Re-evaluating the Ecological Constraints model with red colobus monkeys (*Procolobus rufomitratus tephrosceles*)

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Abstract

The Ecological Constraints model was proposed to explain limits to group size and the observation that larger groups of primates often travel farther per day than smaller groups. It argues that larger groups are forced to travel to more patches of food to compensate for more rapid patch depletion. While the evidence from highly frugivorous primates is consistent with this argument, evidence from folivorous primates is contradictory. Many folivorous species, including the extremely folivorous red colobus (*Procolobus rufomitratus tephrosceles*), have long been thought to show no group size-adjusted changes in daily travel distance (DTD). More recent research suggests, however, that larger groups of red colobus do travel farther per day than smaller groups, and it has been argued that earlier research obscured real effects of group size on DTD because of differential but unacknowledged habitat quality. This study challenges that explanation with a comparison of red colobus feeding and ranging behavior and activity budgets in two distinct compartments of Kibale Forest, Uganda, one of which was selectively logged 11 years earlier. Logging would have accentuated natural floristic differences that might have existed between compartments, thus increasing the likelihood that DTD would differ significantly between compartments. Findings reveal, however, that although there were compartmental differences in canopy cover, understory density, size of trees, and food tree species, the group did not respond to these differences by altering DTD (or their activity budgets). If the floristic differences between compartments are interpreted as insufficient to affect DTD, then it weakens the explanation that earlier studies were confounded by habitat differences. Alternatively, if the differences between compartments are interpreted as theoretically or ordinarily sufficient to affect DTD (e.g., in primates that routinely adjust DTD to group size), then the mechanism underlying the Ecological Constraints model must be questioned for red colobus. Feeding behavior coupled with group movements suggest that the group did not feed in discrete patches, an important element of the Ecological Constraints model. Instead, the group typically fed from multiple tree species per 0.25-ha quadrat and moved slowly, suggesting that their food trees were more uniformly distributed. Estimates from botanical transects and behavioral data also support the interpretation of a more uniform food distribution. Nearly all stems were food tree

species and food trees occurred at a density much higher than for folivorous primates that do show a group size effect on DTD. The group increased its DTD more when funneling across gaps in the forest. Funneling is a group movement that is expected to occur more frequently during travel when group size is large, travel routes are few and narrow, and target locations are sparse or patchy and small relative to group size. It is proposed here to be more fundamental than patch depletion as a mechanism to explain group size-adjusted DTD in other primates.

1. Introduction

Primates display wide dietary and social diversity that can help shed light on ecological and social influences on female reproductive success, group size, and population dynamics. For instance, in Old World monkey (cercopithecoid) species whose diet includes a high proportion of fruit, females tend to live throughout their lives in their natal groups (Pusey & Packer, 1987; Isbell & Van Vuren, 1996), whereas in Old World monkey species whose diets include a high proportion of leaves, females are apparently less constrained socially and can join other groups (Isbell & Van Vuren, 1996; Fashing, 2011). Similarly, a positive relationship between group size and daily travel distance (DTD) exists for most frugivorous primates (Clutton-Brock & Harvey, 1977; Isbell, 1991; Wrangham et al., 1993; Janson & Goldsmith, 1995) (guenons, *Cercopithecus* spp., are exceptions: Struhsaker & Leland, 1988; Butynski, 1990), whereas no such relationship has historically been found in folivory-adapted primates (Clutton-Brock & Harvey, 1977; Struhsaker & Leland, 1987; Isbell, 1991; Janson & Goldsmith, 1995; Fashing, 2001).

   A group size effect on DTD suggests that there can be energetic consequences of living in larger groups. The logic and mechanism behind a group size effect on DTD is detailed in the Ecological Constraints model, which posits that as groups increase in size, for any patch of a given size, there will be less food per individual. This leads to faster depletion of available food, forcing larger groups to travel farther to get sufficient food for the entire group if they cannot spread out (Waser, 1977; Chapman, 1990; Isbell, 1991; Chapman et al., 1995; Chapman & Chapman, 2000a,b; Wrangham, 2000; Snaith & Chapman, 2005). For this to occur, foods would necessarily occur in discrete patches, commonly defined for primates as an individual tree or group of trees of the same species separated from other trees of that species

by trees without food (Chapman, 1988; White & Wrangham, 1988; Chapman et al., 1995; Chapman & Chapman, 2000a; Strier, 2007). The Ecological Constraints model is supported by studies of primates that are ripe fruit specialists, such as spider monkeys (*Ateles geoffroyi*) and chimpanzees (*Pan troglodytes*) whose fruiting trees occur in obvious, discrete patches (Chapman et al., 1995).

For some species that do not increase DTD with increasing group size (e.g., patas monkeys (*Erythrocebus patas*), redtail monkeys (*Cercopithecus ascanius*), and blue monkeys (*C. mitis*): Chism & Rowell, 1988; Struhsaker & Leland, 1988; Butynski, 1990), foods are hypothesized to be distributed in such a way that they allow group members to spread out and forage in a broad swath formation, with less overlap in foraging paths of group members, thereby minimizing the energetic costs of traveling in larger groups (Isbell, 1991). Patas monkeys, for example, feed heavily on arthropods that are extraordinarily abundant and widely distributed in their environment (Isbell, 1998; Isbell et al., submitted). Primates that do not exhibit group size-adjusted DTD may encounter foods that are relatively less patchily distributed than are fruiting trees.

Red colobus monkeys (*Procolobus rufomitratus tephrosceles*, recent syn. *Colobus badius tephrosceles*, *Pr. badius tephrosceles*, *Pr. pennantii*, *Piliocolobus tephrosceles*, *Pi. rufomitratus*) live in large multi-male, multi-female groups of 50 to 80 or more and have a diet that consists almost entirely of young and mature leaf blades and petioles (Struhsaker, 1975, 2010). Long-term data from multiple red colobus groups studied during the 1970s and 1980s in Kibale National Park, Uganda, showed that DTD was not correlated with group size (Struhsaker & Leland, 1987; Struhsaker, 2010).

These findings have been challenged, however, by more recent studies of red colobus in the same forest in which it was found that larger groups of red colobus did travel farther per day than smaller groups (Gillespie & Chapman, 2001; Snaith & Chapman, 2008). Additionally, red colobus were recently found to feed more slowly and travel faster in individual trees as they spent more time in those trees, and they spent less time in smaller trees when there were more animals in those trees (Snaith & Chapman, 2005). The interpretation of these findings was that the food trees of even extremely folivorous primates occur as depletable patches, thus making the Ecological Constraints model widely generalizable (Snaith & Chapman, 2005).

Gillespie & Chapman (2001) and Snaith & Chapman (2008) argued that the discrepancy between earlier and more recent studies of group size-adjusted DTD in red colobus exists because earlier studies did not control for variation in habitats when comparing multiple groups observed at different times and in different parts of the forest. Temporal and spatial variation in food tree density and abundance exists in Kibale (Chapman et al., 1997, 2002, 2010), and contributing to this variation is a history of selective logging in some areas but not others (Skorupa, 1988). Differences in habitat quality can potentially equalize DTD in groups of different sizes by forcing smaller groups in poorer habitats to travel farther per day and allowing larger groups in better habitats to travel less far per day (Gillespie & Chapman, 2001; Snaith & Chapman, 2008).

There are two approaches to testing the effects of habitat differences on DTD. One is to compare multiple groups of different sizes while controlling for habitat differences statistically (e.g., Snaith & Chapman, 2008). In this case, it is also necessary to control for social factors that might affect DTD, e.g., intergroup encounters between groups (Struhsaker, 1975) and male–male competition within groups (Isbell, 1983), which has thus far not been done. The other is to compare the same group in different habitats, the approach used here. I studied a group that ranged in both logged and unlogged compartments of the forest in the 1980s specifically to determine whether their ranging and feeding behavior and activity budgets differed in logged and unlogged habitats as a result of logging that had occurred 11 years earlier. In addition to opening up the forest canopy in multiple spots, logging activities created a vehicle track that ran through the home range of the study group, separating the two compartments and creating a long, continuous gap in the canopy that affected the movements of individuals. The tracks did not prevent the group from moving between logged and unlogged compartments, but when the group approached the tracks to cross, they funneled to leap across at only a few spots.

Given the different logging histories of the two compartments, I expected that the differences between them would be greater than any difference arising from natural causes alone. Here I describe some of the differences, and on the basis of those differences, I make and test several predictions about the ranging and feeding behavior and activity budgets of this study group:

First, if natural habitat differences are sufficient to affect red colobus DTD and obscure group size effects, then natural habitat differences exacerbated by selective logging should also affect DTD, and the study group's DTD

Table 1.
Potential outcomes and causes, the level of support for habitat differences as an explanation for discrepant findings between earlier and later studies and for the Ecological Constraints model, and interpretation of each outcome.

