



Ranging Behavior of Two Species of Guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda

Beth A. Kaplin¹

Received March 30, 2000; revision May 10, 2000; accepted July 5, 2000

*I studied the ranging behavior of one group of L'Hoest's monkeys (*Cercopithecus lhoesti*) and one group of blue monkeys (*C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. This study is the first to examine the ranging behavior of the more terrestrial L'Hoest's monkeys. Fruits composed 47% of blue monkey diet and 24% of the L'Hoest's monkey diet; terrestrial herbaceous vegetation composed 35% of the diet of the latter. While overall abundance of fruit resources in the home range and overall proportion of fruit in the diet were not related to ranging behavior in either group, temporal and spatial availability of specific fruit species was related. Measures of ranging behavior indicated a more concentrated ranging pattern when fruit resources were scarce and dietary diversity increased and when fruit resources were abundant and the groups focused on a few abundant fruit species. Current hypotheses concerning primate ranging behavior suggest that frugivorous species are expected to have greater day ranges and larger home ranges than folivorous species, and invertebrate consumption is expected to produce a more wide-ranging pattern. However, the L'Hoest's monkey group, which was more folivorous and consumed fewer invertebrates, traveled greater daily distances, had a more diverse and longer ranging pattern, and had larger home range areas than the blue monkey group in every month of the study. Both species were highly selective of forest habitats; L'Hoest's monkeys used secondary forest, while blue monkeys preferred primary forest.*

KEY WORDS: *Cercopithecus*; frugivory; habitat selection; home range; ranging behavior; Rwanda.

¹All correspondence should be addressed to Beth A. Kaplin, Ph.D., Department of Environmental Studies, Antioch New England Graduate School, 40 Avon St., Keene, NH 03431, e-mail: bkaplin@antiochne.edu.

INTRODUCTION

I explored the ranging behavior and habitat use of two species of forest guenons, L'Hoest's monkeys (*Cercopithecus lhoesti*) and sympatric blue monkeys (*C. mitis doggetti*). Home range is traditionally defined as the area traversed during the routine activities of food gathering, mating, seeking shelter, and caring for young (Burt, 1943). For the purpose of analysis it may be identified as an outline enclosing a specified proportion of an animal's trajectory over a specified period, wherein the trajectory is the line of movement through space and time described by the animal (Robertson *et al.*, 1998). A species dependent on uniformly distributed, self-renewing resources would be expected to cover its home range relatively evenly, while exploitation of highly patchy resources would result in an irregular pattern of space use focused on shifting patches (Terborgh, 1983). Studies of habitat use and ranging patterns facilitate understanding the complexities in aspects of animal behavior and ecology, including feeding strategies, physiological and morphological specialization, and community interactions (Boinski, 1987).

Several studies of arboreal frugivorous primate species have shown that food abundance and distribution influence daily travel distances and the frequency with which habitats or quadrats are used (Rudran, 1978; Struhsaker, 1978; Raemakers, 1980; Gautier-Hion *et al.*, 1981; Terborgh, 1983; Bennett, 1986; Boinski, 1987; Strier, 1987; Garber, 1993; O'Brien and Kinnaird, 1997; Olupot *et al.*, 1997). Other studies evidenced no correlation with either fruit availability or the fruit component of the diet and home range use (Gautier-Hion, 1988). Additional factors cited as determinants of ranging and habitat use in primates include distribution of water (Altmann and Altmann, 1970), social interactions (Struhsaker, 1974; Isbell, 1983), parasite avoidance (Freeland, 1980), weather conditions (Wu and Lin, 1993), and forest structure (Gautier-Hion *et al.*, 1981; Lemos de Sá and Strier, 1992). However, fruit abundance can be expected to influence ranging behavior in frugivorous primates, as they spend a considerable proportion of their activity budgets foraging for fruits that fluctuate in abundance spatially and temporally (Medway, 1972; Kinnaird, 1992; Sun *et al.*, 1996). Studies of *Cercopithecus* species have shown that their diets are composed of between 43 and 85% fruit (Gautier-Hion, 1988). However, L'Hoest's monkeys consume less fruit and a greater proportion of terrestrial herbaceous vegetation than other guenons (Kaplin and Moermond, 2000).

This is the first study on ranging behavior of the more terrestrial L'Hoest's monkey, which I compare with the sympatric arboreal blue monkey. My two main goals are to determine what forest types are used by each species group and to explore the variables that may influence ranging behavior. I examined ranging behavior by measuring 1) daily ranging

distance, 2) home range area, 3) quadrat use within home ranges, 4) forest habitat type use, and 5) sleep site locations. I measured these parameters during all-day follows of one group of each species with overlapping ranges during a 10 mo study. I evaluated the effects of season, food availability, dietary composition, and aspects of forest structure on measures of ranging behavior. Concurrently, I collected phenological data to follow the pattern of resource abundance in the environment.

