

Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda

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Abstract Recently, considerable intraspecific variation in the diets and ranging behavior of colobine monkeys has been described, although in most cases this has involved documenting variation between, not within, sites. Some African colobines, such as guerezas (*Colobus guereza*), are relatively abundant in disturbed habitats that are very heterogeneous, raising the intriguing possibility that even groups with overlapping home ranges may exhibit large behavioral differences. If such differences occur, it will be important to understand what temporal and spatial scales adequately portray a species' or population's diet and ranging behavior. This study documents within-site variation in the diet and ranging behavior of guerezas in the habitat types in which they are described to be most successful—forest edge and regenerating forest. We collected data on eight groups of guerezas with overlapping home

ranges for 3–5 months each in Kibale National Park, Uganda. The guerezas were highly folivorous, with leaves constituting 78.5–94.0% of the groups' diets. The percentage of mature leaves and fruit in the diet varied widely among and within groups. We show that differences among groups in the intensity with which they fed on specific tree species were not just related to phenology, but also to differences in the forest compositions of groups' core areas. Range size estimates varied more than fivefold among groups and the minimum distance from groups' core areas to eucalyptus forest (which all groups regularly fed in) was a better predictor of range size than was group size. These results reveal considerable variation in the diet and ranging behavior among groups with overlapping ranges and have implications for comparative studies, investigations of within- and between-group feeding competition, and the potential for populations to adapt to anthropogenic or natural environmental change.

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Introduction

Recent studies and reviews have documented considerable variation in diet and ranging behavior within and between species of colobine monkeys (Asian colobines: Bennett and Davies 1994; Koenig 2000; Kirkpatrick 2007; African colobines: Oates 1994; Chapman and Chapman 1999; Davies et al. 1999; Fleury and Gautier-Hion 1999; Fashing 2001a, 2001b, 2007; Chapman et al. 2002a), as well as within other primate species and genera (see reviews in Campbell et al. 2007). Such studies are important for a variety of reasons. First, comparative studies often use

single values to represent diet and/or ranging variables for an entire species or population (Mitani and Rodman 1979; Harvey and Clutton-Brock 1981; Nunn and Barton 2000; Wich and Nunn 2002; Nunn et al. 2003). Studies of intraspecific variation may demonstrate that this is inadequate and, depending on the question being addressed, this could produce spurious results. For example, a major goal of physical anthropology is to understand the extraordinary morphological diversity found within the Order Primates. A number of authors have suggested that there are predictable causal relationships between morphology, locomotor behavior, and aspects of the animal's behavior, including diet (Fleagle and Mittermeier 1980; Gebo and Chapman 1995a, 1995b). If considerable variation in behavioral traits exists between populations, or between groups within a population, then categorizing a species or population based on a single study may be inadequate.

Second, large dietary differences within or between sites could also have implications for studies of contest competition for food, particularly if these reflect differences in availability/abundance of particular food species over space, thus potentially producing monopolizable clumps. For example, some primates rely on foods with patchy distribution (Chapman et al. 1995), or that occur only in very specific habitats (e.g., high-sodium swamp plants; Oates 1977a, 1978), and thus may be contestable. Differences between groups in their use of and access to important food resources may also have implications for the study of scramble competition. When this type of feeding competition is important for a species/population, it is expected that among-group differences in daily path length will be related to group size. If important resources are shared by multiple groups, however, some groups may have to travel longer distances than others to obtain these resources and, thus, they may show ranging differences that are independent of group size.

Lastly, documenting intraspecific variation in diet and ranging can help researchers and managers evaluate which populations are likely to be more or less vulnerable to anthropogenic or natural environmental change. Species that show high dietary variability within or between sites, e.g., blue monkeys (*Cercopithecus mitis*; Lawes 2002), might be able to cope better with habitat alterations than species with a narrowly focused diet (e.g., bamboo lemurs; Grassi 2006). Documenting such variation can help identify which food species or nutritional components are most and least essential—information that may be useful for decisions concerning conservation strategies, including reforestation. Examining the range use of multiple groups within a single site may also help identify important resources that all or many groups rely on.

When primatologists have documented intraspecific variation in diet and ranging, it has usually involved con-

trasting studies made at sites that are geographically widely separated (Oates 1994; Bennett and Davies 1994; Hunt and McGrew 2002) or at multiple sites within a relatively large forest (e.g., Chapman et al. 2002b; Ganas et al. 2004). Comparisons of diet and ranging of neighboring groups, studied for similar amounts of time within the same site, are relatively rare (e.g., mongoose lemurs: Curtis and Zaramody 1998), but may show that considerable intraspecific variation can be observed at very local scales (e.g., ring-tailed lemurs: Yamashita 2002). Some African colobines, such as guerezas (*Colobus guereza*), are relatively abundant in disturbed habitats that are very heterogeneous. This raises the intriguing possibility that even groups with overlapping home ranges may show large behavioral differences.

This study documents within-site variation in the diet and ranging behavior of guerezas in the habitat types in which they are most successful—forest edge and regenerating forest (Struhsaker 1975, 1997; Oates 1977; Thomas 1991; Chapman et al. 2000; Chapman and Lambert 2000). It examines whether differences in forest composition in the groups' core areas predict dietary differences among groups and whether group sizes and/or distances from groups' core areas to nutritionally important, spatially clumped food resources predict differences among groups in range size. We selected spatial (i.e., neighboring groups with overlapping home ranges) and temporal scales (i.e., groups studied a few months apart) that would be expected to illustrate relatively few among-group differences. If differences are found on these scales, then larger differences could be expected on larger spatial and temporal scales.

Materials and methods

We conducted this study at the Kanyawara research site in Kibale National Park, Uganda (0.13–0.41'N and 30.19–30.32'E) from July 2002 to November 2003, July to August 2004, and June to December 2005. The forest is classified as "medium altitude tropical moist forest" (Wing and Buss 1970; Kasenene 1987) and parts of Kanyawara have been logged to varying degrees (Kasenene 1987; Struhsaker 1997; Chapman and Lambert 2000). Struhsaker (1997) details the location, climate, soil chemistry, flora, and logging history of this site.

With the help of three Ugandan field assistants and two undergraduate research assistants, we followed eight groups of guerezas with overlapping home ranges. The forest types they used were diverse, ranging from unlogged forest to recently cleared (in ~1990) forest and from swamp forest to eucalyptus plantation, along the park boundary (Fig. 1). All groups regularly used forest edge habitat and regenerating forest.