DTD different between compartments: causes investigated in this study	Earlier studies did not control for habitat differences	Ecological Constraints model	Interpretation
Yes: Habitat differences exacerbated by logging sufficient to affect DTD	+	+	Red colobus conform to the Ecological Constraints model
No: Habitat differences exacerbated by logging insufficient to affect DTD	–	NA	Lack of group size effect on DTD in earlier studies is not because habitat differences were not considered, and alternatives for the discrepancy between studies need to be considered; the Ecological Constraints model cannot be evaluated
No: Activity budgets modified instead of DTD	NA	–	Cannot evaluate the discrepancy between studies in DTD relative to group size; challenges the primacy of group size-adjusted DTD as a measure of intragroup scramble competition but cannot explain why DTD is often longer in larger groups
No: Food trees not patchily distributed	–	–	Lack of group size effect on DTD in earlier studies is not because habitat differences were not considered, and alternatives for the discrepancy between studies need to be considered; challenges the applicability of the EC model to red colobus

+, support; –, does not support; NA, neither supports nor fails to support.

should have been different between compartments. A significant difference in DTD would be consistent with both the Ecological Constraints model and the proposed explanation for the discrepancy between studies of red colobus in Kibale (Table 1).

Alternatively, if no significant difference in DTD is found between compartments, at least three possible causes exist: (1) habitat differences were insufficient to affect DTD; (2) the group adjusted time spent feeding instead of DTD; or (3) red colobus foods did not occur in patches.

These three possible causes would offer different levels of support for the Ecological Constraints model and the explanation that habitat differences were responsible for the apparent lack of group size-adjusted DTD in red colobus. If the differences between logged and unlogged compartments are interpreted as insufficient to affect DTD, then this study would neither support nor weaken the Ecological Constraints model as it applies to red colobus. It would, however, substantially weaken the argument that natural floristic differences confounded results in studies that did not find group size-adjusted DTD. In that case, other alternatives for the discrepancy between studies would need to be explored. In addition to potential confounding effects of social influences on DTD mentioned above, another explanation for the discrepancy might be that all studies accurately described red colobus behavior but that conditions in Kibale have changed over time, leading to changes in red colobus ranging and feeding behavior.

A difference in activity budgets (Majolo et al., 2008) between compartments would challenge the generality of the Ecological Constraints model because it would offer an option besides longer DTD for dealing with competition within groups. However, it would not address the discrepancy between studies of red colobus DTD nor would it explain why larger groups travel farther per day than smaller groups in so many primate species.

Insignificant differences in DTD between compartments could also indicate that red colobus did not feed in discrete patches at the spatial scale that is most relevant to the Ecological Constraints model (individual trees). In this case, the discrepancy between studies would still need to be explained but most importantly, the Ecological Constraints model as it pertains to red colobus would not be supported. These predictions, their potential outcomes, and the interpretation of those outcomes are summarized in Table 1.

Finally, insights from red colobus movements will suggest that although the Ecological Constraints model may be correct in positing energetic limits to group size, the underlying mechanism that increases travel costs in larger groups may not be more rapid depletion of food patches. Larger groups will always consume foods in their vicinity faster than smaller groups regardless of how those foods are distributed, but DTD is not invariably longer in larger

groups. When group members have multiple choices in the paths they can take, they can spread out and avoid increasing their travel costs. Patchily distributed food trees may cause groups to increase DTD because they narrow the choice of paths and targets available to group members, not because they are depleted faster by larger groups. Patchy food trees provide but one example of several situations in which animals may be required to compress, or funnel, into smaller spaces, causing those ahead to move farther than they otherwise would. The space limitations inherent in funneling are proposed here to be more fundamental than patchy food tree distributions in increasing DTD and the energetic costs of travel in larger groups of primates.

2. Methods

2.1. Study site and subjects

Red colobus monkeys have been studied in the Kanyawara study area of Kibale Forest (now Kibale National Park), Uganda (766–795 km^2; 0°13′ to 0°41′N and 30°19′ to 30°32′E) since the 1970s by several field workers (e.g., Struhsaker, 1975, 1997; Isbell, 1983; Skorupa, 1988; Gillespie & Chapman, 2001; Snaith & Chapman, 2008; Chapman et al., 2010). Rainfall is typically bimodal, with wetter months in March–April and September–November. Annual rainfall averaged approximately 1650–1700 mm from 1977–1981 (Skorupa, 1988). When the fieldwork for this study was conducted in the early 1980s, Kibale incorporated a mid-altitude (1110–1590 m) mosaic of habitat types that included mature native evergreen tropical forest on gently sloping hillsides, grassy hilltops, and swamps. Parts of Kibale were selectively harvested for timber in the 1960s, resulting in a heterogeneous landscape that included forestry compartments that were either selectively logged (e.g., forestry compartment K14) or largely untouched other than minimal pit-sawing (e.g., forestry compartment K30) (Skorupa, 1988; Struhsaker, 1997). Compartments K14 and K30 were clearly separated from each other by a former logging track. Another logging track diverged from the main track and separated a lightly felled part of K30 (here designated K30LFA) from both K14 and the undisturbed part of K30. By the time of my data collection, 11 years had passed since K14 had been selectively logged.

I studied red colobus monkeys for 2086 h from February 1980 through December 1981. Among these groups, the Blaze, or B, group regularly used both K14 and K30. I observed the B group for 1818 h, of which 1622 h

involved systematic data collection from March 1980 to December 1981. Group size averaged 67.2 individuals ($N = 13$ counts, range: 64–70). By April 1980, eight adult and subadult males could be easily identified as individuals by natural markings. By November 1980, all 17 adult and subadult males and 17 other individuals could be identified as individuals. Three subadult males matured and stayed in the group for the duration of the study, and one adult male disappeared. Based on the 13 group counts, there were also, on average, 22.2 adult females, 4.9 subadult females, 9.6 juveniles and 14.1 infants.

2.2. Data collection

2.2.1. Disturbance index

As one way to document the differences between K14 and K30, I determined degree of disturbance from logging by estimating canopy cover and understory density within the two compartments. While walking roughly parallel lines along an established grid of trails intersecting one another at 50–100-m intervals within the study group's home range, I visually assessed each 50-m section on either side of the trail for the extent of canopy cover and understory density using a scale of 0–3 for canopy cover (0 = total cover to 3 = no cover) and 0–2 for understory response to disturbance (0 = sparse understory to 2 = dense understory). Each 50 m × 50 m section was thus assigned two values for canopy cover and two for understory density. These values were then averaged separately for canopy cover and understory density, and the two means were summed to obtain an index of disturbance that ranged from 0 to 5 for each section (some sections (19 of 75 in K14 and 20 of 67 in K30) could only be assessed on one side; their values were simply summed). A sum of 0 indicates total canopy cover along with a sparse understory, i.e., undisturbed old growth forest, whereas a sum of 4 indicates many breaks in the canopy along with a dense understory, i.e., heavily disturbed forest. Note that a value of 1 could not discriminate between human-induced disturbances and natural disturbances such as treefalls. Valley bottoms were excluded because they were rarely, if ever, logged and yet had characteristically sparse canopy coverage and dense understories. An exotic *Pinus* and *Eucalyptus* plantation was also excluded. I also noted any stumps where trees had been cut during logging.

2.2.2. *Botanical transects*

As another way to characterize the differences between K14 and K30, I determined the density and richness of tree species by using the trail system's grid intersections within the home range of the study group to randomly survey strip transects that were 50 m in length and enumerate all trees at least 9 m in height within 2.5 m of either side of the trail. Trees were identified to species using a reference collection provided by T.T. Struhsaker and T.M. Butynski. I measured diameter at breast height (DBH, at 1.4 m) of each tree. I enumerated trees in 49 transects (1.22 ha total area) in K14 and added eight transects in K30 to the 32 transects enumerated by T.M. Butynski, who used the same methods (1 ha total area). Since the variance of density estimates for common species of trees (many of the major food trees of red colobus) levels off at 25–30 transects (Skorupa, 1988), this sampling intensity was thought to be sufficient. These data provided information on density and size of trees belonging to food and non-food species in the group's home range within both logged and unlogged compartments.

2.2.3. *Ranging behavior*

I collected ranging data on the B group beginning in February 1980 but include here only ranging data collected after April 1980 because the group was not habituated to human presence before my study, which increased the potential for inadvertent observer influence on ranging behavior in the early months. I include here ranging data collected over 18 months, from May 1980 through October 1981. I collected data largely following Struhsaker (1975). Each month, once I found the group, I systematically followed it from dawn to dusk (typically 0700 h to 1900 h) for 4–5 consecutive days, regardless of its location to obtain an unbiased sample of compartmental use. I also followed the group for up to four additional full days each month to equalize compartmental sampling per month, but these data were used only for describing feeding behavior, not in the analysis of ranging behavior.