METHODS

Study Site

The study groups had overlapping home ranges in the Nyungwe Forest Reserve, (2°17'–2°50'S and 29°07'–29°26'E), a 950 km² tropical montane rain forest in Rwanda (Figure 1). I collected climatic data from January 1990 throughout the study. Daily temperatures varied little throughout the study period, with average maximum and minimum temperatures of 19.6°C and 10.9°C, respectively. The forest received a mean annual rainfall of 1744 mm, with a dry season from July through August and a short dry season in December and January (Figure 3). The study site, defined by the overlapping home ranges of the two focal monkey groups, ranged in elevation from 2100 to 2700 m.

Foraging Behavior

I habituated a blue monkey group of 27 individuals and a L'Hoest's monkey group of 29 individuals between April 1990 and January 1991. Between February and September 1991 and July and August 1992, I followed first one group and then the other for 4–8 complete days per month, from approximately 0600 to 1845 h. I combined consecutive partial days to provide a full day of observations when the hours sampled during each partial day covered complementary periods of the 0600–1800-h time period.

I used two different methods to sample feeding behavior. I used the first method—the frequency method (Struhsaker, 1975; Rudran, 1978; Butynski, 1990)—from February 1991 to June 1991. During an interval with duration of 10-min every quarter hour I scanned the group and recorded food items eaten. I scored individuals more than once if they switched items (plant part or species) within the same scan sample. This method lacks a systematic procedure to observe individuals and their switches within one scan sample and assumes that one can observe all switches simultaneously. The

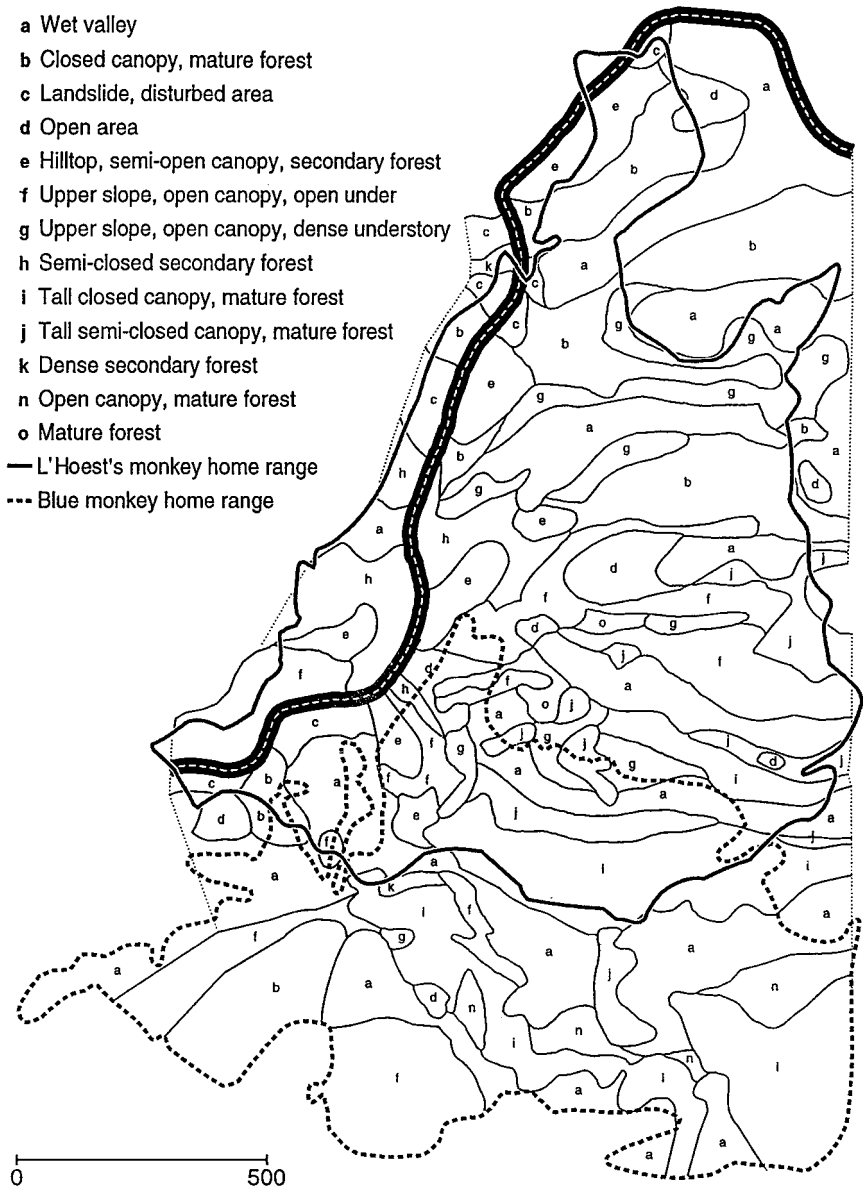


Fig. 1. Study site showing forest habitat types and maximum home range areas of the blue and L'Hoest's monkey groups obtained at the end of the 10-mo study. The thick black line represents a paved road that crosses the study site.

