Activity and Ranging Patterns of Guerezas in the Kakamega Forest: Intergroup Variation and Implications for Intragroup Feeding Competition

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From March 1997 to February 1998, I investigated the activity patterns of 2 groups and the ranging patterns of 5 groups of eastern black-and-white colobus (Colobus guereza), *aka guerezas, in the Kakamega Forest, Kenya. Guerezas at Kakamega spent more of their time resting than any other population of colobine monkeys studied to date. In addition, I recorded not one instance of intragroup aggression in 16,710 activity scan samples, providing preliminary evidence that intragroup contest competition may be rare or absent among guerezas at Kakamega. Mean daily path lengths ranged from 450 to 734 m, and home range area ranged from 12 to 20 ha, though home range area may have been underestimated for several of the study groups. Home range overlap was extensive with 49–83% of each group's range overlapped by the ranges of other groups. Despite the high level of home range overlap, the frequently entered areas (quadrats entered on ≥30% of a group's total study days) of any one group were not frequently entered by any other study group. Mean daily path length is not significantly correlated with levels of availability or consumption of any plant part item. Mean daily path length is also not significantly correlated with group size, though the largest group did have the longest mean daily path length. This finding suggests that intragroup scramble competition may have been rare or absent among guerezas at Kakamega except perhaps in the largest group, which was unusually large.*

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INTRODUCTION

Primates exhibit wide interspecific variation in activity and ranging patterns. Some species adopt a strategy of energy conservation, travelling short distances each day, spending most of the day resting and feeding on relatively ubiquitous food items (e.g., *Alouatta palliata*: Milton, 1980; *Colobus guereza*: Oates, 1977a; *Trachypithecus pileatus*: Stanford, 1991). Other species spend much of their time foraging while travelling over long distances each day and subsisting on patchy, high quality food sources (e.g., *Cercopithecus ascanius*: Cords, 1987; *Lagothrix lagotricha*: Defler, 1996; *Pan troglodytes*: Wrangham, 1977).

Even within species, considerable variation in ranging patterns may exist between groups at different sites (Oates, 1977a; Richard, 1977; Crockett and Eisenberg, 1986) or at a single site (Waser, 1977; van Schaik *et al*., 1983; O'Brien and Kinnaird, 1997; Curtis and Zaramody, 1998; Gathua, 2000). Primate ranging patterns are influenced by a variety of ecological and behavioral factors, including rainfall patterns (Raemakers, 1980; McKey and Waterman, 1982; Isbell, 1983; Olupot *et al*., 1997), food availability, distribution and quality (Clutton-Brock, 1975; Milton, 1980; Raemakers, 1980; Marsh, 1981; Curtin, 1982; McKey and Waterman, 1982; Harrison, 1983; Bennett, 1986; Boinski, 1987; Nunes, 1995; Zhang, 1995; Olupot *et al*., 1997), water availability (Altmann and Altmann, 1970; Chapman, 1988), group size (Waser, 1977; van Schaik *et al*., 1983; de Ruiter, 1986; Ostro *et al*., 1999), reproductive situation (Rasmussen, 1979; Overdorff, 1993), sleeping site or resting site location (Rasmussen, 1979; Sigg and Stolba, 1981; Harrison, 1983), intergroup relationships (Struhsaker, 1974; Curtin, 1980; Harrison, 1983; Isbell, 1983; Kinnaird, 1992), and parasite avoidance (Freeland, 1976; Hausfater and Meade, 1982).

The ranging behavior of colobine monkeys has been studied extensively at many locations, e.g. by Struhsaker (1974), Oates (1977), Marsh (1981), McKey and Waterman (1982), Bennett (1986), Olson (1986), Stanford (1991), Bocian (1997), Kirkpatrick *et al*. (1998), Fleury *et al*. (1999), and Boonratana (2000). Most studies show that colobines have shorter daily travel distances and smaller home ranges than most other primates (Clutton-Brock and Harvey, 1977; Chapman and Chapman, 2000). These ranging patterns may be related to (1) energetic constraints placed on colobines by their specialized digestive tracts and relatively folivorous diets, and (2) the relative ubiquity of potential colobine food sources.

Because colobines appear more capable than most other primates of subsisting on the most common plant items and species in their habitats (Oates, 1977a; Chapman and Chapman, 1999), they may also be buffered to some extent against intragroup feeding competition. Investigations of primate ranging behavior provide one way to assess whether competition over food is occurring within groups (van Schaik 1989; Isbell 1991a; Chapman and Chapman, 2000). In several noncolobine species, daily path lengths increase significantly with increasing group size (*Macaca fascicularis*: van Schaik *et al.*, 1983; *Cebus olivaceous*: de Ruiter, 1986; *Alouatta pigra*: Ostro *et al.*, 1999). This pattern may indicate intragroup scramble competition for food (Isbell, 1991a; Sterck *et al.*, 1997; Chapman and Chapman, 2000). Less is known about scramble competition within groups of colobine monkeys because most prior studies were focused on a single study group (Struhsaker, 1974; Oates, 1977a; Marsh, 1981; McKey and Waterman, 1982; Olson, 1986; Bocian, 1997). Struhsaker and Leland (1987) demonstrated that mean daily path length is not significantly correlated with group size in 9 groups of *Procolobus badius*, though they were studied at different times over a 12-year period. Recent research on *Presbytis thomasi* by Sterck (1995) and Steenbeek (1999) included enough groups studied simultaneously at a single site (Ketambe, Indonesia) to evaluate whether intragroup scramble competition was occurring. They found that daily path length increased with increasing group size, suggesting that there is some level of intragroup scramble competition in *Presbytis thomasi* at Ketambe.

The other form of competition that occurs within some primate groups is contest competition (van Schaik, 1989), though it probably is not as important in colobines as it is in other primates (van Schaik, 1989; Sterck and Steenbeek, 1997). Although intragroup contest competition occurs in *Presbytis thomasi* (Sterck and Steenbeek, 1997), because rates of intragroup aggression are low and dominance hierarchies are weak or absent in several other colobines (Stanford, 1991; Cheney, 1992), intragroup contest competition may be rare or absent in many colobines. The apparent rarity of intragroup contest competition in colobines may be related to the presumed abundance and even distribution of food resources exploited by colobines versus those of other primates.

I conducted a one-year study of the activity and ranging patterns of eastern black-and-white colobus (aka guerezas), *Colobus guereza,* in the Kakamega Forest, Kenya. I sought (1) to describe the activity budgets of Kakamega guerezas and to compare them to those of colobines at other sites, (2) to determine the ecological and behavioral variables that affect guereza ranging patterns at Kakamega, and (3) to determine the extent to which intragroup scramble competition, intragroup contest competition, or both are occurring in Kakamega guereza groups.

METHODS

Study Site and Study Groups

I conducted research on guereza activity budgets and ranging patterns at Isecheno field site in the Kakamega Forest of western Kenya [0°19′N; 34°52′E; Elev. 1580m]. The study area covers approximately 2 km² (Cords, 1987) and is part of a forest block that was last estimated to be 86 km² in size (Brooks *et al.*, 1999). After three periods of preliminary research (July 1993, November–December 1995, November 1996–February 1997), I collected the data presented in this paper from March 1997–February 1998. Over the course of the study, I observed guerezas at Isecheno for more than 3,000 hours.

Research on time budgets focused on 2 study groups, T and O, while research on ranging patterns focused on 5 study groups, T, O, GC, ML, and BS. Group sizes and compositions are detailed in Table I.

Data Collection

Activity Budgets

I collected activity budget data on 5 consecutive study days each month for T and O groups. Five-day samples for T group began between the 1st and 4th of each month, while 5-day samples for O group began between the 14th and 18th of each month. During 5-day samples, I conducted activity scan samples of 5 min duration every 15 min from dawn-to-dusk. I recorded data for the first 6 adults or juveniles and all infants ≥2 mo old seen at the time of each scan (Fashing, 1999).

Adults were monkeys that had reached full size and that appeared to have reached reproductive maturity. Subadult males were at least equal in body size to adult females but smaller than adult males in body size, testicular size, or both. Juveniles were not yet adult size and were not carried by their mothers. Infants were small monkeys still being carried by their mothers. It was easy to tell the two sexes apart because, in addition to the obvious differences in genital morphology between them, only males had a large unbroken line of white hairs across the perineum.

The activity recorded for each individual during a scan sample was the first activity that it held for ≥3 sec once I had sighted her or him. This requirement prevented eye-catching, ephemeral activities from being over-represented in the data set.