Each day that the group was followed for at least 11.5 h, I plotted the estimated center-of-mass of all animals visible to me (Altmann & Altmann, 1970) and the number of visible animals every 15 min on range maps (1:2500) provided by T.T. Struhsaker. Repeatedly seen individuals among those visible suggested that my position relative to the group was fairly constant throughout the day. The trail grid provided landmarks to plot the points accurately. I calculated DTDs by summing straight-line distances between successive chronological points for each day. Degree of tortuosity of

movements was measured by dividing the distance between first and last center-of-mass points for each day by this estimate of DTD, and by summing the distance between the two farthest center-of-mass points on the ranging maps for each month. Degree of tortuosity was measured because animals that move to sparsely distributed or patchy resources tend to follow a more goal-directed, straighter route than animals that move to denser, more uniform, or randomly distributed resources (insects: McIntyre & Wiens, 1999; birds: Roshier et al., 2008; ungulates: Etzenhouser et al., 1998; de Knegt et al., 2007; primates: Milton, 1980, 2000; Pochron, 2001; Noser & Byrne, 2007, 2010; Beisner & Isbell, 2009). Finally, I superimposed a grid map representing 50 m × 50 m quadrats (0.25 ha) on the range maps following Struhsaker (1975), and assigned quadrats to the plotted 15-min group locations. Although most quadrats were clearly within one or the other compartment, 10 quadrats were not and were split between K14 and K30. The lightly felled part of K30 (K30LFA) was treated as separate from the rest of K30 for analyses dealing with ranging behavior for two reasons. Although it was officially a part of K30, its logging history was more similar to that of K14. In addition, it was separated by both K14 and K30 by logging tracks, which required the group to leap across large gaps in the canopy when entering or leaving it. This could have affected travel distance (see Results).

2.2.4. Activity budgets

Following Struhsaker (1975), I scanned the group every 10 min centered on the hour and half-hour and recorded the first activities lasting at least 5 s of all animals clearly seen, along with their age/sex class and individual identity when known. Mutually exclusive categories for adults included feeding, moving, inactive, social grooming, auto-grooming, and 'other'. Percentages for each activity were first calculated per hour each month for adult males and adult females separately to control for uneven sample sizes per hour and then averaged across months. Analyses are based on data collected for 15 months, from May 1980–July 1981.

2.2.5. Feeding behavior

During each all-day follow of the group, I recorded the time, food species, and food item whenever I observed an individual ingesting a food item. The data included here are those from May 1980 through October 1981. An individual was not scored for the same food item more than once within 1 h unless it ate the same food item from a different individual of the same

food species. The following food categories were used: fruits, seeds, floral buds, indistinguishable buds of flowers or leaves (mostly from *C. africana*), flowers, young leaves (further categorized as very small, small, medium and large), petioles of young leaves, mature leaves, petioles of mature leaves, probable arthropods, and miscellaneous (e.g., mosses, lichens and bark).

For general descriptions of diet and feeding behavior, the contributions of individual food tree species to the overall diet were calculated first as percentages by month to avoid bias that might result from uneven monthly sample sizes and then averaged across months to obtain mean percentage contributions to the 18-month diet.

2.2.6. Feeding behavior in relation to use of space

I used an animal-based approach to identify the quadrat locations of food trees by extracting from the feeding data all records within 5 min of each center-of-mass location during each of the first 4–5 sample days of each month. This approach is more thorough than the botanical transects because it provides estimates of food tree distribution, density, and abundance for both common and rarer tree species throughout the home range based on the locations of feeding individuals at the scale of 0.25 ha (the size of quadrats). For example, *Pygeum africanum* (syn. *Prunus africana*), an important food species for the study group, was not enumerated in the transects but was plotted in association with 27 quadrats based on the group's feeding behavior. Although this approach runs the risk of assigning food trees to the wrong quadrat, two facts suggest that the risk was minimal. First, the locations of animals were plotted according to where the food actually occurred, i.e., in the canopy, and canopies of individual trees could be in more than one quadrat (transects cannot locate individual trees in the entire home range, but if they could, each counted stem could only occur in one quadrat). In addition, the number of quadrats with which staple food trees were associated based on these feeding records corresponded well with the density of staple food tree species as estimated by the strip transects ($r_s = 0.71$, $t = 3.46$, $N = 14$, df $= 12$, $p = 0.002$, 1-tailed). Here I define staple food tree species as those that accounted for at least 1% of the diet, on average, regardless of compartment (after Snaith & Chapman, 2008), and also were fed from during at least 12 of the 18 study months.

I used the VassarStats statistical computation website (http://faculty. vassar.edu/lowry/VassarStats.html) for statistical analyses, all of which in-

volved non-parametric two-tailed tests unless specified otherwise. Statistical significance was set at $\alpha = 0.05$.

3. Results

3.1. General use of compartments

During 84 all-day follows from May 1980 through October 1981, the B group spent 49.6 days in K14 (59.0% of total time) and 33.6 days in K30 (40.0%), including 3.7 days in K30LFA. They also spent 0.7 days in an exotic pine/eucalyptus plantation (0.9%). The group used both compartments in all but two months (range: K14 0–4.4 days/month; K30 0–3.7 days/month). Forty-two days were spent entirely in K14 and 15 days in K30, excluding K30LFA. The center-of mass of the group was plotted 4116 times in 254 50 m $\times$ 50 m quadrats (63.5 ha) over 84 days. Of those 254 quadrats, 121.5 were in K14 (47.8%), 107.5 were in K30 (42.3%), 21 were in K30LFA (8.3%), and four were in the pine/eucalyptus plantation (1.6%) (Figure 1).

The group did not spend significantly more time than expected in either compartment, as estimated by the proportional representation of each compartment in the home range multiplied by the number of sample days in K14 and K30 ($\chi^2 = 2.47$, $p = 0.12$, $N = 79.5$, df $= 1$). This is consistent with an earlier study (Isbell, 1983) based on field notes rather than actual quadrat locations on ranging maps.

3.2. Habitat differences between logged and unlogged compartments

Approximately 30% of the study group's home range was rated as undisturbed or very lightly disturbed (disturbance indices 0–1.5) and 26% was rated as heavily disturbed (disturbance indices 4–4.5), excluding valley bottoms and the pine/eucalyptus plantation. In K14, 7% of the B group's home range was rated as undisturbed or very lightly disturbed, whereas 39% was rated as heavily disturbed. Several sections (3%) were rated as extremely disturbed (disturbance index $= 5$); these were combined with disturbance indices 4–4.5 during analysis. In K30 (K30LFA was not included in the analysis), 55% of the B group's home range was undisturbed or very lightly disturbed, whereas 12% was heavily disturbed. No sections were considered extremely disturbed. The two compartments differed significantly in their degree of disturbance ($\chi^2 = 48.76$, $p < 0.0001$, $N = 142$ sections, df $= 4$). Evidence of past logging activity in K14 was also apparent from the 27 tree
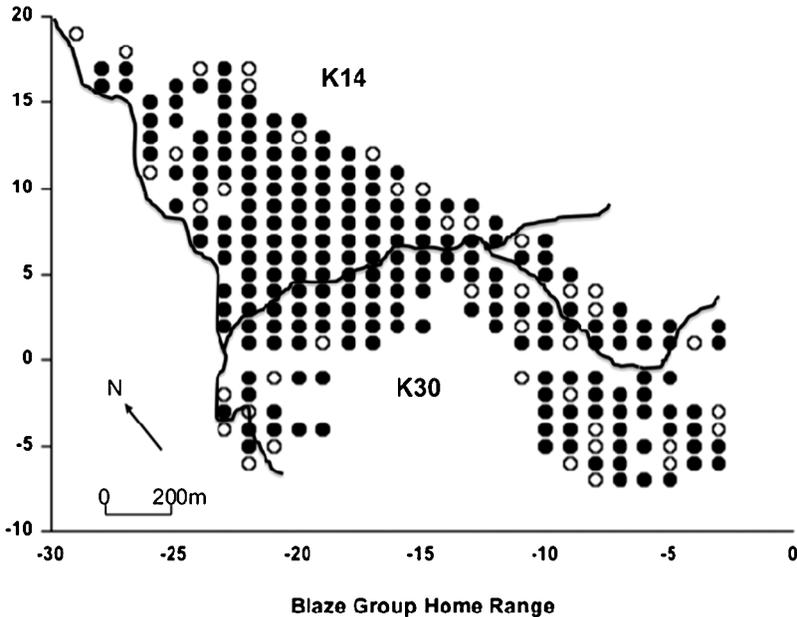
Figure 1. Home range of the B study group. Circles represent 0.25 ha quadrats. Filled circles are the quadrat locations of the B group's 14 staple food tree species. Staples were those species that accounted for at least 1% of the overall diet, regardless of compartment, and were also fed from during at least 12 of the 18 study months. The logged compartment, K14, was separated from the unlogged compartment, K30, by a logging track, shown here by lines traversing the home range. Compartment K30LFA was the area separated by both K14 and K30 proper by two logging tracks.

stumps identified from the trails in K14. In contrast, no tree stumps were seen along the trails in K30.