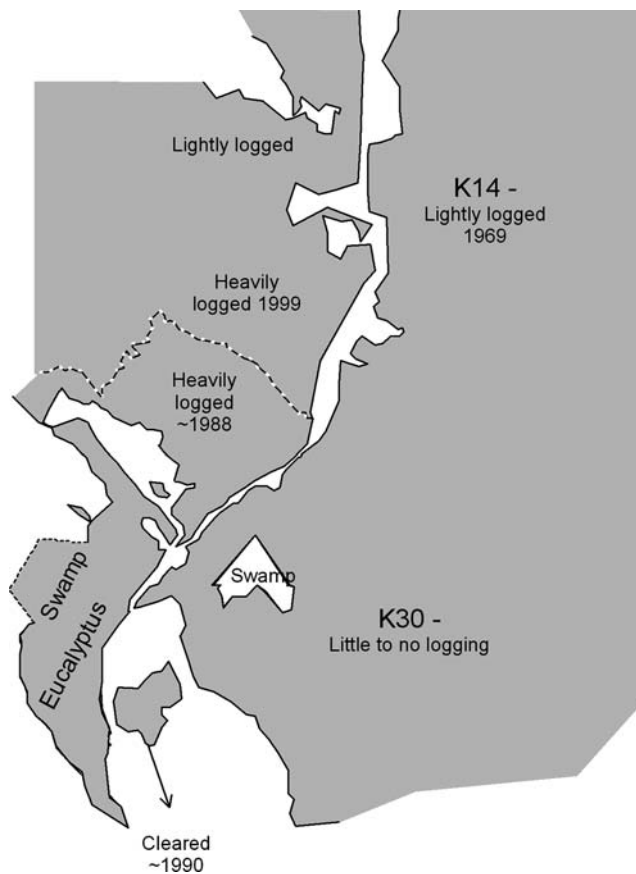


Fig. 1 Forested area in which neighboring groups of *Colobus guereza* were located, with continuous forest shown in gray. Forest edge was mapped using a Garmin GPS unit, with points taken approximately every 15 m along the forest edge. The dotted line edge next to the swamp is only approximate. The dotted black and white line demarcates the forest edge that existed in 2002/2003, but that is now part of continuous forest

Diet and ranging data

We studied six fully habituated groups for ~90 days each (Batekaine group, between July and October 2002; Zikuru group, between October 2002 and January 2003; Mugenyi group, between October 2002 and March 2003; Basaija group, between March and July 2003; Kasembo group, between May and August 2003; and Bwango group, between July and November 2003) with similar observation times per group (see feeding scan sample sizes below). We followed two other habituated groups for ~150 days (Mzee group, between June and November 2005 and Birungi group, between July and December 2005). We often followed and collected data on two groups at a time. To minimize seasonality effects we distributed observation time for each group approximately equally over rainy and dry seasons (see Chapman et al. 1998 for description of seasons).

We followed groups typically from 0800 h (near the time of first activity) to dusk and recorded feeding behavior

of all members, except infants, using 15-min scans for the first six groups, and 30-min scans for the last two groups. We collected data during 3,340, 3,729, 3,504, 3,569, 3,438, and 3,561 scans for the first six groups: Batekaine, Zikuru, Mugenyi, Basaija, Kasembo, and Bwango groups respectively, as well as 2,981 and 3,004 scans for the Mzee and Birungi groups. For each scan, we noted which individuals were feeding and the species and plant part they fed on. We identified plants with the aid of botanical keys, including Hamilton (1991) and Katende et al. (1995), and in situations where difficulties in identification occurred, we took samples to the Herbarium at Makerere University. Adults and often other individuals within groups were individually recognizable using facial markings, tail shape, and body size. Groups were small, ranging from 4 to 11 individuals (excluding infants), so we attempted to locate every individual during scans. When multiple individuals fed during a scan, we noted which individuals fed on the same tree.

When we scored individuals as feeding during scans, we used a Garmin GPS unit to obtain the feeding locations. Where we were unable to obtain accurate GPS points for trees (≤ 20 m accuracy), we assigned them the points of trees with the exact same location description (e.g., trail intersection). For the first two groups we studied, Batekaine and Zikuru, we took only a single feeding location/scan (the geometric mid-point of all feeding individuals). For the other six groups, we marked all trees we recorded during scans using flagging tape, and recorded their GPS points. Every time an individual fed on a marked tree, we used the same GPS point that had been recorded previously.

Diet and ranging analysis

For each group, we determined all species and plant parts consumed and the total number of times we recorded them being fed upon. We then calculated the percentage of feeding records group members devoted to each species and plant part. For each group and each food species, we also calculated the mean number of individuals (excluding infants) that fed per tree per scan.

We examined ranging behavior for each group using the feeding records from the scans. We compiled a list of groups' feeding records (each record corresponding to one individual feeding during a single scan) and their corresponding UTM coordinates and uploaded them to ArcView 3.2. We used the Kernel method, available in the Animal Movement extension to ArcView (<http://www.absc.usgs.gov/glba/gistools/>), to calculate and map the 50 and 95% likelihood of occurrence areas for feeding records for each group. We used a smoothing factor of 30 m to reduce the number of polygons that the algorithm calculates. We defined groups' core areas as their 50% Kernel areas, roughly corresponding to Oates' (1974, 1977) core area description. We defined groups'

feeding ranges as their 95% Kernel areas and used these to visualize where, within their home ranges (see description below), groups were doing most of their feeding. For comparability with other studies and to more fully assess the extent of each group's home range, we also used the Animal Movement extension to calculate the minimum convex polygon area for each group's feeding records.

For each group, we calculated the amount and percentage of its core area, feeding range, and minimum convex polygon range that was overlapped by each of the other groups from the same research period (i.e., 2002–2003 or 2005), as well as by all of the other groups from that period combined. To examine how well we were able to determine home range in 3 months, we calculated weekly minimum convex polygon ranges for all groups. We considered home ranges to have been adequately determined in 3 months if the weekly areas covered by the minimum convex polygons reached asymptotes (with a slight rise over time acceptable), as evaluated visually, within the period. To examine how well we were able to determine groups' core areas in 3 months, we compared the sizes of the Mzee and Birungi groups' 3- and 5-month core areas and determined the percentage areas of their 5-month core areas that were also part of their 3-month core areas.

Lastly, we used linear regression to examine whether group size or distance to eucalyptus plantation (a spatially-clumped, high-sodium resource used by guerezas—Rode et al. 2003) predicts the sizes of groups' ranges, after 3 months of observation, as calculated using the minimum convex polygon method. Specifically, we hypothesized that both modal group size during each group's study period, and shortest straight-line distance from any point in a group's core area to any point in the eucalyptus forest patch most frequently used by the group would predict and vary positively with group range size.

Phenology data and vegetation sampling

We evaluated phenology patterns using a trail system that monitored 300 individuals from 33 species (average number of individuals per species = 8.8, range = 2–12). For each monitored tree, we visually examined the crown to determine the presence of different leaf stages, flowers, and unripe and ripe fruit. We evaluated the relative abundance of these plant parts on a scale of 0–4, with all data recorded by only one observer.