I recorded rest, peer, move, feed, groom, greet, social play, and loco-motor play. Rest includes instances when a monkey was inactive, usually

Table I. Group size and composition for the 5 study groups (Note: the first and last numbers in the ranges of group size and group composition do not necessarily represent the values for the first and last months of the study.)

Group	Study period	Group size		Group composition				
		Mean	Range	Adult males	Adult females	Subadult males	Juveniles	Infants
T	11/96–3/98	11	10–13	1–4[a]	5	0	3–4	0–4
O	11/96–3/98	7	5–8	1	3	0	0–1	1–3
GC	3/97–3/98	10	10–11	1	3	0	4	2–3
ML	4/97–3/98	15	13–16	2–3[b]	3–4	1	4–5	3–4
BS[c]	6/97–3/98	21	19–23	3–6	4	1–3	6–9	0–2

[a] T-group became a 1-male group in 5/97 and remained so to the end of the study period.
[b] ML-group had 2 adult males during most of the study period.
[c] BS-group may have been slightly larger than reported here since it was often difficult to make complete counts of them.

while sitting or lying down. Vigilant includes instances when a monkey sat and peered intensely in a certain direction. Move includes any locomotor behavior, including walking or running, that resulted in a monkey changing its spatial position. Feed includes instances when a monkey plucked food items, pulled food items towards the mouth, masticated, and swallowed. Groom includes instances in which one monkey used its hands to explore or to clean the body of another monkey. Greet includes instances in which one monkey approached another monkey and placed its abdomen and genitals in its face while draping its own body over the back of the other monkey. This behavior is probably equivalent to that described by Oates (1977b) as a non-sexual mount, over-the-head. Social play includes chasing, hitting, wrestling and other vigorous activities involving exaggerated movements and gestures by ≥ 2 monkeys that were clearly interacting with each other in a nonaggressive manner. Locomotor play includes instances when a monkey moved about solitarily using exaggerated movement patterns or gestures not normally seen during regular locomotion. Although never observed during scan samples, aggression includes instances when a monkey chased, bit, grabbed, supplanted, or threatened another monkey.

Ranging Patterns

I estimated and plotted the center of mass (Cords, 1987; Butynski, 1990) of each study group, and the patterns of movement between consecutive centers of mass, at half-hourly intervals on a map of the study site created by M. Cords in 1989. It was easy to estimate center of mass since group spread was generally small (Fashing and Cords, 2000). I measured distances between centers of mass for consecutive half-hourly intervals along the route taken by the majority of group members. If the route between two consecutive center of mass locations was not noted, I considered the shortest distance between the two points to be the route taken by the monkeys.

I mapped ranging patterns on 59 days for T group, 60 days for O group, 23 days for GC group, 21 days for ML group, and 22 days for BS group. For T and O groups, I usually began follows around dawn (0600–0645 h depending on the time of year), while for GC, ML, and BS groups, I usually began follows between 0730 and 0830 h. I took afternoon breaks of 0.5–1.5 h on most of the days when groups GC, BS, and ML were followed. They usually began in the early to mid-afternoon at a time when a group did not appear likely to move soon. The routes the groups followed during these breaks were sometimes described to me by one of my research assistants. Otherwise, I measured the shortest distance between where a group was left before the break and where it was found after the break, and considered that to be

the distance traveled. Follows of all 5 groups concluded around dusk (1830–1915 h depending on the time of year).

At the end of the study, I remeasured the trails at Isecheno with a tape measure and created an updated version of Cords' 1989 map, which I used to analyze all ranging data collected during the study. I analyzed daily path length data in two ways. First, I calculated an adjusted daily path length (ADPL) by adding the shortest straight line distance between a group's sleeping site the night before and its location at 0830 h to the distance the group traveled during the remainder of the day. Since ADPL controlled for the fact that follows of different groups began at different times, it could be used to compare ranging patterns between groups. Secondly, I calculated an unadjusted daily path length (UDPL) by adding the distances traveled during all observed group movements, including those before 0830 h, to the shortest distances between centers of mass for any group movements that were missed during the day. Although not as useful for comparing ranging patterns between groups, UDPL provides a larger, more accurate estimate of daily path length for each group than ADPL.

To investigate differential use of each group's home range, I superimposed a grid of 50×50-m quadrats over daily ranging maps and noted the quadrats utilized and the number of quadrats entered each day. On several occasions, groups left the trail system and were soon lost for several hours. On these occasions, groups almost certainly entered new quadrats that were never noted. Therefore, the estimates of daily path length and home range size that I report below are probably slight underestimates of the actual values for at least some of the study groups.

I calculated home range overlap between groups based on the number of quadrats each group shared relative to the total number of quadrats each group entered. I calculated both a minimum known total home range overlap and a minimum suspected total home range overlap. Minimum known total home range overlap is the amount of overlap known to exist between a study group and all other groups in the forest. Minimum suspected total home range overlap is the amount of overlap believed to exist between a study group and all other groups in the forest based on both known areas of overlap and other areas where strong circumstantial evidence suggests there should be overlap. Quadrats of suspected overlap tended to be on the home range periphery and were rarely entered by a study group and thus not regularly monitored. These quadrats almost certainly supported unstudied guereza groups that were sometimes observed nearby. Thus, the values for suspected total home range overlap probably better approximate the actual amount of home range overlap for each group than values for known total home range overlap.

Group Progressions

Preliminary observations revealed that group movements, especially in smaller groups, commonly consisted of single-file progressions with one individual clearly in the lead. Therefore, I identified and noted the identity, or at least the age/sex class, of the leader of as many progressions as possible. Though leadership of a progression sometimes changed during an individual progression, I considered the individual first noted in the lead to be the leader of the progression.

RESULTS

Activity Budgets

Table II is a comparison of the activity budgets of groups T and O. Both groups spent most of their time resting and little time moving. T-group spent more time feeding than O-group did, while O-group spent more time playing, moving, and grooming than T-group did.

Figure 1 is a comparison of activity budgets between members of different age/sex classes for both study groups. Adult females spent slightly more time resting than adult males did in T-group, while the adult male spent much more time resting than the adult females did in O-group.

Adult males were by far the most vigilant members of both groups. They were, however, rarely involved in grooming in either group. Adult females were the group members most commonly involved in grooming in O-group, while adult females and juveniles groomed relatively equal amounts in T-group. The juveniles most often involved in grooming were females.

T-group had 4 infants ≥2 months old by the end of the study, but activity data on them are too sparse to be included in Figure 1. Conversely, activity

Table II. Activity budgets of groups T and O (in terms of percentage of total activity samples). T-group: n = 7793; O-group: n = 8917

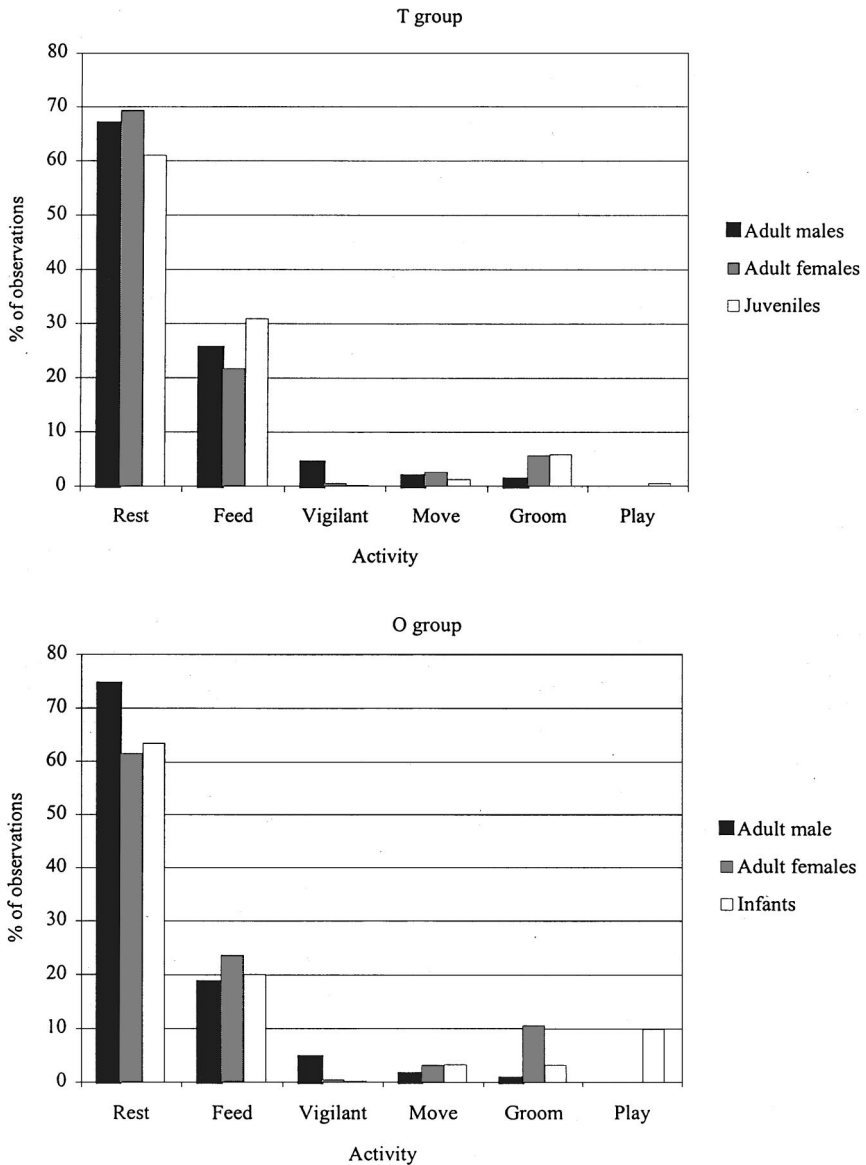| Activity	T	O
Rest	63.2	63.5
Vigilant	0.8	1.1
Feed	28.3	22.9
Move	1.8	2.8
Groom	5.6	6.7
Greet	0.1	0.0
Social Play	0.2	1.6
Locomotor Play	0.0	1.4

