998).

We have presented data to suggest that red colobus and red-tailed guenons will respond to an increase in the potential food resources available to a population by increasing group size. Future studies should also consider that changes in food availability could have other effects, such as increasing population density. For example, we have previously shown that red colobus population density in Kibale is related to resource availability, when one apparently anomalous site was excluded (Chapman and Chapman, 1999). When population density increases, neighboring groups may deplete food resources through exploitation competition. Future studies would benefit from taking a multiple regression approach to examine the influence of increasing potential food resource availability when controlling for linear effects of population density.

Although fundamental to several models of primate social organization (Cheney, 1992; Isbell, 1991; van Schaik; 1989), there are little data on patch depletion in folivores. Chapman (1988a) found that howlers (*Alouatta palliata*) generally deplete fruit patches, but found little evidence to indicate that they depleted the trees when they were feeding on their leaves. It appeared that howler group size may have been constrained during instances in which they were feeding on fruit. This howler population spent only 49% of their time eating leaves (Chapman, 1988b). We know of no study on patch depletion in a species that relies more heavily on leaves. The general lack of information on patch depletion in folivores calls for detailed studies of foraging ecology of folivores addressing questions such as: Do folivores deplete the patches in which they feed? How should a patch for a folivore be defined? How does the ingestion of secondary compounds affect the length of time an individual uses a patch and subsequent group movements?

Red-tailed guenons monkeys may deplete the patches they use, or alternatively, as their 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. Unfortunately, since van Schaik *et al.* (1983) originally proposed this pushing-forward behavioral mechanism, there has been little research done to understand if and how it operates (Barton *et al.*, 1996; Byrne *et al.*, 1993). This calls for further studies of the ecology of species that feed on dispersed food items, which address questions, such as: Does the pushing forward mechanism operate to influence group movement? Do certain classes of individuals tend to be influenced by this mechanism more than others, and, if so, what are the consequences? What prevents species from increasing group spread to avoid increasing search field overlap?

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