Table I. Results of ANOVA test

Source	DF	SS	F	p value
Method	1	0.45	0.07	0.7992
Item	4	566.00	21.19	0.0001
Month	1	11.25	1.68	0.2168
Error	13	86.80		

method may underestimate common items and overestimate uncommon ones.

I used the second method—instantaneous scan sampling (Altmann, 1974; Martin and Bateson, 1986)—from July 1991 through the remainder of the study. I used a 3-min sample interval in which an individual was scored only once during each scan. Observations of an individual were kept to a few sec, and I scored the first item consumed by each visible individual (Kaplin *et al.*, 1998). This method may overestimate common items and underestimate uncommon ones; however, it is systematic in the duration for observing and scoring individuals. I conducted three 3-min scans every 15 min. In both methods, items were food only if inserted into the mouth. Herbs are terrestrial herbaceous vegetation. I combined all terrestrial herbaceous plant parts consumed in the category herbs.

I sampled the dietary composition of L'Hoest's monkeys for 9 mo (none in June 1991) and blue monkeys for 10 mo. I collected data from the blue monkey group via both methods in July and August 1991 and used an ANOVA test applied to the data as ranks to determine if the two methods differ significantly (Conover, 1980); I included month and item to account for sources of variation in the model. There is no significant difference between the two methods (Table I), so I combined months of data within species only to analyze the dietary composition of each species across the study period. Otherwise, I analyzed data on dietary composition by pooling scores for each sample month (sampling method constant within months) and computing proportions of items from the total, because I consider that sample days and scans within days are not independent.

Ranging Behavior

I used only complete day follows for analyses of ranging behavior. Following each scan sample for foraging behavior, I located the estimated center of the mass of the group (Rudran, 1978; Cords, 1987) on a topographical map (1:6389). I connected each location point marked during the all day follows by a line estimating the directional movement of the center of the group. I scanned and digitized the ranging maps via the computer program

CANVAS (Deneba, 1992). I used CANVAS to measure daily travel distances as the sum of the straight line distances between successive location points from daily group movements. I also recorded the locations of sleep sites where the monkeys climbed into trees at the end of the day. During the months when I did not follow the groups (October 1991 through June 1992), field assistants followed them for 2–3 days per month and recorded their movements on the topographical maps, which I used to determine if there were range shifts during my absence.

I estimated home range areas for the period of time I sampled the groups via the minimum convex polygon method, the most commonly-used index (White and Garrott, 1990; De Solla *et al.* 1999). In a study comparing various methods of estimating home range area, Ostro *et al.* (1999) found that the minimum convex polygon method generally overestimates home range area but is a good estimator for cross-study analysis, though the coarseness of the method requires that the results be interpreted with caution. I also estimated home range areas via grid-cell analysis (White and Garrott, 1990) to check my estimates. The grid-cell method of home range estimation provides the smallest estimate compared with the minimum convex polygon method (which gave the largest estimate) and several other methods widely used by wildlife biologists, including the 95% harmonic mean and 95% adaptive kernel analysis (Ostro *et al.*, 1999). I chose a grid size of 0.25 ha (50 × 50 m) because I observed the greatest spread of the monkey groups to be approximately 50 m. I present both monthly home range areas and maximum home range area sampled at the end of the study period for both species groups.

I measured home range use by counting the number of different quadrats entered per day, the total number of quadrats entered per day, and the cumulative number of different quadrats entered per month. This was accomplished by superimposing a grid of 0.25 ha quadrats (50 × 50 m) over the topographical maps of daily ranging. I also examined range use by examining differences in quadrat use between pairs of days and computing C values (Strier, 1987). I computed C values as the ratio of b/a , in which b = the number of new quadrats entered the second day of the pair and a = the total number of quadrats entered on the second day. If no new quadrat was entered on the second day, C values equal zero; if only new quadrats were entered on the second day, C values equal one. A higher C value results from more new quadrats entered on the second day, and indicates a long-distance ranging pattern. A lower C value implies a more concentrated pattern of range use (Strier, 1987).