Fig. 1. Differences between age/sex classes in time spent on different activities within T- and O-groups. [T-group: 1–2 adult males (n = 854), 5 adult females (n = 2459), and 3–4 juveniles (n = 1304)—Note: 5 infants were born (though one disappeared after 2 mo) in T-group between June–November 1997, but too few data were collected on infant activities to be included in this figure; O-group: 1 adult male (n = 1468), 3 adult females (n = 4124), and 1–4 infants (n = 2727)—Note: 1 infant became a small juvenile during the study but is considered an infant for the purposes of this analysis].

data for infants in O-group were relatively easy to collect and are included in Figure 1. The greater amount of time spent playing by members of O-group can be attributed to the fact that virtually all play involved infants.

Neither group had even one incidence of aggression in 16,710 total scans. I occasionally observed instances of intragroup aggression outside of scan samples. Although this aggression was not carefully quantified, it appeared to occur at very low rates except during intergroup encounters, when adult males often directed flashy leaps towards other members of their own group (Fashing, in press). Intragroup aggression over food patches occurred several times in small, but common food patches, such as vines of *Piper guineense* where only 1 or 2 individuals could feed simultaneously.

Ranging Patterns

Daily Path Length

The five study groups varied significantly in mean unadjusted daily path length, ranging from 450 m in T-group to 734 m in BS-group (Table III; Kruskal-Wallis: $H = 39.7$; $p < .0001$). Mean adjusted daily path length was also significantly different between groups ($H = 41.2$; $p < .0001$), ranging from 434 m in T-group to 708 m in BS-group. The shortest single day journey was made by T-group on October 7, 1997, when they traveled only 166 m, while the longest single day journey was made by BS-group on January 28, 1998, when they traveled ≥ 1360 m.

Mean daily path length is not significantly correlated with either group size ($r_s = .100$, $p = .842$) or group biomass ($r_s = .100$, $p = .842$), though the power of the tests is low given the small sample size, i.e., 5 groups. The largest group, BS, had the longest mean daily path length, but the smallest group, O, had the second longest mean daily path length. The group with by far the shortest daily path length, T-group, was the third largest group.

Table III. Unadjusted (UDPL) and adjusted (ADPL) daily path lengths (m) for the 5 study groups

Group	Study days	Mean ± S.E. UDPL	Range	Mean ± S.E. ADPL	Range
T	59	450 ± 33	166–1358	434 ± 32	166–1300
O	60	625 ± 26	218–1162	614 ± 26	214–1166
GC	23	565 ± 62	200–1242	552 ± 58	200–1150
ML	21	564 ± 29	350–866	551 ± 29	303–821
BS	22	734 ± 51	260–>1360	708 ± 49	250–1314

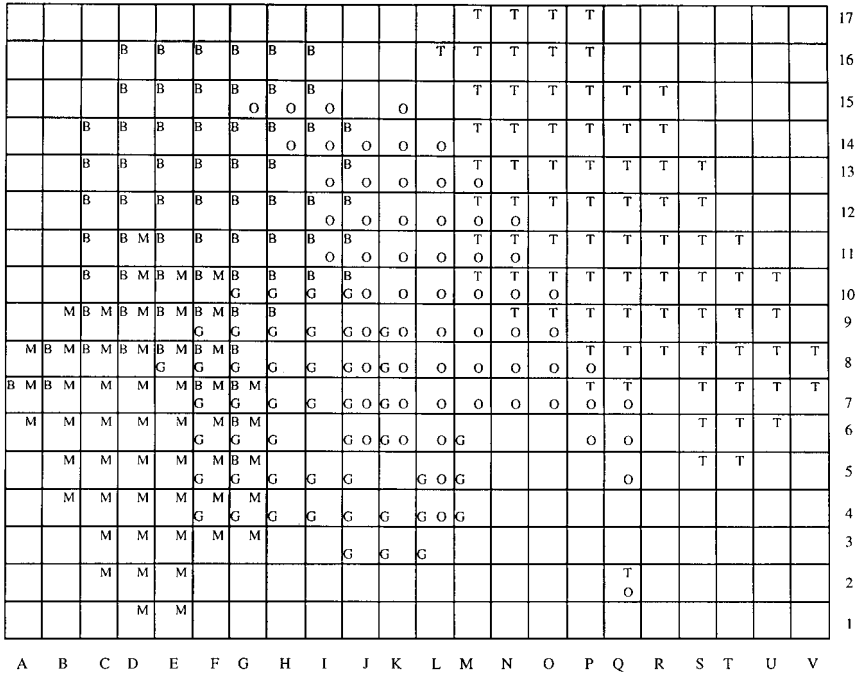|	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	
17														T	T	T	T						
16			B	B	B	B	B	B					T	T	T	T	T						
15			B	B	B,O	B,O	B,O	B	O					T	T	T	T	T	T				
14		B	B	B	B	B	B,O	B,O	B,O	O	O			T	T	T	T	T	T				
13		B	B	B	B	B	B,O	B	B,O	O	O	O	T,O	T	T	T	T	T	T				
12		B	B	B	B	B	B,O	O	O	O	O	O	T,O	T,O	T	T	T	T	T				
11		B	B,M	B	B	B	B	B,O	B,O	O	O	O	T,O	T,O	T	T	T	T	T	T			
10		M,B	M,B	M,B	M,B	M,B	B,G	B,G	B,G	G,O	O	O	O	T	T,O	T	T	T	T	T	T		
9	M,B	M,B	M,B	M,B	M,B	B,G	B,G	G	O	O	O	O	O	O	T,O	T	T	T	T	T	T		
8	M,B	M,B	M,B	M,B	M,B	M,B	B,G	B,G	G	G	O	O	G,O	O	O	O	T,O	T	T	T	T	T	
7	B,M	B,M	M	M	M,B	M,B	B,G	B,G	G	G	O	O	G,O	O	O	O	T,O	T,O	T	T	T	T	
6	M	M	M	M	M,B	M,B	G	G	G	O	O	G,O	O,G			O	O		T	T	T		
5	M	M	M	M	M,B	M,B	G	G	G	G	G	G,O	O,G				O			T	T		
4	M	M	M	M	M,B	M	G	G	G	G	G	G,O	O,G										
3	M	M	M	M	M		G	G	G														
2	M	M	M														T,O						
1	M	M																					

Fig. 2. Home range overlap among the 5 study groups. (Note: borders on this figure do not represent the borders of the forest).

Home Range Size

Figure 2 represents a 50 × 50-m grid of the quadrats entered by groups T, O, GC, ML, and BS. T-group entered a total of 79 0.25-ha quadrats on 59 study days, O-group entered 62 quadrats on 60 study days, GC-group entered 48 quadrats on 23 study days, ML-group entered 51 quadrats on 21 study days, and BS-group entered 69 quadrats on 22 study days. In addition to the quadrats known to have been entered by groups T and O, I infer that both groups must have entered ≥ 2 additional quadrats in order to reach quadrat Q2. Accordingly, I estimated home range sizes to be 19.75 (or 20.25) ha for T-group, 15.50 (or 16.00) ha for O-group, 12.00 ha for GC-group, 12.75 ha for ML-group, and 17.25 ha for BS-group. When I plotted increases in home range size estimates over time, home range sizes appeared to reach asymptotes for groups T, O, and BS 55–80% of the way through the study, while home range sizes never appeared to reach asymptotes for groups GC and ML (Fashing, 1999). Furthermore, BS-group entered 8 quadrats (2 ha) during unsystematic observations that they did not enter during systematic follows,

demonstrating that their home range size was not fully estimated during systematic observations. These findings suggest that home range size was fully estimated only for T and O, the two groups studied most intensively.