Because guerezas' core areas are small, we attempted to determine the true abundance (in terms of basal area/m²) of the most heavily fed-on species in the groups' core areas. After determining the ranges for all groups, we plotted and overlaid in ArcView a set of GPS points, spaced 15–20 m apart, corresponding to the outer edge of each group's core area polygon(s), and then found these points in the forest

using a GPS unit. When we were not able to receive accurate GPS readings in the forest, we started at a location with a good reading (≤ 15 m accuracy) and used a compass and measuring tape to find the next point(s). We marked all points in the forest with flagging tape and roped off the core areas for each group.

We compiled a list of the top five fed-on species for the eight study groups, for a total of 15 species: *Acanthus arborescens* (syn. *A. pubescens*), *Albizia grandibracteata*, *Balanites wilsoniana*, *Celtis africana*, *C. durandii* (syn. *C. gomphophylla*), *Dombeya kirkii* (syn. *D. mukole*), *Eucalyptus grandis*, *Ficus exasperata*, *Markhamia lutea* (syn. *M. platycalyx*), *Olea capensis* (syn. *O. welwitschii*), *Premna angolensis*, *Prunus africana*, *Spathodea campanulata*, *Strychnos mitis*, and *Zanthoxylum gillettii*. On average, a group's top five food species constituted $73.8 \pm 1.3\%$ (mean \pm SE) of their feeding records and these 15 species constituted $84.2 \pm 0.9\%$ of their feeding records. We did not include vines in our list because we were not able to identify many of them or to estimate their abundance, as described below. If all vines are grouped together, they constitute 8.5% of the diet, on average, for the eight groups. The study groups fed on at least five different species of vine, however, with no single species constituting most of the feeding percentage on vines, thus reducing the importance of each species in the diet.

In groups' core areas, we enumerated and measured the diameter at breast height (DBH) of all trees and shrubs ≥ 5 cm DBH belonging to the 15 species above. We chose DBH as a measure of tree size because inter-observer reliability for this measure is high (Chapman et al. 1992) and the square of DBH, as well as the basal area (DBH²/1.273), is a good predictor of leaf biomass (Enquist 2002). Also, crown volume would have been impractical to measure, because the canopy in the secondary forest where we worked was often entangled with vines that made crown edges very difficult to see.

Phenology and vegetation analysis

We used basal area data for food tree species to predict differences among groups in how intensively they relied on them, controlling for phenology differences between groups. We chose to examine species for which we monitored at least ten trees for phenology, and for which we had basal area data from groups' core areas (e.g., *E. grandis* was excluded because it was not found in any group's core area). This resulted in a list of nine commonly fed-on species, representing, on average, $77.3 \pm 1.0\%$ of groups' feeding records: *A. grandibracteata*, *C. africana*, *C. durandii*, *D. kirkii*, *F. exasperata*, *M. lutea*, *O. capensis*, *P. africana*, and *S. campanulata*.

We calculated the basal area for each tree species in each group's core area using the DBH measurements (A

= πr^2) and summed them for each species. Because some of the groups' core areas consisted of open spaces that were not regularly used, we calculated the amount of each group's core area that was covered by continuous forest (Fig. 1). We then used this number to calculate the basal area (m^2)/forested ha for each species in each group's core area, and the percentage of the total basal area of food trees in groups' core areas (using data from the 15 measured tree species) that each of the nine species constituted. For each food species, we used its percentage basal area measures, for each of the eight groups' core areas, to predict groups' percentage feeding scores on those species for months, or combinations of 2 months (in cases where groups were followed for <15 days for a single month), with comparable phenology scores. Because guerezas at Kibale generally prefer young leaves (YL) to mature leaves (ML; Oates 1977; Chapman et al. 2004; Chapman and Pavelka 2005), we analyzed monthly phenology scores for young leaves. However, if any group devoted more than 10% of its feeding on a given species to fruit (FR) or flowers (FL), we analyzed monthly combined YL + FL or YL + FR scores.

We used one-tailed linear regression, with positive relationships expected in all cases, for our analyses. For each of the nine regressions (one per species), the percentage feeding records for the groups were normally

distributed. Because we ran multiple comparisons, these analyses should be taken as an exploration of relationships. There is much controversy about how to deal with multiple comparisons (Pereneger 1998), so we have not adjusted for them.

We also investigated whether monthly differences in feeding on a particular species were related to its phenology. For the Mzee and Birungi groups, for which we had feeding data from six different months, we used monthly phenology scores for the nine food species listed above to predict the groups' monthly percentage feeding records on those species. We used one-tailed linear regression for these analyses, with positive relationships expected in all cases.

Results

Diet

Guerezas' diets consisted mostly of leaves, ranging among groups from 78.5 to 94.0% (Table 1). Groups generally fed on young leaves more than mature leaves (Tables 1, 2), but the use of mature leaves in the diet differed more than fourfold among groups (Table 1: 11.7–50.2%). However, monthly variation within some groups in the usage of

Table 1 Summary of feeding data for the eight neighboring groups of *Colobus guereza*

	Batekaine	Zikuru	Mugenyi	Basajja	Kasembo	Bwango	Mzee	Birungi	Minimum	Maximum	Mean
Number of feeding records	4,624	4,055	3,314	2,538	5,036	4,855	3,686	5,230	2,538	5,230	4,167
Mean number of feeding/tree/scan	1.41	2.46	2.29	2.00	1.95	3.23	1.97	2.43	1.41	3.23	2.22
Median number of feeding/tree/scan	1	2	2	2	1	3	2	2	1	3	
Group size range ^a	7	6	4–5	5	6	8–9	5–10	10–11	4	11	
Leaves (%)	90.80	83.61	78.52	93.97	90.28	89.59	88.82	84.44	78.52	93.97	87.50
Petioles (%)	1.08	0.05	0.18	0.00	0.10	0.02	0.08	0.02	0.00	1.08	0.19
Bark (%)	3.20	0.93	1.44	1.76	1.35	0.50	1.95	1.25	0.50	3.20	1.55
Flowers (%)	2.31	4.04	0.86	1.00	1.33	0.71	5.48	1.95	0.71	5.48	2.21
Seeds (%)	0.05	0.38	1.29	0.00	0.10	0.00	0.03	0.00	0.00	1.29	0.23
Fruit (%)	1.55	10.77	17.72	2.68	4.09	6.76	3.64	11.44	1.55	17.72	7.33
Gum (%)	0.07	0.03	0.00	0.00	2.21	0.04	0.00	0.02	0.00	2.21	0.30
Soil (%)	0.20	0.05	0.00	0.00	0.12	1.17	0.00	0.25	0.00	1.17	0.22
Concrete (%)	0.59	0.15	0.00	0.60	0.35	1.21	0.00	0.65	0.00	1.21	0.44
Stems/twigs (%)	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.02
Lichens (%)	0.02	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.06	0.01
Leaves: unclassified (%)	12.05	4.08	5.38	4.17	6.24	5.49	3.18	1.18	1.18	12.05	5.22
Identified leaves: mature (%)	34.36	16.06	11.66	22.80	50.15	31.26	33.05	18.16	11.66	50.15	27.19
Identified leaves: young (%)	65.64	83.94	88.34	77.20	49.85	68.74	63.78	80.66	49.85	88.34	72.27