Enumeration transects also revealed a significant difference between K14 and K30 in the size of trees. Within the group's home range in K14, 219 trees (68% of 341 trees) had a DBH less than 31 cm, whereas 129 trees in K30 (54.6% of 247 trees) had a DBH less than 31 cm. Conversely, only four trees (1.2%) in K14 had a DBH of more than 90 cm whereas 10 trees (4.2%) in K30 were at least that large ($\chi^2 = 14.2$, $p < 0.05$, $N = 558$, df $= 6$) (larger trees can support more individuals, all else being equal) (Figure 2). This was associated with a higher tree density in K14 (277 trees/ha) than in K30 (247 trees/ha). Much of this could be attributed to the presence of small, colonizing species that often fill in light gaps created by logging. *Trema guineensis*, for example, occurred at a density of 40.8 trees/ha in K14 but was
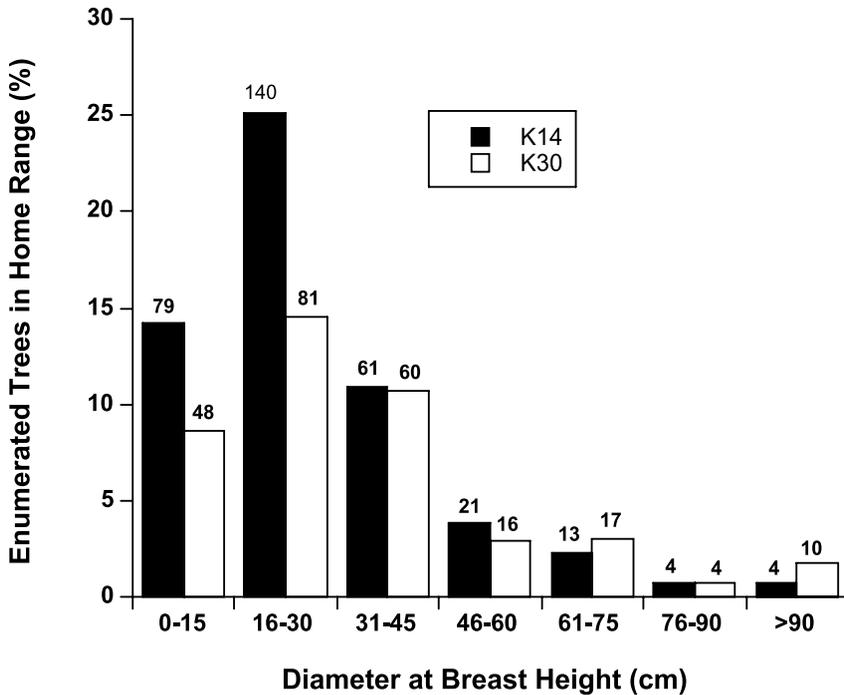
Figure 2. Tree size (DBH) of enumerated trees in K14 (logged) and K30 (unlogged) compartments of Kibale Forest within the home range of the red colobus study group. Sample sizes are above the bars.

absent in the K30 enumeration, and the density of *Markhamia platycalyx* in K14 was more than double that in K30 (Table 2).

Finally, of 56 tree species enumerated along transects in the group's home range, 22 were common to both K14 and K30, 13 were found only in K14, and 21 were found only in K30 (Table 2). In summary, selective logging that occurred 11 years earlier in K14 resulted in (1) greater vegetational disturbance, (2) greater numbers of smaller trees and (3) higher densities of trees. Selective logging also increased the density of colonizing species, changing the overall composition of tree species in K14.

3.3. Daily travel distance within compartments

Mean ± SE DTD on days in which the group traveled entirely within K30 was 579.8 ± 54.3 m ($N = 15$), only 4% longer than the mean DTD on days in which the group traveled entirely within K14 (557.4 ± 30.2 m, $N = 42$). There was no significant difference in DTD between compartments either

Table 2.

Tree species enumerated in vegetation transects in K14 (logged) and K30 (unlogged).

Species	N, K14	K14 stems/ha	N, K30	K30 stems/ha
Markhamia platycalyx[*,a]	77	62.8	27	27.0
Trema guineensis[*,a]	50	40.8		
Celtis durandii[*,a,b]	42	34.3	32	32.0
Diospryos abyssinica	42	34.3	9	9.0
Funtumia latifolia	20	16.3	26	26.0
Bosqueia phoberos[*]	16	13.1	34	34.0
Teclea nobilis[*]	13	10.6	9	9.0
Uvariopsis congensis	12	9.8	7	7.0
Chaetacme aristata[*]	10	8.2	9	9.0
Dombeya mukole[*,a,b]	7	5.7	2	2.0
Celtis africana[*,b]	6	4.9	1	1.0
Aphania senegalensis	6	4.9	1	1.0
Fagaropsis angolensis	5	4.1	2	2.0
Olea welwitschii	5	4.1	4	4.0
Neoboutonia macrocalyx	3	2.4	2	2.0
Bersama sp.	3	2.4		
Albizia grandibracteata	3	2.4		
Cordia millenii	2	1.6		
Haloptelia grandis	2	1.6		
Strombosia scheffleri[*]	2	1.6	35	35.0
Allophylus sp.	1	0.8		
Mitragyna rubrostipulata	1	0.8		
Chrysophyllum gorungosanum	1	0.8	3	3.0
Ehretia cymosa	1	0.8	1	1.0
Ficus brachylepis	1	0.8	1	1.0
Ficus capensis	1	0.8		
Ficus exasperata	1	0.8	1	1.0
Ficus natalensis	1	0.8	1	1.0
Millettia dura[*,a,b]	1	0.8	1	1.0
Premna angolensis	1	0.8		
Strychnos mitis	1	0.8	2	2.0
Vangueria apiculata	1	0.8		
UID sp. 1[c]	1	0.8		
UID sp. 2[c]	1	0.8		
UID sp. 200[c]	1	0.8		
Symphonia globulifera			8	8.0
Cassipourea ugandensis			4	4.0
Pancovia turbinata			3	3.0
Aningeria altissima[*,b]			2	2.0
Drypetes battiscombei			2	2.0

Table 2.
(Continued.)

Species	N, K14	K14 stems/ha	N, K30	K30 stems/ha
Erythrina abyssinica			2	2.0
Fagara angolensis			2	2.0
UID sp. 202[c]			2	2.0
UID sp. 203[c]			2	2.0
Anthocleista nobilis			1	1.0
Gabunia odoratissima			1	1.0
Euadenia eminens			1	1.0
Linociera johnsonii			1	1.0
Lovoa swynnertonii			1	1.0
Mimusops bagshawei			1	1.0
*Newtonia buchananii**			1	1.0
*Parinari excelsa**			1	1.0
Pterygota mildbraedii			1	1.0
Randia urcelliformis			1	1.0
Trichilia spendida			1	1.0
UID sp. 201[c]			1	1.0
Total	341	277.9	247	247.0

* Staple food tree species (those with at least 1% of all feeding records and which were fed on in at least 67% of all months).
[a] Colonizing staples (from Struhsaker, 1978, 1997).
[b] Deciduous staples (from Struhsaker, 1978, 1997).
[c] Unidentified species.

when controlling for phenology by comparing mean DTD between compartments within the same months (Wilcoxon matched-pairs test: $W = 2$, $p > 0.05$, $N = 7$) or when phenology was not considered (Mann–Whitney U-test: $U = 360.0$, $z = -0.81$, $p = 0.42$, $N_1 = 42$, $N_2 = 15$). These results are consistent with those of an earlier study on the same group using a somewhat different data set (Isbell, 1983). Logging tracks had a greater effect on DTD than compartment type. Mean DTD on days when the group crossed logging tracks was 662.3 ± 57.8 m ($N = 24$), 14–18% longer than when they stayed entirely within either compartment (Mann–Whitney U-test: $U = 781.5$, $z = -1.0$, $N_1 = 57$, $N_2 = 24$, $p = 0.16$, one-tailed), a statistically non-significant but potentially biologically significant difference (see Discussion). The influence of the logging tracks on DTD could be consequential (the group simply encountered logging tracks more often the farther it traveled) or causal (the logging tracks caused the group to travel farther).

The former seems unlikely because DTDs on days with multiple crossings (range 430–1240 m; $N = 4$) were within the range of DTDs on days with only one crossing (310–1357.5 m; $N = 20$).

3.4. Activity budgets within and between compartments

Group size-adjusted DTD is but one indicator of competition within groups. If DTD does not change with group size, time spent feeding may change instead if animals increase their feeding effort in larger groups. Alternatively, time spent moving may change if animals conserve their energy in poorer habitats. Neither occurred in this study, however. Adult females spent 31.2% of their time feeding and 10% moving in K14, whereas they spent 32.2% of their time feeding and 11.8% moving in K30 ($N = 4398$ activity records (K14, 2512; K30, 1886)). There was no significant difference in adult female activity budgets between the two compartments (all activities except 'other'; percentages back-transformed; $\chi^2 = 0.49$, $p = 0.48$, df $= 1$). Similarly, adult males spent 29.7% of their time feeding and 8.5% moving in K14, and 30.3% feeding and 7.3% moving in K30 ($N = 4021$ activity records (K14, 2287; K30, 1734)) (Table 3). There was also no statistically significant difference in adult male activity budgets between compartments (all activities except 'other'; percentages back-transformed; $\chi^2 = 2.26$, $p = 0.69$, df $= 1$).