Home Range Overlap

Figure 2 also shows the pattern of home range overlap among the 5 study groups by indicating the 0.25-ha quadrats used by each group during systematic observations. Range overlap among the 5 study groups varied considerably between dyads. Four dyads had no range overlap because their ranges were not adjacent to each other while BS-group used ≥37% of ML-group's range.

Minimum known total home range overlap with all other groups in the forest is 61% for T-group, 83% for O-group, 73% for GC-group, 49% for ML-group and 69% for BS-group. Minimum suspected total home range overlap with all other groups in the forest is 90% for T-group, 87% for O-group, 78% for GC-group, 53% for ML-group, and 77% for BS-group.

Patterns of Home Range Use

Each group had a series of (usually) contiguous quadrats within its range that it entered frequently (Figure 3). I defined quadrats of frequent use as ones that the group entered on ≥30% of all study days. Only 9% of the quadrats in T-group's range were frequently used, while 25% of the quadrats in GC-group's range, 26% of the quadrats in O-group's range, 33% of the quadrats in ML-group's range, and 35% of the quadrats in BS-group's range were frequently used. Figure 3 also shows that of the 76 frequently-used quadrats occupied by the 5 groups, none was frequently used by >1 group.

Correlates of Ranging Behavior

Table IV.A shows Spearman rank correlations for groups T and O between variables related to ranging and variables related to diet, rainfall and intergroup encounters—occasions when ≥2 groups were ≤50 m from each other—for the pooled 12-mo samples. Dietary, rainfall, and intergroup encounter data used in this analysis are from Fashing (1999). No significant correlation exists between any of the ranging variables and any of the dietary variables for both groups. There is also no significant correlation between any of the ranging variables and rainfall patterns and intergroup encounters
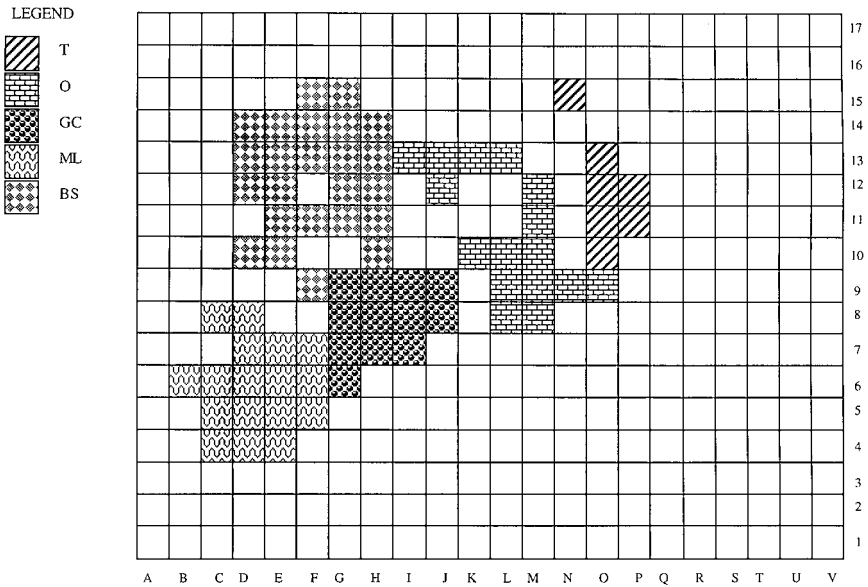
Fig. 3. Areas of frequent use (quadrats entered on ≥30% of study days) for the 5 study groups. (Note: borders on this figure do not represent the borders of the forest).

for both groups. Significance level was reduced for these correlations via the Bonferroni correction for multiple tests on the same variable (Sokal and Rohlf, 1995).

Because ranging behavior, diet, weather and frequency of intergroup encounters vary considerably from day to day, it may be misleading to perform statistical analyses on the monthly mean for each variable. Instead, it may be more appropriate to analyze the relationship between these variables with each day as an independent data point. Accordingly, I performed Spearman rank correlations between ranging variables and dietary and intergroup encounter-related variables on the 59 days of data for T-group and the 60 days of data for O-group. The results of the correlations are in Table IV.B. Again, significance levels were reduced via the Bonferroni correction (Sokal and Rohlf, 1995).

For T-group, there is a positive, though not significant ($p = 0.051$), association between daily path length and number of intergroup encounters per day involving T-group. For O-group, there is a significant positive correlation between daily path length and number of intergroup encounters per day. There is also a significant correlation for O-group between the number of quadrats entered per day and the number of intergroup encounters per day.

Table IV. Spearman correlations between ranging and ecological and behavioral variables. [Note: dietary, rainfall, and intergroup encounter data are taken from Fashing (1999)]; DPL = daily path length; Mean no. Q = mean number of quadrats used per day; Area used = area used per month; ylvs = young leaves in diet; mlvs = mature leaves in diet; No. IEs = number of intergroup encounters; * $p < 0.05$; † $p < 0.10$; ^{f} $p < 0.01$; correlation coefficients that are statistically significant after applying the Bonferroni correction for multiple tests on the same variable are underlined (Sokal and Rohlf, 1995)

A. Monthly correlations based on pooled data from 5-day samples on T-and O-groups (Note: there were only 4 days in the March 1997 sample for T-group). The Bonferroni correction sets statistical significance at $p < 0.00625$ for these correlations (Sokal and Rohlf, 1995)

	Fruit in diet		Fruit avail.		YL in diet		YL avail.		ML in diet		ML avail.		No. IEs		Rainfall	
	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O
Mean DPL	.245	−.112	.357	.112	.389	.056	.329	−.140	.000	−.077	−.601†	.217	.687†	−.047	−.028	−.524*
Mean no. Q	.315	−.249	.508*	−.088	.435	.190	.182	−.222	.088	.074	−.441	.201	.703†	.366	−.014	−.413
Area used	.245	−.343	.580*	−.193	.399	−.432	.063	−.492	.014	.682†	−.245	.443	.616†	.295	−.056	−.239

B. Daily correlations based on 59 all-day follows for T-group and 60 all-day follows for O-group. (Note: data on daily patterns of rainfall and food availability were not collected) at $p < 0.013$ for these correlations (Sokal and Rohlf, 1995). The Bonferroni correction sets statistical significance

	Fruit in diet		YL in diet		ML in diet		No. IEs	
	T	O	T	O	T	O	T	O
DPL	.071	.098	.101	−.152	−.036	−.144	.256*	.365^f
No. Q	.046	.001	.154	−.158	−.031	−.040	.212	.411^f

Group Progressions

Table V shows that group progressions were most often led by adult females in 4 of the 5 study groups (T, O, GC, and BS), though sample sizes are small for all groups except O-group. Despite the fact that adult females usually led progressions in most groups, the number of progressions led per adult female was actually lower than the number led per adult male in 3 groups (T, O, and ML).

Sufficient data were available to examine group progressions at the individual level in O group (Figure 4), in which one adult female, D'arcy, led ≥77% of the progressions led by adult females and ≥54% of all progressions. The adult male, Oliver, was the second most likely group member to lead progressions, and the other two adult females, Saffron and Veruca Salt, only rarely led progressions. Differences between the 4 adults in the number of progressions led by each are significant (G test, df = 3, p < .0001). Infants never led progressions.