^a Infants not included; group size range is only reported for the time period in which feeding data were collected

Table 2 Variation among the eight study groups in density of, feeding intensity on, and plant parts fed upon, for food species/items that constituted at least 1% of feeding records for at least one group

Species	n	BA/ha-core area	% Total feeding records	% YL	% ML	% L, overall	% Pet	% Bark	% Fl	% Seeds	% RF	% UF	% F, overall	% Other
<i>Acanthus arborescens</i> ^a	Mean	0.35	1.4	79.1	17.8	99.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1 stems
	Range	0.00–1.91	0.0–6.8	46.3–100.0	0.0–51.2	98.6–100.0	0.0–0.7	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.7
<i>Albizia grandibractea</i>	Mean	1.31	6.9	80.5	6.9	99.2	0.0	0.3	0.4	0.1	0.0	0.0	0.0	0.1 gum
	Range	0.00–3.70	0.2–16.4	54.5–98.3	1.7–22.7	97.7–100.0	0.0–0.0	0.0–1.4	0.0–2.3	0.0–0.6	0.0–0.0	0.0–0.2	0.0–0.2	0.0–0.3
<i>Balanites wilsoniana</i>	Mean	0.13	0.7	51.5	46.2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Range	0.00–0.92	0.0–5.3	33.3–81.3	12.0–66.7	100.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
<i>Celtis africana</i>	Mean	1.50	4.8	65.8	17.2	99.2	0.2	0.0	0.7	0.0	0.0	0.0	0.0	0.0
	Range	0.87–3.85	1.7–10.4	51.2–90.2	6.3–35.1	94.8–100.0	0.0–1.3	0.0–0.0	0.0–5.2	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
<i>Celtis durandii</i> ^b	Mean	4.89	41.9	64.3	27.3	94.4	0.0	0.0	1.2	0.0	1.4	2.8	4.3	0.0
	Range	1.26–10.83	20.9–70.8	37.3–96.9	2.0–51.6	84.8–100.0	0.0–0.2	0.0–0.1	0.0–7.1	0.0–0.0	0.0–8.7	0.0–7.8	0.0–13.9	0.0–0.1
Concrete	NA	NA	0.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Diospyros abyssinica</i>	Mean	NA	0.0–1.2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Range	NA	0.0–1.2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Dombeya kirkii</i> ^c	Mean	–	1.2	34.2	14.7	61.0	0.0	0.0	6.1	3.4	8.4	19.6	29.4	0.0
	Range	–	0.0–3.0	12.5–71.2	0.0–50.0	16.5–100.0	0.0–0.0	0.0–0.0	0.0–37.8	0.0–23.7	0.0–30.9	0.0–75.0	0.0–75.0	0.0–0.0
<i>Erythrina abyssinica</i>	Mean	0.50	2.0	85.9	10.7	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Range	0.00–2.11	0.0–4.8	46.7–100.0	0.0–53.3	100.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
<i>Eucalyptus grandis</i>	Mean	–	1.1	34.6	4.1	31.5	0.5	0.3	60.1	0.0	0.0	0.0	0.0	0.0
	Range	–	0.0–3.6	8.5–62.2	0.0–13.3	0.0–62.2	0.0–3.5	0.0–2.4	37.8–88.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
<i>Ficus exasperata</i>	Mean	0.00	3.3	1.5	2.3	4.0	0.0	38.4	0.0	0.0	3.4	0.1	57.6	0.0
	Range	0.00–0.00	2.2–4.5	0.0–7.2	0.0–10.4	0.0–13.9	0.0–0.0	12.1–74.5	0.0–0.0	0.0–0.0	0.0–20.0	0.0–1.1	22.3–87.9	0.0–0.0
<i>Ficus sansibarica</i> ^d	Mean	0.42	2.1	55.4	13.2	81.3	0.0	0.0	0.0	0.0	4.2	12.6	18.7	0.0
	Range	0.00–2.22	0.1–11.9	0.0–89.3	0.0–60.0	17.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–33.5	0.0–49.5	0.0–83	0.0–0.0
<i>Markhamia lutea</i> ^e	Mean	–	0.5	67.9	20.3	88.2	0.0	0.0	0.0	0.0	0.0	11.8	11.8	0.0
	Range	–	0.0–1.7	22.0–100.0	0.0–65.9	72.7–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–27.3	0.0–27.3	0.0–0.0
<i>Olea capensis</i> ^f	Mean	2.29	3.9	82.5	9.0	96.2	0.2	0.0	0.0	3.6	0.0	0.0	0.0	0.0
	Range	0.09–9.82	0.4–11.5	57.1–100.0	0.0–33.3	71.4–100.0	0.0–1.4	0.0–0.0	0.0–0.0	0.0–28.6	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
<i>Pittosporum manii</i>	Mean	1.91	2.5	64.3	24.7	98.6	0.2	0.0	1.1	0.0	0.1	0.0	0.1	0.0
	Range	0.08–6.72	0.5–6.3	36.5–88.0	8.0–40.5	90.3–100.0	0.0–1.6	0.0–0.0	0.0–8.6	0.0–0.0	0.0–1.1	0.0–0.0	0.0–1.1	0.0–0.0
<i>Polyscias fulva</i>	Mean	–	1.5	51.3	16.7	80.6	0.0	0.0	0.0	0.0	2.9	0.4	19.3	0.1
	Range	–	0.1–6.2	0.0–100.0	0.0–51.5	20.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–11.1	0.0–3.1	0.0–80.0	0.0–1.0
	Mean	–	0.3	36.9	29.2	72.5	0.0	0.0	0.0	0.0	2.5	25.0	27.5	0.0
	Range	–	0.0–1.1	0.0–70.6	0.0–52.0	0.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–10.0	0.0–100.0	0.0–100.0	0.0–0.0