3.5. Feeding behavior within compartments

Over 18 months, the B group fed from 60 tree species, 51 of them in K14 and 43 in K30 ($N = 3793$ feeding records in K14 and 2372 in K30). Two-thirds of the total food tree species (34/60; 65.4%) were common to both

Table 3.
Activity budgets (%, mean $\pm$ SD) of adult females and adult males in compartments K14 (logged) and K30 (unlogged).

Activity	Adult females		Adult males	
	K14 ($N = 2512$)	K30 ($N = 1886$)	K14 ($N = 2287$)	K30 ($N = 1734$)
Feed	31.2 ± 5.2	32.2 ± 6.9	29.7 ± 5.5	30.3 ± 6.7
Locomotion	10.0 ± 4.6	11.8 ± 4.8	8.5 ± 2.7	7.3 ± 4.6
Inactive	50.0 ± 5.6	46.5 ± 6.8	55.0 ± 5.2	54.2 ± 8.4
Social groom	7.2 ± 1.5	7.6 ± 3.8	3.6 ± 1.4	4.0 ± 1.9
Auto-groom	1.1 ± 1.0	0.9 ± 0.8	1.4 ± 0.9	1.2 ± 0.9
Other	0.3 ± 0.5	0.8 ± 0.8	1.8 ± 1.6	3.0 ± 3.1

compartments (Table 4). Fourteen food tree species were staples, i.e., food tree species that contributed at least 1% to the diet and that were fed from in at least 67% of the study months. The group fed on 13 staples in K14 and all 14 staples in K30. Non-staple food tree species accounted for 38 of 51 (74.5%) tree species in K14, and 29 of 43 (67.4%) tree species in K30. The two compartments did not differ significantly in the number of staple versus non-staple species ($\chi^2 = 0.28$, $p = 0.60$, $N = 94$, df $= 1$).

The group was observed to eat 125 species-specific food items over 18 months ($N = 6165$ feeding records). Among classes of food items, young leaves were eaten most often (37.5%), followed by mature leaves (21.8%) petioles of mature leaves (11.8%), petioles of young leaves (7.1%), buds (usually of leaves) (6.1%), flowers and floral buds (3.8%), fruits and seeds (3.7%), and arthropods (0.7%). Young leaves comprised a significantly greater percentage of the diet in K30 (43.7%, $N = 2372$) than in K14 (33.6%, $N = 3793$; $\chi^2 = 63.13$, $p < 0.0001$, df $= 1$). The lower young leaf consumption in K14 was largely replaced by greater consumption of mature leaves (K14: 26.6%; K30: 14.2%), mainly from *Trema*. Indeed, the most frequently eaten species-specific food item was mature leaves of *Trema*, accounting for 10.3% of the overall diet. *Trema* was only found along K14 transects. The differences in the group's diet between the two compartments indicate that group members were opportunistic in what they ate, a finding that is consistent with studies reporting extraordinarily broad diets in other red colobus groups (Struhsaker, 1975, 2010; Gillespie & Chapman, 2001; Snaith & Chapman, 2008).

The ability of red colobus to take advantage of what is available is supported by transect enumerations. The density of food trees and food tree species richness were high in both compartments (density: K14, 257.1 food trees/ha; K30, 229 food trees/ha; χ^2 goodness of fit $= 1.52$, $p = 0.22$, $N = 486.1$, df $= 1$; richness: K14: 25 of 35 species; 71.4%; K30: 33 of 42 species; 78.6%; $\chi^2 = 0.21$, $p = 0.65$, $N = 77$, df $= 1$). Transect enumerations showed 315 food trees of 341 (92%) stems in K14, and 229 food trees of 247 (93%) stems in K30. Staple food species contributed 65.8% of enumerated stems (182.8 of 277.9 stems/ha) in K14 and 62.3% of enumerated stems (154 of 247.0 stems/ha) in K30. Non-staple food species contributed an additional 26.7% (74.1 of 277.9 stems/ha) in K14 and 30.4% (75 of 247.0 stems) in K30 (Table 2). A low percentage of non-food trees was also similarly represented in each compartment (K14, 7.6%, 21 stems/ha; K30, 7.3%, 18 stems/ha).

Table 4.
Food species in the diet of red colobus in compartments K14 (logged) and K30 (unlogged) ($N = 6165$ feeding records) and the number of quadrats in each compartment with which they were associated ($N = 1598$ feeding records within 5 min of center-of-mass ranging points). Species marked with asterisks were fed from in both compartments.

K14 food species eaten ($N = 3793$)	Mean % in diet	No. of quadrats	K30 food species eaten ($N = 2372$)	Mean % in diet	No. of quadrats
*Trema guineensis	21.0	54	*Pygeum africanum	18.3	14
*Markhamia platycalyx	19.2	66	*Celtis africana	12.3	24
*Celtis africana	10.3	47	*Markhamia platycalyx	11.7	47
*Dombeya mukole	9.4	30	*Strombosia scheffleri	10.7	45
*Celtis durandii	6.3	46	*Celtis durandii	5.8	17
*Millettia dura	4.9	33	*Aningeria altissima	4.8	15
*Strombosia scheffleri	2.8	17	*Newtonia buchananii	4.8	15
*Pygeum africanum	2.4	11	*Bosqueia phoberos	3.9	19
*Aningeria altissima	2.3	7	*Parinari excelsa	2.5	17
*Bosqueia phoberos	2.3	21	Albizia gummifera	2.4	4
*Chaetacme aristata	1.8	12	*Sapium ellipticum	2.4	4
*Parinari excelsa	1.5	7	*Chrysophyllum	2.2	14
*Teclea nobilis	1.5	15	gorungosanum		
*Ficus brachylepis	1.5	12	*Trema guineensis	1.8	5
*Olea welwitschii	1.0	9	*Teclea nobilis	1.4	11
Liana spp.	0.9		*Funtumia latifolia	1.2	17
*Funtumia latifolia	0.8	13	*Chaetacme aristata	1.1	8
Fagara macrophylla	0.8	5	*Dombeya mukole	1.1	6
*Arthropods	0.7		*Arthropods	1.0	
*Albizia grandibracteata	0.7	1	*Mimusops bagshawei	0.8	6
*Ehretia cymosa	0.6	5	*Pancovia turbinata	0.7	6
*Chrysophyllum	0.6	5	*Millettia dura	0.7	2
gorungosanum			*Ficus natalensis	0.6	3
*Acacia monticola	0.5	5	*Ehretia cymosa	0.6	2
Premna angolensis	0.5	5	*Urera cameroonensis	0.5	
*Urera cameroonensis	0.5		Cassipourea	0.5	1
*Sapium ellipticum	0.5	1	ruwensorensis		
Aphania senegalensis	0.5	4	*Macaranga	0.5	1
*Linociera johnsonii	0.4	3	schweinfurthii		
*Mimusops bagshawei	0.4	0	Fagara angolensis	0.5	0
UID #19	0.3		*Liana spp.	0.4	
UID #45	0.3		Symphonia globulifera	0.4	2
UID	0.3		*Diospyros abyssinica	0.4	3

Table 4.
(Continued.)

K14 food species eaten ($N = 3793$)	Mean % in diet	No. of quadrats	K30 food species eaten ($N = 2372$)	Mean % in diet	No. of quadrats
*Newtonia buchananii	0.2	1	*Ficus brachylepis	0.4	7
*Bark	0.2		*Lovoa swynnertonii	0.4	5
UID #43	0.2		UID	0.4	
*Lovoa swynnertonii	0.2	0	UID #14	0.3	
*Ficus capensis	0.2	1	*Albizia grandibracteata	0.2	0
*Macaranga schweinfurthii	0.1	2	*Ficus dawei	0.2	2
			*Lichen	0.2	
*Pterygota mildbraedii	0.1	0	*Bark	0.2	
*Myrianthus arboreus	0.1	2	*Pterygota mildbraedii	0.2	1
Erythrina abyssinica	0.1	0	*Linociera johnsonii	0.2	0
*Diospyros abyssinica	0.1	3	*Olea welwitschii	0.1	3
Ficus cyathistipula	0.09	1	UID #52	0.1	
*Pancovia turbinata	0.09	1	UID #50	0.1	
*Galls	0.09		UID #47	0.09	
*Ficus natalensis	0.08	0	*Ficus capensis	0.08	0
Cordia milleni	0.08	0	*Galls	0.08	
Dead wood	0.06		*Fagaropsis angolensis	0.07	1
Strychnos mitis	0.05	0	*Acacia monticola	0.07	0
*Herbaceous plant spp.	0.05		*Herbaceous plant spp.	0.05	
*Fagaropsis angolensis	0.03	0	Gabunia odoratissima	0.05	0
Ficus exasperata	0.03	0	*Moss	0.04	
Stems	0.03		Epiphyte	0.04	
*Lichen	0.03		*Myrianthus arboreus	0.04	1
*Ficus dawei	0.03	0			
Alafia grandis	0.03	0			
UID # 49	0.03				
UID # 51	0.03				
UID # 53	0.03				
UID # 44	0.02				
*Moss	<0.01				
Total	99.8%	445		99.9%	327

3.6. Spatial distribution of red colobus food trees

To locate food trees in the group's home range, I extracted only those data on feeding behavior recorded between 5 min before and after data were recorded on quadrat location ($N = 1598$). The 14 staple food tree species ac-

Table 5.