In GC-group, an individual adult female, Harriet, led >50% (6 of 11) of the group's progressions. Therefore, in both groups in which all group

Table V. Age/sex classes of progression leaders in the 5 study groups

Group	Age/sex class	Progressions led	Number of individuals in group between March 1997–February 1998*
T	Adult females	13	5
T	Adult males	7	1–2
T	Juvenile males	4	1
T	Juvenile females	0	2–3
T	Infants	0	0–4
O	Adult females	66	3
O	Adult males	29	1
O	Infants	0	3–4
GC	Adult females	7	3
GC	Adult males	1	1
GC	Juvenile males	3	4
GC	Infants	0	2
ML	Adult females	3	4
ML	Adult males	5	2–3
ML	Subadult males	0	1
ML	Juveniles	1	4–5
ML	Infants	0	3–4
BS	Adult females	5	4
BS	Adult males	0	3–6
BS	Subadults or juveniles	1	10–11
BS	Infants	0	0–2

*Group composition data are only available for BS-group for the period of June 1997–February 1998, and even during this period, some individuals may have been missed.
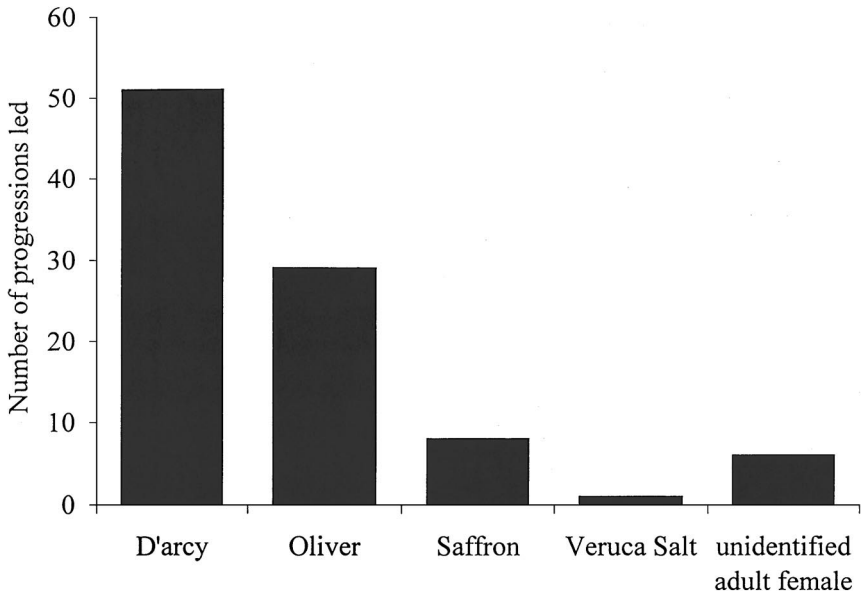
Fig. 4. Number of group progressions (n = 95) led by each adult in O-group between March 1997–February 1998. (Note: Oliver is an adult male; D'arcy, Saffron, and Veruca Salt are adult females; unidentified adult female refers to either D'arcy, Saffron, or Veruca Salt on those occasions when individual identity could not be determined.

members were individually recognized, O and GC, an individual adult female led >50% of group progressions.

DISCUSSION

Activity Budgets

At all three sites where they have been studied extensively (Kibale Forest, Uganda: Oates, 1977b; Ituri Forest, D.R. Congo: Bocian, 1997; Kakamega Forest, Kenya), guerezas spend ≥50% of the time resting. In fact, with both study groups spending ≥63% of the time resting, guerezas at Kakamega are the least active colobines for which time budget data are available (Clutton-Brock, 1974; Struhsaker, 1975; Oates, 1977b; Marsh, 1981; McKey and Waterman, 1982; Stanford, 1991; Starin, 1991; Newton, 1992; Dasilva, 1993; Decker, 1994; Gupta and Kumar, 1994; Fuentes, 1996; Bocian, 1997; McGraw, 1998). Dasilva (1992, 1993) provided evidence that the relatively high levels of inactivity in *Colobus polykomos* on Tiwai Island, Sierra

Leone (59% of time resting), could be attributed to a strategy of behavioral thermoregulation. The tendencies of *Colobus guereza* at Kibale and Kakamega to lead inactive lifestyles, sunbathe in the canopy during the cool early morning, and hunch over during rainstorms (Oates, 1977b; Fashing, personal observation), suggest that guerezas may also engage in behavioral thermoregulation, though more quantitative data like those collected by Dasilva (1992, 1993) are necessary to properly test this hypothesis.

Intersite Variation in Daily Path Length

Guerezas at Kakamega proved to be considerably more frugivorous than those at Kibale and Ituri (Fashing, 2001). Despite this greater reliance on fruit, a resource usually assumed to be scarcer and more patchily distributed than leaves (Wrangham, 1980; Oates, 1987), guerezas at Kakamega did not travel further per day (mean = 588 m, n = 5 groups) to meet their dietary needs than the more folivorous guerezas at other sites (Kibale: 535 m, n = 1 group; Ituri: 609 m, n = 1 group). Most of the important fruit species—*Antiaris toxicaria, Trilepisium madagascariense (*syn. *Bosqueia phoberos), Ficus exasperata, Teclea nobilis*—in the diet of guerezas at Kakamega occurred at high stem densities and exhibited relatively strong within species synchrony in their fruiting patterns (Fashing, 2001), allowing groups to feed extensively on fruit without traveling long distances each day. For example, during the 5-day sample in November 1997, *Trilepisium madagascariense* had such a high fruit availability index that T-group was able to attain a diet composed of 81% fruit, while travelling an average of only 300 m per day.

Factors Influencing Black-and-White Colobus Monkey Ranging Patterns

Studies have revealed that patterns of home range use in *Colobus angolensis, C. polykomos*, and *C. satanas* vary in accordance with variation in primary food item availability. In contrast, there appears to be little or no relationship between patterns of home range use and variation in primary food item availability in *Colobus guereza.* For example, *Colobus satanas* at Douala-Edea, Cameroon, traveled shorter distances in times of primary food item (seed) abundance and longer distances during periods of primary food item scarcity (McKey and Waterman, 1982). Similarly, *Colobus angolensis* at Ituri Forest, D.R. Congo traveled further when their primary food item (young leaves) was scarce (Bocian, 1997).

Colobus polykomos on Tiwai Island, Sierra Leone, however, exhibited the opposite pattern. They increased daily path length and ranged over a larger area when primary food items (seeds and young leaves) were abundant. *Colobus satanas* at Makande, Gabon, also traveled furthest when seeds and fruits were abundant and least when seeds and fruits were rare (Fleury and Gautier-Hion, 1999). *Colobus satanas* at Lope, Gabon "used more of their range" when seeds were abundant, though it is unclear whether this means that they also increased their daily path length in times of seed abundance (Harrison pers. comm. cited in Oates, 1994:99).

As for *Colobus guereza,* Oates (1977a) concluded that neither primary food item (young leaves of *Celtis gomphophylla* [syn. *C. durandii*]) availability nor primary food item consumption influenced ranging patterns at Kibale, Uganda. Similarly, Bocian (1997:138) found that "*C. guereza* movements (at Ituri, D.R. Congo) were not associated with measures of food density or availability." Finally, I found that daily path lengths and quadrat use patterns of *Colobus guereza* did not vary significantly with either the availability or consumption of particular food items at Kakamega.

Despite temporal and spatial variation in the abundance of their primary food items, guerezas appear able to maintain their pattern of short daily travel distances throughout the year. Items that are infrequently eaten, but of great nutritional importance, may actually have more influence on guereza ranging patterns than general primary food item availability and consumption. For example, Kibale guereza groups made periodic journeys to a swamp where they fed on plants believed to be rich in minerals otherwise missing from the diet (Oates, 1978). While Oates's main study group (IV) lived near the swamp, another group (XIII) had to travel ≥ 800 m from its normal ranging area to reach the swamp.

Kakamega guerezas also occasionally made long journeys (≥ 600 m in each direction) to feed on an item—bark of *Eucalyptus* sp.—that was only rarely included in the diet. Because accessible eucalyptus trees were not available within the usual ranging areas of most of the study groups at Kakamega, these groups were forced to travel long distances to obtain the bark. The nutritional or medicinal benefits that guerezas acquire by consuming the bark of this exotic tree species are unknown.

A relationship also existed between ranging patterns and proximity to conspecific groups in one of the Kakamega guereza groups. In O-group, there is a significant correlation between the number of intergroup encounters engaged in per day and the number of quadrats entered per day. The relationship between these two variables may be related to the fact that by increasing the area over which it travels on a given day, a group also increases the area over which it can encounter other groups.

Home Range Size

Home range areas for all 5 Kakamega groups are considerably smaller than those reported for guereza groups at Kibale and Ituri. At Kakamega, home range sizes ranged from 12 to 20 ha (n = 48–79 50 × 50-m quadrats), while at Kibale and Ituri, home range sizes measured 32 ha (n = 128 50 × 50-m quadrats) and 100 ha (n = 64 125 × 125-m quadrats), respectively. These differences in home range size exhibit an inverse relationship with population density. Guereza population density is highest at Kakamega (150 individuals/km^2: Fashing and Cords, 2000), intermediate at Kibale (100 individuals/km^2: Oates, 1974), and lowest at Ituri (3 individuals/km^2: Bocian, 1997). Data from a fourth large forest block ($\geq$50 km^2) where guerezas have been studied, the Budongo Forest, Uganda, however, do not fit this pattern. Suzuki (1979) reported that guerezas at Budongo had a mean home range size of 14 ha and a population density of 49 individuals/km^2, but provided no information on his methods of data collection and analysis or on the number of hours he spent observing each of 25 groups.