Table 2 continued

Species	<i>n</i>	BA/ha– core area	% Total feeding records	% YL	% ML	% L, overall	% Pet	% Bark	% Fl	% Seeds	% RF	% UF	% F, overall	% Other
<i>Premna angolensis</i>	6	Mean 0.09	2.3	86.8	4.1	91.7	1.5	0.0	0.0	0.0	1.4	3.4	6.8	0.0
		Range 0.00–0.25	0.0–15.4	50.8–100.0	0.0–11.1	59.3–100.0	0.0–9.1	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–8.5	0.0–20.3	0.0–40.7
<i>Prunus africana</i>	8	Mean 0.90	9.0	27.6	61.0	97.8	1.2	0.1	0.1		0.7	0.2	0.8	0.0
		Range 0.00–2.70	0.4–22.1	9.8–44.9	33.3–80.5	90.3–100.0	0.0–9.2	0.0–0.4	0.0–0.9		0.0–4.2	0.0–1.1	0.0–5.3	0.0–0.2
<i>Sapium ellipticum</i>	1	Mean –	0.6	21.8	0.0	21.8	0.0	0.0	0.0	3.4	0.0	74.7	74.7	0.0
<i>Sesbania sesban</i>	1	Mean –	0.0–4.4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Range –	0.3	10.9	1.0	11.9	0.0	77.2	9.9	0.0	0.0	0.0	0.0	0.0
Soil	NA	Mean NA	0.0–2.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Range NA	0.0–1.2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Spathodea campanulata</i>	7	Mean 0.54	2.9	68.7	6.7	79.3	3.9	0.0	17.1	0.0	0.0	0.0	0.0	0.0
<i>Strychnos mitis</i>	2	Mean 0.00–1.91	0.0–7.0	40.7–93.4	0.0–18.4	53.3–100.0	0.0–19.8	0.0–0.0	0.0–35.2	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
		Range 0.05	0.6	52.4	11.9	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Triplisium^g madagascariensis</i>	2	Mean 0.00–0.38	0.0–4.7	4.8–100.0	0.0–23.8	100.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
		Range –	0.2	98.5	1.5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Vernonia auriculifera</i>	3	Mean –	0.0–1.1	97.0–100.0	0.0–3.0	100.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
		Range –	0.4	41.0	38.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vine (unknown species)	8	Mean NA	0.0–1.8	21.1–73.9	0.0–72.0	100.0–100.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0
		Range NA	6.9	57.8	25.0	94.0	0.0	0.0	0.6	1.8	2.8	0.2	4.1	0.0
<i>Zanthoxylum gillettii</i>	2	Mean NA	0.8–11.6	36.6–83.1	4.1–47.8	82.2–100.0	0.0–0.0	0.0–0.0	0.0–3.0	0.0–12.3	0.0–7.5	0.0–0.7	0.0–15.9	0.0–0.0
		Range 0.90	0.4	40.2	3.8	44.0	0.0	7.9	0.0	0.0	0.0	0.0	0.0	48.1 gum
	Range 0.00–6.52	0.0–3.0	12.0–68.4	0.0–7.5	19.5–68.4	0.0–0.0	0.0–15.8	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	15.8–80.5

Data from all eight groups were used to calculate percentage feeding records for each species as well as basal area, where it is reported. Only data from groups that fed on the species for ≥ 5 scans were used to calculate the percentages of plant parts fed on. Column ‘*n*’ = number of groups used in plant part calculations

BA basal area (overall units are m²/forested ha), YL young leaves and leaf buds, ML mature leaves, overall %L %YL + %ML + % unclassified leaves, which are not listed, Pet leaf petioles, Fl flowers or flower parts, RF ripe fruit, UF unripe fruit, overall % F %RF + %UF + % unclassified fruits, which are not listed

^a Syn. *Acanthus pubescens*; ^b Syn. *Celtis gomphophylla*; ^c Syn. *Dombeya mukole*; ^d Syn. *Ficus sansibarica*; ^e Syn. *Markhamia platycalyx*; ^f Syn. *Olea welwitschii*; ^g Syn. *Bosqueia phoberos*

mature leaves was even greater than this (e.g., monthly percentage of mature leaves for the Birungi group ranged from 5.9 to 91.6%). The only species from which all guereza groups ate more mature leaves than young leaves was *P. africana* (Table 2).

Fruit constituted a relatively small percentage of the guerezas' diets, but its percentage in the diet differed more than 11-fold among groups (Table 1: 1.6–17.7%). Fleshy fruits were more commonly eaten unripe than ripe. The most commonly eaten fleshy fruits were those of *F. exasperata*, *C. durandii*, and *Diospyros abyssinica* (Table 2). *E. grandis* fruits, which are not fleshy, were commonly eaten by all groups (Table 2) and constituted most of the fruit eaten by members of the Batekaine, Zikuru, Basaija, and Kasembo groups. Phenology data were not available for all fruiting species, precluding statistical analysis. However, the Mugenyi group had a relatively large percentage of fruit in their diet (17.7%) and this may be explained by the presence of a large fruiting *F. exasperata* tree within their home range, and the fact that *C. durandii* was fruiting during the period they were observed. The Birungi group (11.4% fruit in diet) also fed relatively heavily on *C. durandii* fruits and the Zikuru group (10.8% fruit in their diet) fed relatively heavily on the fruits of *Sapium ellipticum*, which we did not observe fruiting during other groups' study periods. The Basaija, Kasembo, Batekaine, and Mzee groups, which fed the least on fruit, ranged more in areas that had been recently and heavily logged (for pine and cypress), and the smaller trees that were typical of these areas typically produce less fruit (Chapman et al. 1992; excluding *Trema orientalis*, which the guerezas rarely feed on).

Twenty-seven species/items (including soil and concrete from buildings) constituted at least 1% of feeding records for at least one study group (Table 2). For all eight groups, *C. durandii* made up the highest percentage of feeding records. The largest differences among the groups in the percentage feeding records (among-group range >15%) were for the species *A. grandibracteata*, *C. durandii*, *Premna angolensis*, and *P. africana* (Table 2).

When we followed groups during the same months (thereby controlling for phenology differences), they often devoted very different percentages of their diets to the top three fed-on species (Table 3). For example, in October 2002, we observed three groups, and the percentage of feeding records devoted to *A. grandibracteata*, *C. durandii*, and *P. africana* ranged from 0.00 to 32.04, 30.49 to 72.22, and 0.00 to 23.95 respectively. In most cases, where more than one group was followed per month, the group that fed least on a given species had less of that species in its core area than the group that fed on it most (Table 3). Differences in forest composition among groups' core areas (specifically, differences in the percentage basal areas comprising individual food tree species) predicted the percentage of feeding records groups devoted to those species in 6 out of 9 cases (Table 4). Two groups, Mzee and Birungi, were followed during six different months and for these groups, in only 2 out of 18 cases did monthly phenology scores for a given species predict and vary positively with the percentage monthly feeding records a group devoted to it—1 out of 9 cases for the Mzee group (*A. grandibracteata*: $R^2 = 0.582$, $P = 0.039$, $n = 6$) and 1 out of 9 for the Birungi group (*O. capensis*: $R^2 = 0.772$, $P = 0.011$, $n = 6$).