The proportion of 0.25 ha quadrats in which the B group fed on staple tree species in K14 and K30.

Tree species	K14, proportion of quadrats ($N = 121.5$)	K30, proportion of quadrats ($N = 107.5$, excluding K30LFA)	Total, proportion of home range ($N = 254$ quadrats)
Aningeria altissima	0.06	0.14	0.09
Bosqueia phoberos	0.17	0.18	0.17
Celtis africana	0.39	0.22	0.29
Celtis durandii	0.39	0.16	0.27
Chaetacme aristata	0.10	0.07	0.09
Dombeya mukole	0.25	0.06	0.17
Markhamia platycalyx	0.54	0.44	0.49
Millettia dura	0.27	0.02	0.14
Newtonia buchananii	0.008	0.14	0.06
Parinari excelsa	0.06	0.16	0.09
Pygeum africanum	0.09	0.13	0.11[*]
Strombosia scheffleri	0.14	0.42	0.35
Teclea nobilis	0.12	0.10	0.13
Trema guineensis	0.44	0.04	0.23

[*] *Pygeum africanum* also occurred in the pine plantation.

counted for over three-quarters (76.3%) of the group's diet and were spatially widespread. Staple food tree species were eaten in 209 of 254 quadrats in the recorded home range (82.3%) (Figure 1). The other 46 food tree species increased the percentage of quadrats associated with food trees by only 6.7%, indicating that non-staples typically occurred in the same quadrats with staples. Individual staple tree species could be patchily distributed, however. For instance, whereas *Markhamia* was associated with nearly half of all quadrats, *Aningeria altissima* and *Newtonia buchananii*, two large, emergent species, were associated with only 6 and 9% of all quadrats, respectively (Table 5). An examination of the cumulative number of quadrats associated with food divided by the number of tree species in Table 4 reveals that 8.4 food tree species occurred per 0.25 ha quadrat in K30 and 10.6 per 0.25 ha quadrat in K14.

Although individuals of the same tree species could be patchily distributed, the monkeys rarely fed consecutively on different individual trees within the same species. Of 1586 feeding records in which individuals were identified, only 12 (0.8%) involved an individual feeding on the same food

item from different trees of the same species within the same hour. On a given day, red colobus typically fed on more than one species within each quadrat (mean ± SD 2.0 ± 1.22 species/quadrat per day, range 1–8, $N = 84$).

The monkeys also moved as if their foods were fairly uniformly distributed. On average, I recorded the center of mass of the group in 10.5 ± 3.8 quadrats per day (mean ± SD, $N = 84$), and the majority of these (mean ± SD 7.8 ± 2.3; 75%) were associated with food. Normally they moved fairly slowly each day (mean quadrats/h ± SD: 0.9 ± 0.3; range 0.2–1.9 quadrats/h; mean m/h ± SD 52.6 ± 20.3; range 1.7–118 m/h). One day was exceptional in that the monkeys were recorded during 18 scans (4.5 h) as feeding exclusively in one quadrat. In that quadrat, they fed on *Pygeum*, *Sapium ellipticum*, *Albizia gummifera*, and the liana *Urera cameroonensis*. In addition, the group regularly moved more gradually (as one would expect of animals that feed on more uniform resources) than in punctuated bursts of rapid movement over longer distances (as one would expect of animals feed on patchier resources). When the group moved out of one quadrat, in the following 15-min interval it was almost always recorded in an adjacent quadrat. The group moved to non-adjacent quadrats an average of only once per day (average ± SD 0.98 ± 1.09; range 0–6), which accounted for 2% of all scans per day (mean scans per day ± SD 45.2 ± 2.4, $N = 84$ days).

Another way to investigate whether their foods occurred in patches is to examine the extent of tortuosity of their movements. Direct movements are often interpreted as revealing goal-directed movements, often to patchily distributed foods (Milton, 1980, 2000; Pochron, 2001; Noser & Byrne, 2007, 2010; Beisner & Isbell, 2009). One measure of directness of travel is the ratio of the group's net displacement, i.e., the distance between the group's location at the start and the end of day, to the group's DTD, called the straightness index (Beisner & Isbell, 2009). Values closer to 1 indicate more directed daily travel whereas values closer to 0 indicate more tortuous daily travel. The mean straightness index per day ± SD was 0.39 ± 0.20 (range 0.0–1.0, $N = 84$), indicating more tortuous than direct daily movements.

The tortuosity of their travel can also be examined with monthly paths. Mean DTD per month was positively correlated with the straight-line distance between the two farthest quadrats for each month ($r_s = 0.63$, $t = 3.21$, $N = 18$, df = 16, $p = 0.003$, one-tailed) (Figure 3), suggesting that in months when the group traveled more linearly, they traveled farther, on average. However, as expected from the low straightness index for daily travel,
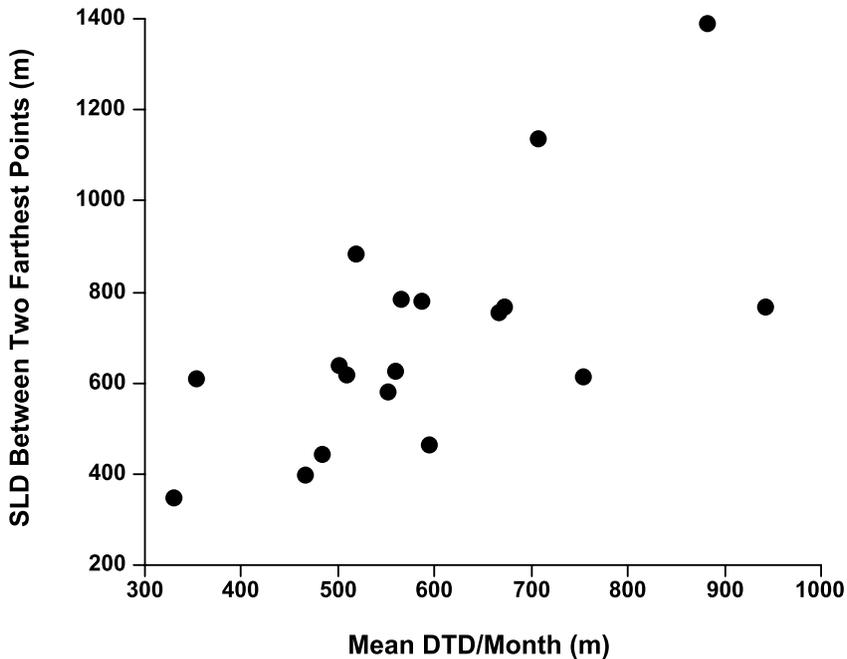
Figure 3. Relationship between mean daily travel distance (DTD) per month and the straight-line distance (SLD) between the two farthest points. Smaller DTDs per month involved staying in the same general area. The longest DTDs per month involved moving in a more linear path to more distant areas, suggesting more goal-directed travel over a five-day period.

in 15 of 18 months the path of the group was relatively tortuous, with widest spatial displacements of 350.0–787.5 m from the two farthest points of the month. Again, this suggests that the group was not typically goal-directed in its movements.

Three months that were exceptional in having the three widest spatial displacements between farthest quadrats (885–1390 m) involved travel to or from the same far edge of the group's home range in K30 (the group was recorded there in only one other month). In addition to the staples *Chaetacme aristata* and *Teclea nobilis*, the group ate from numerous non-staples in this area: *Ficus brachylepis*, *F. natalensis*, *Lovoa swynnertonii*, *Mimusops bagshawei*, *Pancovia turbinata*, and *Pterygota mildbraedii*. These non-staples were relatively rare in the group's home range. Transect enumerations picked up these species at densities of 0.4–1.3/ha. Feeding observations associated with quadrat use were consistent with transect enumerations in that they fed from these food tree species at low levels in few quadrats.

Ficus brachylepis was associated with feeding in 18 of 254 quadrats (7.1%); *Mimusops* 11 (4.3%); *Pancovia* 7 (2.8%); *Lovoa* 5 (2.0%); *F. natalensis* 4 (1.6%); and *Pterygota* 1 (0.4%). Thus, while it was not the norm, the group occasionally traveled in an apparently goal-directed manner to particular quadrats on the periphery of their home range, suggesting some degree of patchiness of food trees, but importantly, it took five days to get there rather than just one day, the time frame relevant to DTD and the Ecological Constraints model.

4. Discussion

Red colobus monkeys have both paved and muddied the way to better understanding of ecological determinants of group size. Initially they provided a clear example of primates in which DTD does not increase with group size (Struhsaker & Leland, 1987). Most such primates were folivory-adapted colobines, in contrast to frugivorous cercopithecines, which showed a clear DTD response to larger group size (Clutton-Brock & Harvey, 1977; Struhsaker & Leland, 1987; Isbell, 1991; Wrangham et al., 1993; Janson & Goldsmith, 1995; Fashing, 2001).