When the results of studies of guerezas from small forests are also considered, the pattern becomes clearer. For the 9 guereza study sites for which values for both mean home range size and population density have been reported (Table VI), there is a significant negative correlation between mean home range size and population density ($r_s = -.891$, p = .008). This result is consistent with Dunbar's (1987) conclusion, based on a smaller data set, that mean home range size is inversely related to population density in guerezas. Further research on guereza behavior and ecology at Budongo might help to explain why Budongo guerezas fail to fit this general pattern.

Wide intraspecific variation in home range sizes between study sites also exists for the other 4 species of colobine monkeys whose ranging patterns have been studied extensively at >1 site (Table VII). For example, home range size for *Semnopithecus entellus* is >16 times larger at Junbesi, Nepal, than that at Kanha, India, while home range size for *Colobus satanas* is nearly 10 times larger at Makande, Gabon, than that at Douala-Edea, Cameroon. This large intersite variation in home range size for several well-studied species attests to the ecological flexibility of some colobine monkeys.

Home Range Overlap

Consistent with the results of an earlier 2-month study by von Hippel (1996), I found that home range overlap for Kakamega guereza groups was extensive (known total range overlap: $\overline{X} = 67 \pm$ S.D. 13%, n = 5; suspected total range overlap: $\overline{X} = 77 \pm$ S.D. 15%, n = 5). Despite this extensive home

Table VI. Population densities and home range sizes for the 4 large forest blocks ($\geq$50 km^2) and 5 small forest fragments ($\leq$10 km^2) at which home range size estimates have been made for guerezas. Home range sizes for guerezas at each site are based on data from 1 study group unless otherwise noted

Site	Forest size	Population density (ind/km^2)	Home range size (ha)	Reference
Ituri, D.R. Congo	Block	3	100.0	Bocian (1997)
Budongo, Uganda	Block	49	14.4[a]	Suzuki (1979)
Kibale, Uganda	Block	100	32.0	Oates (1977)
Lake Shalla, Ethiopia	Fragment	138	5.6[b]	Dunbar (1987)
Kakamega, Kenya	Block	150	18.1[c]	this study
Bole, Ethiopia	Fragment	315	2.1[d]	Dunbar (1987)
Kyambura Gorge, Uganda	Fragment	347	3.7[e]	Kruger et al. (1998)
Lake Naivasha, Kenya	Fragment	396	4.8	Rose (1978)
Limuru, Kenya	Fragment	500	2.0	Schenkel and Schenkel-Hulliger (1967)
Murchison Falls, Uganda	Fragment	800	1.5	Leskes and Acheson (1971)

[a] mean for 25 groups; [b] mean for 6 groups; [c] mean for 2 groups; [d] mean for 7(?) groups; [e] mean for 24 groups.

Table VII. Daily path lengths (DPL) and home range areas for 19 colobine monkey species at 29 long-term study sites

Species	Study site	Mean DPL (m)	DPL [Range] (m)	Home range area (ha)	Reference
Colobus angolensis	Ituri, D.R. Congo	983	312–1914	371	Bocian (1997)
Colobus guereza	Kakamega, Kenya	588[a]	166–1360	18[b]	this study
Colobus guereza	Kibale, Uganda	535	288–1004	32	Oates (1977b)
Colobus guereza	Ituri, D.R. Congo	609	268–1112	100	Bocian (1997)
Colobus guereza	Budongo, Uganda	—	—	14[c]	Suzuki (1979)
Colobus polykomos	Tiwai, Sierra Leone	832	350–1410	24	Dasilva in Oates (1994)
Colobus satanas	Makande, Gabon	852	20–1983	573	Fleury and Gautier-Hion (1999)
Colobus satanas	Lope, Gabon	510	40–1100	184	Harrison (1986); Oates (1994)
Colobus satanas	Douala-Edea, Cameroon	460	<100–>800	60	McKey (1979)
Colobus vellerosus	Bia, Ghana	307	75–752	48[d]	Olson (1986); Oates (1994)
Procolobus badius	Kibale, Uganda	649	223–1185	65	Struhsaker (1975)
Procolobus badius	Kibale, Uganda	553 < X < 596	≤350–≥1050	—	Isbell (1983)
Procolobus badius	Gombe, Tanzania	—	—	114[e]	Clutton-Brock (1975)
Procolobus badius	Mchelelo—Tana, Kenya	603	170–990	9	Marsh (1981); Decker (1994)
Procolobus badius	Mchelelo—Tana, Kenya	532	210–870	12	Decker (1994)
Procolobus badius	Baomo—Tana, Kenya	461	180–780	13	Decker (1994)
Procolobus badius	Abuko, Gambia	—	—	34[f]	Starin (1991)
Procolobus badius	Fathala, Senegal	—	—	9–20	Gatinot in Marsh (1981)
Procolobus badius	Jozani, Zanzibar	—	—	60[g]	Mturi (1995)
Procolobus badius	Tiwai, Sierra Leone	—	—	55	Davies in Oates (1994)
Procolobus verus	Tiwai, Sierra Leone	—	—	28[h]	Oates (1994)
Presbytis hosei	Lipad, Malaysia	743[i]	425–1088	40[i]	Mitchell (1994)
Presbytis melalophos	Kuala Lompat, Malaysia	—	—	21	Curtin (1980)
Presbytis melalophos	Kuala Lompat, Malaysia	703[i]	300–1360	30[i]	Bennett (1986)
Presbytis potenziani	Betumonga, Indonesia	540[i]	60–1120	33[k]	Fuentes (1996)
Presbytis rubicunda	Sepilok, Malaysia	850	225–1670	85	Bennett and Davies (1994)
Presbytis thomasi	Ketambe, Indonesia	1068[l]	—	27[l]	Steenbeek (1999)

(*Continued*)

Table VII. (*Continued*)

Species	Study site	Mean DPL (m)	DPL [Range] (m)	Home range area (ha)	Reference
Trachypithecus auratus	Pangandaran, Indonesia	486[i]	>300–<800	6[i]	Kool (1989)
Trachypithecus johnii	Kakachi, Indonesia	—	—	24	Oates in Bennett and Davies (1994)
Trachypithecus pileatus	Madhupur, Bangladesh	325	50–700	22	Stanford (1991)
Trachypithecus obscurus	Kuala Lompat, Malaysia	—	—	33	Curtin (1980)
Semnopithecus entellus	Kanha, India	1083	—	75	Newton (1992)
Semnopithecus entellus	Junbesi, Nepal	2990	—	1250[m]	Curtin (1982)
Nasalis larvatus	Tanjung Puting, Indonesia	—	—	130	Yeager (1989)
Nasalis larvatus	Sukau, Malaysia	910	370–1810	221	Boonratana (2000)
Nasalis larvatus	Samunsam, Malaysia	—	—	900	Bennett and Sebastian (1998)
Rhinopithecus bieti	Wuyapiya, China	1310	300–2950	1625[n]	Kirkpatrick et al. (1998)

[a] mean of values for groups T, O, GC, ML, and BS; [b] mean of values for groups T and O; [c] mean home range size for 25 groups, though the number of hours of observation for each group was not reported; [d] home range size based on 361 days of follows over a 12-month period; [e] home range size computed with a 100 × 100 yard grid so probably a large overestimate; [f] home range size between July 1978–September 1982; [g] mean home range size for 2 groups; [h] home range size based on 33 days of follows between June 1983–October 1985; [i] mean DPL and home range size for 2 groups; [j] mean DPL for an unidentified number of groups; [k] mean home range size for 2 groups; [l] mean DPL and home range size for 14 groups; [m] home range size computed with a 0.4 × 0.4 ha grid; [n] home range size for 1 year computed with a 500 × 500 m grid.

range overlap, however, no quadrat was frequently used by >1 group. Unlike von Hippel (1996), I found that groups had priority of access to their frequently-entered quadrats and were consistently able to expel intruding conspecifics from them (Fashing, 1999).

Like Kakamega guerezas, those at Kibale also had high levels of home range overlap (74%) between groups (Oates, 1977b). Home range overlap at Ituri (22%), however, is considerably lower than those at Kakamega and Kibale (Bocian, 1997). Home range overlap also appears to have been low during Suzuki's (1979) study at Budongo. Since Suzuki reported population density as 49 guerezas/km^2, mean home range size as 14 ha, and mean group size as 7 individuals, home range overlap must have been minimal at Budongo, unless portions of Suzuki's study area were not occupied by any guerezas.