Table 3 Range of feeding effort (percentage feeding records) devoted to the top three fed-on species by neighboring groups of *Colobus guereza* that were followed during the same months

Month	<i>n</i>	<i>Albizia grandibracteata</i> , range	<i>Celtis durandii</i> , range	<i>Prunus africana</i> , range
August 2002	2	5.6 (0.0)–14.7 (3.2)	15.1 (1.3)–49.3 (6.2)	5.6 (0.0)–12.8 (0.8)
October 2002	3	0.0 (0.0)–32.0 (3.2)	30.5 (1.3)–72.2 (4.5)	0.0 (0.0)–24.0 (0.8)
November 2002	2	0.0 (0.0)–7.6 (3.7)	31.7 (1.5)–57.7 (4.5)	0.0 (0.0)–14.2 (1.2)
December 2002	2	0.0 (0.0)–8.4 (3.7)	22.3 (1.5)–39.7 (4.5)	1.4 (0.0)–10.6 (1.2)
January 2003	2	0.8 (0.0)–6.0 (3.7)	14.3 (1.5)–34.9 (4.5)	1.0 (0.0)–7.1 (1.2)
March 2003	2	0.0 (0.0)–23.1 (2.6)	13.9 (2.0)–61.1 (4.5)	0.5 (0.0)–18.4 (2.5)
May 2003	2	1.4 (0.01)–8.9 (2.6)	32.0 (2.0)–49.6 (10.8)	9.1 (2.7)–18.6 (2.5)
June 2003	2	1.3 (0.01)–5.2 (2.6)	24.3 (2.0)–45.7 (10.8)	17.0 (2.7)–22.6 (2.5)
July 2003	3	0.3 (2.6)–2.1 (0.0)	26.0 (10.8)–31.4 (6.2)	5.2 (0.0)–31.4 (2.5)
August 2003	2	0.0 (0.1)–0.1 (0.0)	16.2 (10.8)–39.7 (6.2)	1.2 (0.0)–37.8 (2.7)
July 2005	2	0.0 (0.4)–7.0 (0.5)	43.3 (6.1)–55.5 (6.8)	0.0 (0.0)–1.1 (0.0)
August 2005	2	0.6 (0.4)–3.8 (0.5)	65.6 (6.8)–75.0 (6.1)	0.5 (0.0)–0.6 (0.0)
September 2005	2	6.4 (0.4)–16.6 (0.5)	63.1 (6.1)–70.5 (6.8)	0.6 (0.0)–3.1 (0.0)
October 2005	2	1.7 (0.4)–19.8 (0.5)	65.0 (6.1)–82.4 (6.8)	0.2 (0.0)–0.8 (0.0)
November 2005	2	0.4 (0.4)–18.1 (0.5)	61.4 (6.1)–72.4 (6.8)	0.0 (0.0)–0.7 (0.0)

n = number of groups sampled that month. Basal area (m²)/forested ha of the food species in the group's core area is given in parentheses

Table 4 Results of one-tailed linear regressions using among-group variation in core area forest composition to predict the feeding effort study groups devoted to particular tree species. Specifically, for each species, we used the percentage basal area the species contributed to the total (for the top 15 food species) in each group's core area to predict groups' monthly percentage feeding scores on those species, using months with comparable young leaf (unless otherwise noted) phenology scores. $N=8$ for all regressions

Species	P	t	R^2
<i>Albizia grandibracteata</i>	0.010	3.162	0.625
<i>Celtis africana</i>	0.199	-0.909	0.121
<i>Celtis durandii</i> ^a	0.023	2.509	0.512
<i>Dombeya kirkii</i>	0.370	-0.347	0.020
<i>Ficus exasperata</i> ^a	0.002	4.767	0.791
<i>Markhamia lutea</i>	0.001	6.495	0.875
<i>Olea capensis</i>	0.000	7.020	0.891
<i>Prunus africana</i>	0.001	6.070	0.860
<i>Spathodea campanulata</i> ^b	0.104	1.415	0.25

^a Monthly phenology scores, which were matched across groups, represent combined UF, RF, and YL scores

^b Monthly phenology scores, which were matched across groups, represent combined FL and YL scores

Ranging behavior

All groups occupied forest edge habitat, heavily logged and currently colonizing forest, and eucalyptus plantation. The core areas of the Mugenyi, Bwango, Mzee, and Birungi groups, however, were located in more mature forest (K-14 compartment, Fig. 1). Groups' core areas (Figs. 2, 3; 50% Kernel) ranged in size from 0.5 to 1.6 ha and the area they encapsulated ranged from 6.2 to 24.7% of the groups' feeding ranges (95% Kernel) and from 1.7 to 10.4% of the groups' minimum convex polygon (MCP) ranges. Group range sizes calculated using the 95% Kernel method varied from 5.3 to 11.7 ha (Figs. 2, 3); using the MCP method they varied from 6.7 to 32.8 ha (Figs. 2, 3). Using weekly MCP data, range size estimates for all eight study groups leveled off after 3 months of observation (Fig. 4). Additionally, the sizes of the core areas of the Mzee and Birungi groups were similar when calculated using either 3 or 5 months of data (Mzee: 0.69 vs. 0.51 ha; Birungi: 0.62 vs. 0.61 ha) and the locations of these core areas were almost identical after 3 or 5 months (99.5% of Mzee's and 95.9% of Birungi's 5-month core areas were also part of their 3-month core areas).

Overlap in core area (50% Kernel), feeding range (95% Kernel), and MCP range between pairs of the first six groups we studied (in 2002–2003) ranged from 0 to 47%, 4 to 66%, and 13 to 78% respectively. On average, 25% (range: 5.9–47.0%), 67% (range: 43.3–79.8%), and 83% (range: 64.3–98.8%) of the land area encapsulated by these groups' core areas, feeding ranges, and MCP ranges respectively were overlapped by those of all the other six

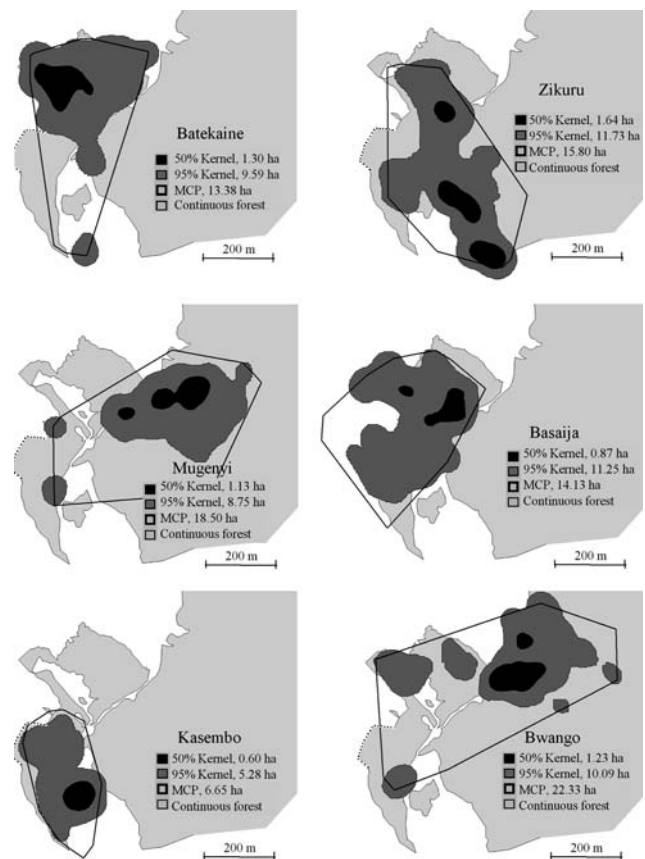


Fig. 2 Feeding ranges (95% Kernel areas), core areas (50% Kernel areas), and minimum convex polygon (MCP) areas for the six neighboring groups of guerezas from the 2002–2003 study period. Map shows the forest edge as it was mapped during that study period