More recently, Gillespie & Chapman (2001) and Snaith & Chapman (2008) have challenged this research by reporting that larger groups of red colobus do travel farther per day than smaller groups. Snaith & Chapman (2005) also found that red colobus spent less time in smaller trees when more animals were present in those trees, and that food intake rate slowed while movement increased within trees. These are important findings. They interpreted these data to mean that red colobus foods occur in patches and that the patches are depletable. Since red colobus are highly folivorous, their results have been used to broaden the generality of the Ecological Constraints model. They suggested that the discrepancy in group size-adjusted DTD between their studies and earlier ones was a result of earlier studies not controlling for floristic differences within the forest.

This study showed, however, that DTD in a group of red colobus monkeys did not differ as a result of natural floristic differences in habitat exacerbated by selective logging. This result can be interpreted in two ways: either the changes in the logged habitat were insufficient to affect DTD, or DTD was not affected by the changes (Table 1). If we accept the former interpretation, then it weakens the argument of Chapman and colleagues that natural habitat

variation obscured real differences in DTD among groups studied earlier, because natural floristic variation in habitats is undoubtedly milder than natural floristic variation compounded by selective logging. We would then need a different explanation as to why earlier and later studies obtained different results. If we accept the latter interpretation, then we must search not only for an explanation for differing results but also one for the lack of adjustment in DTD between compartments that was found in this study. One potential alternative explanation is that animals adjust their activity budgets instead of adjusting DTD in floristically different habitats (Janson & van Schaik, 1988; Chapman & Chapman, 2000a; Majolo et al., 2008) (Table 1). I found, however, that the activity budgets of both adult female and adult male red colobus were similar between compartments despite the differences caused by logging. There is, thus, no evidence that red colobus adjusted their activities instead of DTD in response to habitat differences.

Below I discuss two potential explanations for the discrepancies in group size-adjusted DTD between studies, and follow this with an explanation for the lack of adjustment in the group's DTD. In discussing the latter, I question the applicability of the Ecological Constraints model for red colobus and propose a new mechanism for group size-adjusted DTD in other primates.

4.1. Discrepancies between studies: concerns with more recent studies

Kibale Forest shows small-scale variation in tree species composition and densities (Chapman et al., 1997). Gillespie & Chapman (2001) and Snaith & Chapman (2008) argued that earlier studies reporting no significant increase in DTD in larger red colobus groups (and other folivores) were flawed because they did not control for such variation. One problem with this explanation is that it does not address why frugivores routinely show group size-adjusted DTD even when habitat differences are not considered.

The studies that found group size-adjusted DTD were also much shorter in duration than studies that did not find it (Gillespie & Chapman, 2001, 4 months; Snaith & Chapman, 2008, 2 months versus Strushaker, 1975, 19 months; this study, 18 months). For several reasons, sampling red colobus ranging and feeding behavior over a few months, even if intensive during those months, may not be representative of their behavior over longer periods of time. First, red colobus eat so many foods that it may take several years to obtain a representation of their diet (Struhsaker, 2010). Second, some tree species are seasonal in their food production and shorter studies may either

miss these species entirely or be overly affected by them. Finally, this study showed that ranging behavior can be quite different depending on the month. In some months monkeys may move as if to patchy food trees whereas in other months they may move more tortuously.

Another potential confounding factor in the later studies is male behavior. Red colobus are highly unusual among primates in that males are the stable core of the group (Struhsaker, 1975). Struhsaker (2010) provided evidence that much of the variance in red colobus group size can be attributed to variation in numbers of males in groups rather than ecological constraints of food competition. Groups increase in size because females tend to transfer to groups with more males and small groups dissolve when females abandon them for other groups (Struhsaker et al., 2004; Struhsaker, 2010). Previous research in Kibale also showed that male behavior influences DTD. A small group traveled farther on days when the group encountered other groups (Struhsaker, 1974, 1975), and a larger group traveled farther on days when intragroup male–male competition was more frequent (Isbell, 1983). Future studies could easily examine one aspect of the effect of male behavior on DTD in groups of different sizes by comparing frequencies of rapid-quaver vocalizations, a proxy for male–male competition, against group size. For now, it remains unclear whether recent studies measured DTD as a function of group size or male behavior. Struhsaker (2010) has several additional concerns.

4.2. Discrepancies between studies: has Kibale changed over time?

The discrepancy between studies done decades apart could also exist because Kibale may have changed since red colobus were first studied there. For example, Kibale has become wetter over time: mean annual rainfall in Kibale has increased from 1666 mm in the late 1900s until the 1990s to 1707 mm during the 1990s to 2010 (Chapman et al., 1997; Struhsaker, 1997, 2010; C.A. Chapman, unpubl. data). Additionally, the overall density of trees has increased in both K14 and K30 (Chapman et al., 1997). Finally, densities of some food tree species have increased while others have decreased (Chapman et al., 1997). Some or all of these changes may have facilitated an increase in young leaf consumption by red colobus over time. In the 1970s and 1980s, young leaves constituted 30–40% of their diet (Struhsaker, 1975, 2010; J.P. Skorupa, unpubl. data; this study). In the 2000s, that percentage increased to about 75% (Chapman et al., 2002; Rode et al., 2003; Snaith

& Chapman, 2008). Since the methods used to collect feeding data were similar between time periods, the difference cannot be methodological except for, perhaps, a difference in study duration. Studies also show increased young leaf consumption among sympatric black-and-white colobus (*Colobus guereza*). In the 1970s, 58% of the diet of black-and-white colobus came from young leaves, with young leaves of *Celtis durandii* alone contributing 35% (Oates, 1977). The percentage of young leaves in their diet is now up to 67–87% (Rode et al., 2003; Harris & Chapman, 2007).

Red colobus groups are also larger now than they were in the past (Struhsaker, 1975, 2010; Snaith & Chapman, 2008). In the early 1970s, mean group size was 50 (Struhsaker, 1975); in the mid-2000s, mean group size was 65 (Snaith & Chapman, 2008). At 67 members, the B group was the largest study group in the 1970s–1980s (Struhsaker, 2010). Currently the largest study group has approximately 150 individuals (Tombak et al., 2012). The change in diet could help account for the increase in group size because young leaves are generally higher in quality than mature leaves. If young leaves are more available now than before, and if population size has increased (although there is evidence for a decline in numbers of groups (Struhsaker, 2010: 84)) then it would imply that red colobus have always been limited by food abundance, contra Isbell (1991, 2004). It is also possible that these changes have created greater food patchiness. For example, the deciduous *C. durandii* produces flushes of new leaves fairly quickly in response to rainfall but individuals flush asynchronously (Oates, 1977; Struhsaker, 1997). This species increased in density from the 1970s to at least the 1990s (Chapman et al., 1997). Asynchronous flushing in a greater number of individual trees may create a patchier food tree distribution. Future studies could test this by examining group movements. If red colobus monkeys are now feeding regularly in patches, groups should travel linearly more often than they did in the past. This study shows that red colobus in earlier times only rarely fed as if their food trees were patchily distributed. Below I discuss the implications of this for the Ecological Constraints model.

4.3. Why red colobus did not adjust DTD: food trees were not patchy in space and time

The Ecological Constraints model posits that DTD is longer in larger groups, including red colobus groups, because larger groups deplete 'patches' more quickly and thus need to travel to more patches to obtain the same amount

of food as smaller groups (Chapman, 1990; Wrangham et al., 1993; Chapman et al., 1995). Energetic costs increase for larger groups because they are forced to travel between more patches without eating in between (Chapman & Chapman, 2000a, b). Early evidence supporting the Ecological Constraints model came from frugivorous primates whose food trees clearly occur in discrete patches, i.e., food-bearing trees that are separated from other food-bearing trees by non-food-bearing trees (Chapman et al., 1995; Wrangham, 2000). More recently, studies have shown that DTD is sensitive to group size in folivory-adapted primates when their food trees are relatively sparse or patchy. In highly folivorous ursine colobus (*Colobus vellerosus*) at Boabeng-Fiema, Ghana, larger groups have longer DTDs than smaller groups, and their food trees are patchy. Only 24–38% of the stems in the home ranges of two groups were food tree species (Saj & Sicotte, 2007a, b; Teichroeb & Sicotte, 2009). Similarly, in Thomas's langurs (*Presbytis thomasi*) at Ketambe, Sumatra, and mountain gorillas (*Gorilla beringei*) at Bwindi, Uganda, larger groups travel farther per day than smaller groups (Steenbeek & van Schaik, 2001; Ganas & Robbins, 2005). Although they are both capable of having a highly folivorous diet, their diets include substantial amounts of fruit (Steenbeek & van Schaik, 2001; Ganas & Robbins, 2005), and fruiting trees are expected to be more patchily distributed than trees with palatable leaves. In fact, DTD was positively correlated with the percentage of fruits in the diet of Bwindi gorillas (Ganas & Robbins, 2005). These studies reveal that it is not diet per se that drives group size-adjusted DTD. Regardless of whether primates are frugivorous or folivorous, larger groups do travel farther per day than smaller groups (see also Majolo et al., 2008) when food trees are sparse or patchy.