There appear to be two major differences between Kakamega and Kibale, where home range overlap is extensive, and Ituri and Budongo, where home range overlap appears limited. First, guerezas at both Kakamega and Kibale live at high population densities for large forest blocks. Secondly, both Kakamega and Kibale have one or two small patches of rare resources (eucalyptus bark or swamp plants) that are converged upon by many groups. The greater level of home range overlap at Kakamega and Kibale may be due to one or both of these factors.

Dunbar (1987) suggested that at the very high population densities often found in forest fragments, guereza home ranges will become compressed to such small sizes, and boundaries so ritualized, that virtually no overlap occurs between the home ranges of adjacent groups. Home range overlap does indeed tend to be low in forest fragments (e.g., Bole: Dunbar and Dunbar, 1974; Chobe: Oates, 1977b), though this is not always the case (e.g., Kyambura Gorge: Kruger *et al.*, 1998).

Intragroup Feeding Competition

Although investigating feeding competition was not the primary focus of my study, data on activity and ranging patterns at Kakamega can be used to make some preliminary observations on levels of intragroup feeding competition in guerezas. If intragroup contest competition were common among guerezas at Kakamega, one would expect rates of aggression to have been high within groups, particularly in the vicinity of food patches. Since no instance of aggression was recorded during scan samples in either group regardless of proximity to food patches, it is tempting to conclude that contest competition does not occur within guereza groups at Kakamega. However, since aggression is often brief, scan samples are probably not the

best means to estimate rates of aggression. Fortunately, crude data are also available on patterns of aggression for guerezas at Kibale and Bole based on all-occurrence sampling regimes. Struhsaker and Leland (1979), citing unpublished data from J.F. Oates, found that the rate of intragroup aggression among Kibale guerezas was quite low, with an average of 1 act of aggression within a guereza group every 8.7 hours. Dunbar (1987) did not provide data on rates of intragroup aggression at Bole, but noted that aggression among adult females was rare and that most aggression involving adult males appeared to be related to reproductive access to females rather than to access to food. Therefore, while there has been no thorough investigation of aggression within guereza groups, the available evidence from Kibale, Bole, and Kakamega suggests that contest competition is not common within guereza groups.

The lack of a significant positive correlation between group size and mean daily path length for the 5 study groups suggests that intragroup scramble competition is not occurring at Kakamega. However, this result cannot be considered conclusive since a Spearman rank correlation conducted on only 5 data points has relatively little power. Furthermore, the fact that BS-group, one of the largest guereza groups ever recorded, had the highest mean daily path length suggests that it is possible that beyond a certain group size threshold—15-20 members—it is necessary for group members to increase their daily path lengths to meet their energetic needs.

Nevertheless, based on the available preliminary evidence, neither intragroup contest nor intragroup scramble competition appear to be occurring at more than very low rates in most groups of Kakamega guerezas. This finding is interesting in light of the fact that the population density of guerezas at Kakamega is the highest yet recorded for a large rain forest block (Fashing and Cords, 2000). It may be that the relative abundance of trees in the Moraceae family has led to there being a higher carrying capacity for guerezas at Kakamega than for guerezas at other large rain forest sites.

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REFERENCES

Altmann, S. A., and Altmann, J. (1970). *Baboon Ecology: African Field Research,* University of Chicago Press, Chicago.

Bennett, E. L. (1986). Environmental correlates of ranging behavior in the banded langur, *Presbytis melalophos. Folia Primatol.* 47: 26–38.

Bennett, E. L., and Davies, G. (1994). The ecology of Asian colobines. In Davies, A. G. and Oates, J. F. (eds.), *Colobine Monkeys: Their ecology, behavior and evolution*, Cambridge University Press, Cambridge, pp. 129–171.

Bennett, E. L., and Sebastian, A. C. (1988). Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *Int. J. Primatol.* 9: 233–255.

Bocian, C. M. (1997). *Niche separation of black-and-white colobus monkeys (Colobus angolensis and C. guereza) in the Ituri Forest*. Ph.D. thesis, City University of New York, New York.

Boinski, S. (1987). Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia Primatol.* 49: 151–167.

Boonratana, R. (2000). Ranging behavior of the proboscis monkey (*Nasalis larvatus*) in the Lower Kinabatangan. *Int. J. Primatol.* 21: 497–518.

Bronikowski, A. M., and Altmann, J. (1996). Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol.* 39: 11–25.

Brooks, T. M. (1999). Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 13: 1140–1150.

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low- density subpopulations. *Ecol. Monogr.* 60: 1–26.

Chapman, C. (1988). Patterns of foraging and range use by 3 species of neotropical primates. *Primates* 29: 177–194.

Chapman, C. A., and Chapman, L. J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40: 215–231.

Chapman, C. A., and Chapman, L. J. (2000). Determinants of group size in primates: The importance of travel costs. In Boinski, S. and Garber, P. A. (eds.), *On the Move: How and Why Animals Travel in Groups*, University of Chicago Press, Chicago, pp. 24–42.

Cheney, D. L. (1992). Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behav. Ecol.* 3: 334–345.

Clutton-Brock, T. H. (1974). Activity patterns of red colobus (*Colobus badius tephrosceles*). *Folia Primatol.* 21: 161–187.

Clutton-Brock, T. H. (1975). Ranging behavior of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Anim. Behav.* 23: 706–722.

Clutton-Brock, T. H., and Harvey, P. H. (1977). Species differences in feeding and ranging behaviour in primates. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*, Academic Press, New York, pp. 557–584.

Cords, M. (1987). *Mixed Species Association of Cercopithecus Monkeys in the Kakamega Forest, Kenya.* Univ. Calif. Publ. Zool. Berkeley, University of California Press, 117: 1–109.

Crockett, C. M., and Eisenberg, J. F. (1986). Howlers: Variations in group size and demography. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 54–68.

Curtis, D. J., and Zaramody, A. (1998). Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz. Int. J. Primatol.* 19: 811–835.

Curtin, R. A. (1982). Range use of gray langurs in highland Nepal. *Folia Primatol.* 38: 1–18.

Curtin, S. H. (1980). Dusky and banded leaf monkeys. In Chivers, D. J. (ed.), *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest*, Plenum Press, New York, pp. 105–145.

Dasilva, G. L. (1992). The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.* 61: 79–91.

Dasilva, G. L. (1993). Postural changes and behavioural thermoregulation in *Colobus polykomos*: the effect of climate and diet. *Afr. J. Ecol.* 31: 226–241.

Decker, B. S. (1994). Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratus*). *Int. J. Primatol.* 15: 703–737.

Defler, T. R. (1996). Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagothricha*). *Am. J. Primatol.* 38: 289–302.

de Ruiter, J. R. (1986). The influence of group size on predator scanning and foraging behavior of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98: 240–258.

Dunbar, R. I. M. (1987). Habitat quality, population dynamics, and group composition in a colobus monkeys (*Colobus guereza*). *Int. J. Primatol.* 8: 299–329.

Dunbar, R. I. M., and Dunbar, E. P. (1974). Ecology and population dynamics of *Colobus guereza in Ethiopia. Folia Primatol.* 21: 188–208.

Fashing, P. J. (1999). *The Behavioral Ecology of an African Colobine Monkey: Diet, Range Use, and Patterns of Intergroup Aggression in Eastern Black and White Colobus Monkeys* (*Colobus guereza*). Ph.D. thesis, Columbia University, New York.

Fashing, P. J. (2001). Feeding ecology of guerezas in the Kakamega Forest, Kenya: The importance of Moraceae fruit in their diet. *Int. J. Primatol.* 22: 579–609.

Fashing, P. J. (in press). Male and female strategies during intergroup encounters in black and white colobus monkeys (*Colobus guereza*): evidence for resource defense mediated through males. *Behav. Ecol. Sociobiol.*

Fashing, P. J., and Cords, M. (2000). Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. *Am. J. Primatol.* 50: 139–152.

Fleury, M. C., and Gautier-Hion, A. (1999). Seminomadic ranging in a population of black colobus (*Colobus satanas*) in Gabon and its ecological correlates. *Int. J. Primatol.* 20: 491–509.

Freeland, W. J. (1976). Pathogens and the evolution of primate sociality. *Biotropica* 8: 12–24.

Fuentes, A. (1996). Feeding and ranging in the Mentawai Island langur (*Presbytis potenziani*). *Int. J. Primatol.* 17: 525–548.

Gathua, J. M. (2000). *Intraspecific Variation in Foraging Patterns of Redtail Monkeys* (*Cercopithecus ascanius*) *in the Kakamega Forest, Kenya.* Ph.D. thesis, Columbia University, New York.

Gupta, A. K., and Kumar, A. (1994). Feeding ecology and conservation of the Phayre's leaf monkey *Presbytis phayrei* in northeast India. *Biol. Cons.* 69: 301–306.