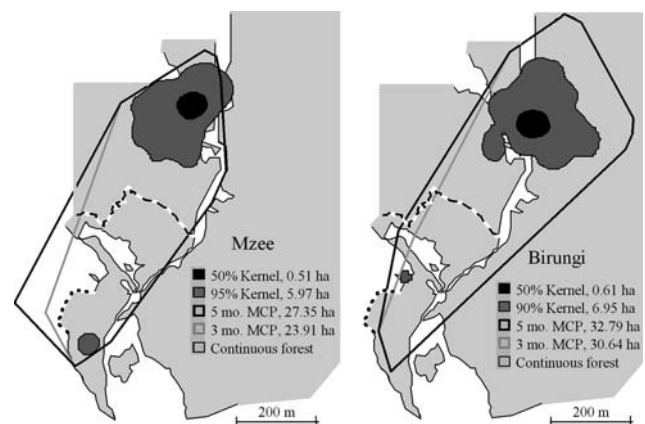


Fig. 3 Feeding ranges, core areas, and minimum convex polygon (MCP) areas for the two guereza groups (Mzee and Birungi) studied in 2005

groups from that study period. The core areas of the other two study groups (from 2005) did not overlap, but were separated by less than 30 m. On average, 19.5 and 56.4% of the Mzee and Birungi groups' feeding ranges and MCP ranges respectively overlapped.

Range size, as determined using 3 months of feeding locations for each group and the MCP method, varies positively with both the minimum distance between groups' core areas and eucalyptus plantation (one-tailed linear regression: $n = 8$, $R^2 = 0.856$, $P < 0.001$; Fig. 5) and group size ($n = 8$, $R^2 = 0.539$, $P = 0.019$) when these relationships are examined separately. The effect of group size, however, drops out when both independent variables are placed in the same regression ($n = 8$, model $R^2 = 0.893$, $P_{\text{eucalyptus}} = 0.005$, $P_{\text{group size}} = 0.122$).

Discussion

Diet

All guereza groups were highly folivorous and relied heavily on *C. durandii* leaves, which may be considered

high-quality due to their high protein-to-fiber ratio and selection by colobus monkeys for leaves with this trait (Wasserman and Chapman 2003; Chapman et al. 2003, 2004). These findings are similar to those of Oates (1977), but contrast with those of Fashing (2001a), who showed that guerezas at Kakamega, Kenya, rely heavily on fruits of trees from the Moraceae family.

There were fourfold differences among our study groups in their reliance upon mature leaves, but these differences may have been related to phenology. Fruit constituted a relatively small percentage of groups' diets, but there were relatively large (11-fold) differences among groups in how much they relied upon it. Differences in fruit consumption were most likely explained by phenology and differences in logging history and availability of specific tree species among home ranges. For example, large fig trees are relatively rare in the heavily logged forest at Kanyawara (Struhsaker 1997). Because all groups were not followed simultaneously, however, it is difficult to isolate which factor is most responsible for these differences. However, since there can be large interannual variation in phenology patterns (Chapman et al. 2004b), it would still be difficult to compare years within a 2-year study.

There were large differences among groups in the intensity with which they fed on some species, such as *A. grandibracteata*, *C. durandii*, and *P. africana*—even for groups that were studied during the same month (i.e., phenology was similar). We demonstrate that variation among groups in feeding effort on a number of commonly fed-on species, was not just related to phenology (which we controlled for), but to variation in forest composition among the groups' core areas. For the two groups, Mzee and Birungi, which we studied longest, monthly phenology scores were unrelated to feeding effort for most commonly fed-on species. While stronger conclusions could be made if all groups were followed simultaneously, these results suggest that much of the dietary variation among these neighboring groups were due to differences in the relative abundance of certain food species in groups' home ranges, and particularly in their core areas. This is somewhat expected, given that the area the groups collectively occupied was very heterogeneous, incorporating forest edge, interior forest, and forest that had been subjected to varying degrees of logging in the past. For example, *A. grandibracteata* and *P. africana* are common on the forest edge and were not present in the core areas of the Mugenyi and Bwango groups.

The intraspecific variation in diet we have shown over a very small geographical scale (i.e., hundreds of meters) within a single site, and the variation known to exist between neighboring and geographically distant sites has implications for studies of contest competition for food. We show that differences among groups, even those with

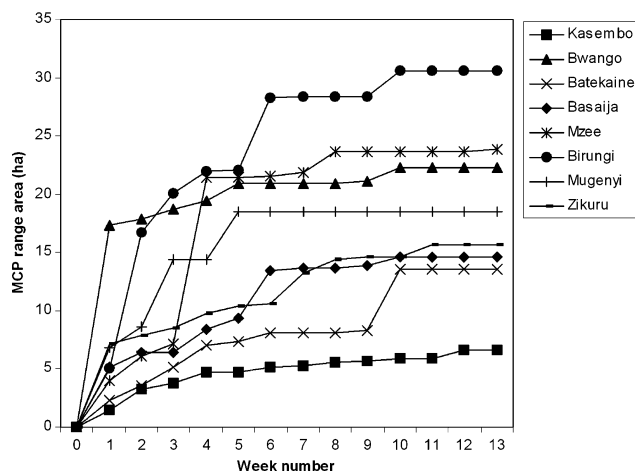


Fig. 4 Minimum convex polygon range areas over a 3-month period for the eight study groups