A functionally patchy food distribution at the scale required by the Ecological Constraints model is difficult to envision for Kibale red colobus of the 1980s, however. As reported here and elsewhere (Struhsaker, 1975, 2010; Gillespie & Chapman, 2001; Snaith & Chapman, 2008), red colobus in Kibale eat a wide variety of food items from a wide variety of tree species. Estimates from vegetation transects indicate that, overall, 92% of the stems in the B group's home range were food tree species, and that food trees occurred at a density of 233–257 stems per ha (58–64 stems per quarter-ha).

Foods were also widespread in the home range on shorter time scales. Fourteen food tree species were considered staples because they were fed from in most months, and these were associated with 82% of all quadrats

in the group's home range. Many of the lesser food trees overlapped in the same quadrats with staple food trees; these 46 species only increased the percentage of quadrats with food by 7%.

On the time scale most relevant to the Ecological Constraints model, red colobus were recorded to eat from an average of two species of trees and as many as eight species per quadrat on a given day. Note that these are conservative estimates because they were derived from data extracted from a larger dataset. In other words, they fed in multiple tree species within each quadrat on the same day.

Finally, those red colobus monkeys that were individually recognizable rarely ate the same food item from two individual trees of the same food species within the same hour. In contrast, animals whose foods do occur in obvious patches often do eat the same food item from successive individuals of the same tree species, and may pass through other trees to get to them. For example, spider monkeys in Santa Rosa, Costa Rica, traveled for an average of 13 min to get to each of four or five individual trees of *Slonea terniflora*, on which they fed in succession (Chapman, 1988; Chapman et al., 1995).

The image that emerges for red colobus is that, rather than having a home range with discrete patches of food trees, the study group's home range consisted of a mega-patch of many food trees with connected canopies nearly as large as the home range itself.

The absence of a group size effect on DTD in this study was likely facilitated by the ability of red colobus to take advantage of a wide variety of tree species, as exemplified by their consumption of *Trema*, a short-lived colonizing species that appears after logging (Struhsaker, 1997). During my study, *Trema* occurred at a fairly high density in K14, and mature leaves of *Trema* were the B group's single most frequently eaten species-specific food item. By 1997, however, *Trema* had disappeared from transect enumerations in K14 (Chapman et al., 1997). *Trema* was never common in K30, and Struhsaker (1997: 112) even considered it unimportant in primate diets unless no other choices were available. Struhsaker (2010: 198–199) describes additional examples of 'new' food tree species, and points out that multiple years of observations are required to obtain a full representation of red colobus diets.

The eclecticism of red colobus diets also undoubtedly reduces patchiness. In this study, the group ate 125 species-specific food items from 60 plant species. Red colobus dietary breadth is similarly revealed by a study in which

268 species-specific food items from 95 tree species among nine red colobus groups with overlapping home ranges were recorded (Snaith & Chapman, 2008). Collectively, these groups had a much broader diet over two months than the present 18-month study of a single group. In comparison, sympatric and equally folivorous black-and-white colobus monkeys have a much narrower range of food tree species and food items (Struhsaker & Oates, 1975; Rode et al., 2003) and as a result, may be more likely to feed in discrete patches. Indeed, at certain times of the year, a large portion of their diet comes from just two tree species (Harris et al., 2010).

Red colobus monkeys are so diverse in what they eat that groups with extensively overlapping home ranges can even have different food preferences unrelated to food density (Chapman et al., 2002). Group-specific preferences for certain foods among the many available suggest a kind of 'food culture' that could help partition resources among multiple groups and encourage their generally peaceful co-existence. Milton (1991) found similar group-specific food preferences among indigenous humans in the Amazon basin, but in that case, groups remained hostile to each other.

The movements of the B group as a whole also suggest that their foods were not typically patchy. Animals that move in a linear, goal-directed manner often move toward specific, patchily distributed resources (Milton, 1980, 2000; Pochron, 2001; Noser & Byrne, 2007, 2010; Beisner & Isbell, 2009). With low linearity, the movements of the study group did not resemble highly goal-directed paths, either daily or monthly, with informative exceptions. It was only when they fed on rarer foods at the periphery of their home range that they moved in a linear, goal-directed way, as if those foods were indeed patchy. Even so, the movements occurred not within a day but over five days. Thus, on multiple space and time scales the red colobus study group did not behave as if its food trees were patchily distributed.

When food trees are more uniformly distributed in space and time, animals in groups have many more paths to move along and may be able to minimize following in the paths of others. This should allow groups to move forward more as a broad front rather than in file formation and so may enable larger groups to avoid traveling farther than smaller groups (Isbell, 1991). On most days the red colobus study group moved forward in a broad front using multiple paths, likely facilitated by their widespread and very diverse diet. A later study (Gillespie & Chapman, 2001) also noted that a larger group of red colobus had a wider group spread than a smaller group, revealing that

even during more recent times Kibale red colobus groups are not prevented from spreading out. Patas monkeys provide another example of primates using this kind of forward movement: group spread is wider in larger groups but DTD is not longer (Chism & Rowell, 1988). The Ecological Constraints model is not applicable to species whose groups can spread out (Gillespie & Chapman, 2001).

This study does not challenge the main premise of the Ecological Constraints model that group size is often constrained by the energetic costs of travel. It does question more rapid patch depletion as the underlying mechanism causing larger groups to move farther than smaller groups. Food depletion in the vicinity of a group can occur independently of the demonstration that the food resource is patchily distributed. Larger groups will invariably consume the same amount of food faster than smaller groups whether groups feed in patches or on more uniformly distributed foods. However, patchily distributed foods are more likely than uniformly distributed foods to cause spatial compression, or funneling, and I suggest that funneling, not depletion, is the actual mechanism driving longer DTDs in larger, cohesive groups.

4.4. Funneling as an alternative mechanism for group size-adjusted DTD

Normally, the extensive canopy and its multiple travel paths allow red colobus groups in Kibale to move in a swath-like manner. On days when the B group approached the logging tracks, however, group members compressed from a broad front into a file formation in which they funneled largely into a single-file line as they leapt (see also Gillespie & Chapman, 2001). On these days DTD increased 14–18%. Because group members used the same few points of departure and arrival, the animals in front were forced to move forward because not all group members could occupy the same place at the same time. The consequences for individuals who do not move forward when others come from behind is exemplified in the extreme by human stampedes that may occur when crowds attempt to pass through narrow passageways such as bridges, doors and staircases. For example, in 2009, too many spectators attempting to squeeze into the Houphouet-Boigny arena in Côte d'Ivoire resulted in the deaths of at least 22 people (British Broadcasting Corporation, 2009).

Other spatial bottlenecks might include stream and river crossings, water points, forest gaps, limited, narrow arboreal pathways, and patchily distributed food trees. Even in a patchy food environment, however, funneling

can be avoided if the routes and targets are diverse, as can occur when dietary diversity is high. Thus, a group of Kibale red colobus that ranged in a very heavily logged compartment with a severely broken canopy often split up into subgroups that took multiple paths to multiple widely separated food trees (Skorupa, 1988; LAI, pers. obs.). Their mean DTD was similar to that of other groups (Struhsaker & Leland, 1987).

Repeated funneling into a limited number of trees is suggested here to be the fundamental mechanism behind group size-adjusted DTD. When cohesive groups attempt to enter a limited number of patchily distributed trees, e.g., fruiting trees, funneling may occur as the group compresses into the trees. Larger groups that travel to a small number of patchily distributed trees are expected to fill trees of a given size faster than smaller groups. First arrivers in larger groups might respond by moving forward farther and earlier than first arrivers in smaller groups because there are more individuals coming from behind. This response might be independent of whether or not they have depleted foods, or have been sated, or indeed, have eaten anything at all. Importantly, it may appear as if foods are being depleted if animals spend less time in smaller trees when more animals are present in those trees, and if food intake rate slows while movement increases within trees (Snaith & Chapman, 2005), but the same responses would be expected from funneling. Patch depletion vs. funneling could be tested by comparing the duration of time that individuals in larger groups, regardless of their activities, are able to stay in one place in trees of a given size as additional animals enter the trees. Funneling as a mechanism would be supported if individuals in larger groups shorten the time others in their groups are able to stay in one place even when they are not eating.

Note that although funneling forces others to move forward, it is different from the 'pushing forward' mechanism proposed by van Schaik and colleagues (1983) (see also Chapman & Chapman, 2000a). They proposed that the need to avoid overlap of search fields while feeding underlies their 'pushing forward' mechanism for longer DTD. Funneling, by contrast, simply involves constraints on physical space that can be independent of food.

In conclusion, understanding the determinants of DTD in groups of different sizes is not straightforward because the same behavior can generate more than one inference. This study suggests that several presumed behavioral indicators of scramble competition for food, including longer daily travel distance in larger groups, the most widely acknowledged one, may actually

indicate something else. The challenge for the future is to devise tests that distinguish behavior driven by food competition from those driven by social factors unrelated to food and by structural features of the habitat that could influence the movements of members of groups.

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