Harrison, M. J. S. (1983). Patterns of range use by the green monkey, *Cercopithecus sabaeus,* at Mt. Assirik, Senegal. *Folia Primatol.* 41: 157–179.

Harrison, M. J. S. (1986). Feeding ecology of black colobus, *Colobus satanas*, in central Gabon. In Else, J. G. and Lee, P. C. (eds.), *Primate Ecology and Conservation*, Cambridge University Press, Cambridge, pp. 31–37.

Hausfater, G., and Meade, B. J. (1982). Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23: 287–297.

Isbell, L. A. (1983). Daily ranging behavior of red colobus (*Colobus badius tephrosceles*). *Folia Primatol.* 41: 34–48.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behav. Ecol.* 2: 143–155.

Kinnaird, M. F. (1992). Variable resource defense by the Tana River crested mangabey. *Behav. Ecol. Sociobiol.* 31: 115–122.

Kirkpatrick, R. C., Long, Y. C., Zhong, T., and Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti. Int. J. Primatol.* 19: 13–51.

Kool, K. M. (1989). *Behavioural Ecology of the Silver Leaf Monkey, Trachypithecus auratus sondaicus, in the Pangandaran Nature Reserve, West Java, Indonesia.* Ph.D. thesis, University of New South Wales, Sydney.

Kruger, O., Affeldt, E., Brackmann, M., and Milhahn, K. (1998). Group size and composition of *Colobus guereza* in Kyambura Gorge, Southwest Uganda, in relation to chimpanzee activity. *Int. J. Primatol.* 19: 287–297.

Leskes, A., and Acheson, N. H. (1970). Social organization of a free-ranging troop of black and white colobus monkeys (*Colobus abyssinicus*). In Kummer, H. (ed.), *Proceedings of the Third International Congress of Primatology, Zurich 1970, Volume 3, Behavior*, S. Karger, Basel, pp. 22–31.

Marsh, C. W. (1981). Time budget of Tana River red colobus. *Folia Primatol.* 35: 30–50.

McGraw, W. S. (1998). Posture and support use of Old World monkeys (Cercopithecidae): The influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items. *Am. J. Primatol.* 46: 229–250.

McKey, D. B. (1979). *Plant chemical defenses and the feeding and ranging behavior of colobus monkeys in African rainforests.* Ph.D. thesis, University of Michigan, Michigan.

McKey, D. B., and Waterman, P. G. (1982). Ranging behavior of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. *Folia Primatol.* 39: 264–304.

Milton, K. (1980). *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics.* Columbia University Press, New York.

Mitchell, A. H. (1994). *Ecology of Hose's langur, Presbytis hosei, in Mixed Logged and Unlogged Dipterocarp Forest of Northeast Borneo.* Ph.D. thesis, Yale University, New Haven.

Mturi, F. A. (1995). Ecology of the Zanzibar red colobus monkey, *Colobus badius kirkii* (Gray, 1968), in comparison with other red colobines. In Lovett, J. C. and Wasser, S. K. (eds.), *Biogeography and Ecology of the Rain Forests of Eastern Africa*, Cambridge University Press, Cambridge, pp. 243–266.

Newton, P. (1992). Feeding and ranging patterns of forest Hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.* 13: 245–285.

Nunes, A. (1995). Foraging and ranging patterns in white-bellied spider monkeys. *Folia Primatol.* 65: 85–99.

Oates, J. F. (1974). *The Ecology and Behaviour of the Black-and-White Colobus Monkey* (*Colobus guereza Ruppell*) *in East Africa.* Ph.D. thesis, University of London, London.

Oates, J. F. (1977a). The guereza and its food. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*, Academic Press, New York, pp. 275–321.

Oates, J. F. (1977b). The social life of a black and white colobus monkey, *Colobus guereza. Z. Tierpsychol.* 45: 1–60.

Oates, J. F. (1978). Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): A relationship with minerals and toxins in the diet? *Biotropica* 10: 241–253.

Oates, J. F. (1987). Food distribution and foraging behavior. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 197–209.

Oates, J. F. (1994). The natural history of African colobines. In Davies, A. G. and Oates, J. F. (eds.), *Colobine Monkeys: Their ecology, behavior and evolution*, Cambridge University Press, Cambridge, pp. 75–128.

O'Brien, T. G., and Kinnaird, M. F. (1997). Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *Int. J. Primatol.* 18: 321–351.

Olson, D. K. (1986). Determining range size for arboreal monkeys: Methods, assumptions, and accuracy. In Taub, D. M. and King, F. A. (eds.), *Current Perspectives in Primate Social Dynamics*, Van Nostrand Reinhold, New York, pp. 212–227.

Olupot, W., Chapman, C. A., Waser, and Isabirye-Basuta, G. (1997). Mangabey (*Cercopithecus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Am. J. Primatol.* 43: 65–78.

Ostro, L. E. T., Silver, S. C., Koontz, F. W., Young, T. P., and Horwich, R. H. (1999). Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America. *Biol. Cons.* 87: 181–190.

Overdorff, D. J. (1993). Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and rufous lemurs (*Eulemur fulvus rufus*). In Kappeler, P. M. and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*, Plenum Press, New York, pp. 167–178.

Raemaekers, J. (1980). Causes of variation between months in the distance traveled daily by gibbons. *Folia Primatol.* 34: 46–60.

Rasmussen, D. R. (1979). Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). I. Sleeping sits, impregnable females, births, and male emigrations and immigrations. *Anim. Behav.* 27: 1098–1112.

Richard, A. (1977). The feeding behavior of *Propithecus verreauxi*. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*, Academic Press, New York, pp. 71–96.

Rose, M. D. (1978). Feeding and associated positional behavior of black and white colobus monkeys (*Colobus guereza*). In Montgomery, C. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, D.C., pp. 253–262.

Schenkel, R., and Schenkel-Hulliger, L. (1967). On the sociology of free-ranging colobus (*Colobus guereza caudatus* Thomas 1885). In Starck, D., Schneider, R., and Kuhn, H. J. (eds.), *Progress in Primatology*, Karger, Basel, pp. 185–194.

Sigg, H., and Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia Primatol.* 36: 40–75.

Sokal, R. S., and Rohlf, F. J. (1995). *Biometry*. W. H. Freeman, New York.

Stanford, C. B. (1991). The capped langur in Bangladesh: behavioral ecology and reproductive tactics. *Contributions to Primatology.* 26: 1–179.

Starin, E. D. (1991). *Socioecology of the red colobus monkey in the Gambia with particular reference to female-male differences and transfer patterns*. Ph.D. thesis, City University of New York, New York.

Steenbeek, R. (1999). Female choice and male coercion in wild Thomas's langurs. Ph.D. thesis, University of Utrecht, Utrecht, the Netherlands.

Sterck, E. H. M. (1995). *Females, foods and fights: A socioecological comparison of the sympatric Thomas langur and long-tailed macaques*. Ph.D. thesis, University of Utrecht, Utrecht, the Netherlands.

Sterck, E. H. M., and Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behavior* 134: 749–774.

Sterck, E. H. M., Watts, D. P., and van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* 41: 291–309.

Struhsaker, T. T. (1974). Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *Amer. Zool.* 14: 177–184.

Struhsaker, T. T. (1975). *The Red Colobus Monkey*. University of Chicago Press, Chicago.
Struhsaker, T. T. and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv. Stud. Behav.* 9: 159–228.

Suzuki, A. (1979). The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. In Bernstein, I. S., and Smith, E. O. (eds.), *Primate Ecology and Human Origins*, Garland STPM Press, New York, pp. 153–173.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In Standen, V. and Foley, R. A. (eds.), *Comparative Socioecology: The behavioral ecology of humans and other mammals*. Blackwell, Oxford, pp. 195–218.

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., and den Tonkelaar, I. (1983). The effect of group size on time budgets and social behavior in wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* 13: 173–181.

von Hippel, F. A. (1996). Interactions between overlapping multimale groups of black and white colobus monkeys (Colobus guereza) in the Kakamega Forest, Kenya. *Am. J. Primatol.* 38: 193–209.

Waser, P. (1977). Feeding, ranging and group size in the mangabey *Cercopithecus albigena.* In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*, Academic Press, New York, pp. 183–222.

Wrangham, R. W. (1977). Feeding behavior of the chimpanzees in Gombe National Park, Tanzania. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*, Academic Press, New York, pp. 5-3-556.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262–300.

Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *Int. J. Primatol.* 10: 497–530.

Zhang, S.-Y. (1995). Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French Guiana. *Int. J. Primatol.* 16: 489–507.