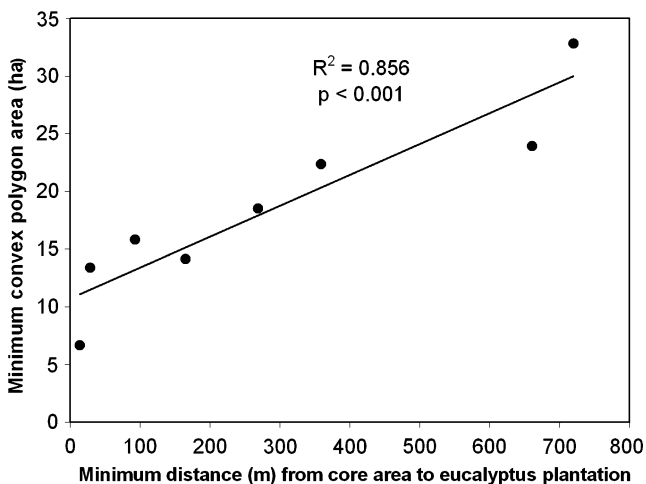


Fig. 5 Range size after 3 months of observation versus minimum distance from core area to eucalyptus forest

overlapping ranges, in the species they feed on may at least partly be explained by differences in the abundance of those species in their ranges. If some of these species are more important food resources than others and high-quality species are, for example, absent in some areas but abundant in others, or if some areas have an overall higher abundance of food than others, there might be a selective advantage for guerezas to engage in between-group contest competition for food (Harris 2006). Primatologists have sometimes assumed that folivores should not engage in contest competition because they have considered their food resources to be abundant, evenly distributed, and of relatively low quality (e.g., Wrangham 1980). However, recent studies (Koenig et al. 1998; Koenig 2000; Fashing 2001c; Korstjens et al. 2002; Harris 2006; Snaith and Chapman 2005) suggest that at least some colobine monkeys engage in contest competition for food. It is also worth testing whether either within- or between-group feeding competition differs between sites where guerezas have different diets: e.g., between Kakamega, where guerezas rely heavily upon fruit (Fashing 2001a), and Kanyawara, where leaves form the staple of their diet.

Ranging behavior

There was an approximately threefold difference among groups in the sizes of their core areas and feeding ranges, and a fivefold difference in the size of their home ranges. Because groups were not studied simultaneously, it is possible that some ranging differences could be due to seasonal variations, but we attempted to minimize this problem by equally distributing observation times for each group over rainy and dry seasons.

Although groups were only studied for 3–5 months each, we have shown that the locations and sizes of the groups' ranges stabilized over this period. The minimum distance between groups' core areas and eucalyptus plantation was a better predictor of home range size than group size. *E. grandis* and the swamp plants, *Hydrocotyle ranunculoides* and *Lemna minor*, which influenced the ranging behavior of Oates' (1977) study group, are spatially clumped, high-sodium resources (Oates 1978; Rode et al. 2003) occurring outside of the guerezas' core areas. Previous descriptions (Oates 1974, 1977; Fashing 1999, 2001b) and our personal observations indicate that guerezas typically feed on plants with high sodium content for long bouts at least once a month. Rode et al. (2003) found that most guereza foods at Kibale have extremely low levels of sodium and both they and Oates (1978) suggested that guerezas are probably sodium-deficient. Use of nutritionally important, spatially clumped resources have been shown to affect ranging

behavior in other primate species (e.g., Phayre's leaf monkeys: Pages et al. 2005; Japanese macaques: Hill and Agetsuma 1995; Western lowland gorillas: Doran-Sheehy et al. 2004), and may have important implications for studies of intraspecific variation in ranging behavior and feeding competition.

Between-group contest competition for food may occur over spatially clumped, nutritionally important resources, especially if numerous groups use them and can benefit from trying to exclude others and/or from establishing core areas that contain, or are close to, these resources (Harris 2006). Travel toward spatially clumped resources may also be a confounding variable that needs to be considered when examining the predictions for scramble competition. When within-group scramble competition is important for a species, there should be a positive relationship between group size and daily path length because larger groups should deplete food patches more quickly than small groups or experience reduced per capita encounter rates with food (Janson and van Schaik 1988; Wrangham et al. 1993; Chapman et al. 1995). If important resources are shared by multiple groups, however, some groups may have to travel longer distances than others to obtain these resources and, thus, groups may show differences in ranging that are independent of group size.

Range overlap among the guereza groups was probably high due to their common use of eucalyptus plantations, but it was also highly variable, with 5.9–47.0, 43.3–79.8, and 64.3–98.8% of groups' core areas, feeding ranges, and minimum convex polygon ranges respectively being overlapped by those of the other study groups. Other groups not followed in this study also used parts of the home ranges of some study groups, although it is unlikely that these groups' core areas overlapped with those of our study groups. Only one non-study group was encountered (i.e., within 50 m of a study group) regularly (16 times in 16 months) in the ranges of our study groups.

Summary and implications

We document considerable variation in the diet and ranging behavior of guerezas with overlapping home ranges. Although we were unable to study all eight groups simultaneously, we have shown that the differences in diet among groups were not just related to phenology, but to differences in the relative abundance of certain tree species in the groups' core areas. Chapman et al. (2002b) similarly found large dietary differences between groups within the same forest, although on a larger spatial scale, for red colobus monkeys. While these findings, as well as those of previous studies (Chapman et al. 2000, 2005), suggest that these two colobus species

have relatively flexible diets and may be able to adapt to moderate environmental changes, there is evidence from this study and other studies (e.g., Oates 1977, 1978; Fashing 2001a, 2001b; Chapman et al. 2002b; Rode et al. 2003) that they are particularly reliant upon high-sodium resources. As has also been shown for Phayre's leaf monkeys (Pages et al. 2005), this dietary requirement also affects their ranging patterns. We have shown that differences in range size among our groups were best explained by the distance from groups' core areas to spatially clumped eucalyptus plantations.

The extent of variation we have documented within the population of guerezas at Kanyawara, as well as the dietary variation Fashing (2001a, 2007) has documented among guereza populations, clearly illustrates that it is difficult to represent this species' diet and range size with a single study of one group. Moreover, the range of variation in diet and range size within *C. guereza* (this study, and summarized in Fashing 2007) is, for the most part, as large as the known between-species variation within African colobines (reviewed in Fashing 2007). Similar, or even greater, variation may be present in other species and populations, and may complicate comparative analyses (Foster and Cameron 1996; Chapman et al. 2002b), because the commonly used independent contrasts method typically does not use data to examine intraspecific variation and assumes that such variation does not exist or is negligible (Martins and Hansen 1996).

This study shows that a single group during a single time period may not be representative of what is typical for a species or population, even at a single site, because it may be atypical in terms of some character (ecological, demographic, or behavioral). Mean or median values for a given species also may be misleading, when traits vary as much as they do in *C. guereza* (e.g., home range size is known to range from 7 to 100 ha and the percentage of fruit in the diet from 2 to 40%: this study, and summarized in Fashing 2007) and when studies from certain habitat types are represented far more in the literature than others.

While, with the data currently available, it is not possible to know how many groups should be studied or how long studies need to be to provide a representative description of a species' or population's diet and ranging patterns, it is clear that the degree of heterogeneity of the habitat, on a spatial scale relevant to the question at hand, must be taken into account. While we advocate that increased effort should be made to describe populations' diet and ranging patterns in different areas and over longer time periods, this does not mean that the academic community should stop making comparisons. Rather, it suggests that researchers should be careful in drawing interpretations and should re-investigate past patterns once new data become available. While such variation may create difficulty in comparative work, it also

offers important opportunities to investigate what leads to differences between groups or populations.

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