I examined forest habitat use by superimposing the 0.25-ha grid over the daily ranging maps, which were overlaid with the map of forest habitat

types (Figure 1). Each time a quadrat was entered, I recorded the forest habitat type covering that quadrat. If the quadrat contained >1 habitat type, I noted each type the group entered.

Vegetation Sampling

The Nyungwe Forest is a mosaic of forest types, including tall closed canopy forest, dense secondary growth, open areas, wet valley bottoms, and habitats in various stages of succession following disturbances such as landslides. I identified forest habitat types by walking trails transecting the home range areas at 50–100-m intervals and recording and mapping changes in the following variables: dominant canopy species, dominant understory species, dominant herbaceous vegetation, canopy height, elevation, aspect and topography. I digitized the resulting map of 13 different forest habitat types and measured the area of each of them (Figure 1).

I used a random stratified sampling method to measure the abundance and distribution of plant species within each forest habitat type during the last 2 mo of the study when the maximum home range areas of the groups were known. I placed 5–7 0.1-ha plots in each of the 13 different forest types within the home ranges for a total of 52 plots, covering an area of 5.2 ha. I identified all trees with diameter at breast height (DBH) ≥ 10 cm in each plot to species, and measured their DBH. There was a total of 38 different tree species in the plots and the species included in the phenology sample are among them. I measured herb density in each plot using a nested plot design, with 25 1-m² plots within each 0.1-ha plot. Plant determinations were facilitated by Troupin (1982) and the herbarium at the Institute of Scientific and Technological Research, Rwanda. From these data I computed densities and basal areas of trees, densities of lianas and epiphytes, mean tree height, specific richness, and herb density. Density and basal area of specific species with fruits important in the groups' diets provide an indication of resource abundance in each forest habitat type.

I distributed the forest habitat types into the following broad forest categories based on ecological parameters to examine how the monkeys use forest on a broader scale: primary or closed canopy forest (frequently on ridge tops), secondary forest (dense stands of pioneer tree species), wet valleys, open areas (dense herbs and ferns with few trees), steep slopes (large trees and open canopy), and disturbed forest (revegetating landslides with exposed soil). The area of each broad forest category was then determined by summing the areas of habitat type belonging to each category.

Phenological Sampling

I collected data on the phenological patterns of 25 fruit-producing species within the groups' home ranges on a monthly basis beginning in January 1991. This sample is a subset of a larger phenological study of 47 species (Sun *et al.*, 1996), and represents 93% of the fruit and seed species in the blue monkey diet, and 70% of the fruit and seed species in the L'Hoest's monkey diet. Individuals in the phenological sample (mean sample size 11 ± 3.87 individuals per species, range 4 to 22, $n = 25$) were reproductively mature, located throughout the home range, and were assumed to represent the phenological patterns within the home ranges of the monkeys. I marked all individual trees in the sample with numbered aluminum tags, and identified them with the assistance of Troupin (1982) and the herbarium at the Institute of Scientific and Technological Research, Rwanda.

Sampling took place over 2–3 days at the same time each month. I estimated the percentage of new leaves, flowering buds, flowers, and fruit in a given tree crown and assigned them a score from 1 to 4: none of the crown = 0, 1–25% = 1, 26–50% = 2, 51–75% = 3, 76–100% = 4 (Sun *et al.*, 1996). I present fruit phenology patterns as the monthly overall density of trees with a fruiting score of ≥ 1 to represent fruit abundance within the home range. Although density does not take into account interspecific differences in the size distribution of trees and the intensity of phenological activities, it takes into account the relative abundance among tree species and improves the accuracy of depicting plant resource abundances (Chapman *et al.*, 1994). For a more fine-scale species-specific approach, I present individual fruit phenology patterns of the five fruit or seed species most commonly eaten by both monkey species.

RESULTS

Home Range Area

The mean monthly home range area of the L'Hoest's monkeys based on the minimum convex polygon method is 56.4 ha \pm 15.6, and based on the grid-cell analysis it is 44.0 ha \pm 10.1. The total area used by the L'Hoest's monkey group at the end of the study is 116.6 ha, with 24–70% of their total area used in any one month (Table II). Mean monthly home range area for the blue monkeys based on the minimum convex polygon method is 28.4 ha \pm 15.3, and from the grid-cell analysis it is 23.8 ha \pm 7.6. The home range of the blue monkeys at the end of the study was 87.8 ha; the group used

Table II. Monthly home range areas and proportion of total used each month

	Blue monkey				Mountain monkey					
	Home range area (ha) MCP ¹	Monthly proportion (%) of total area used	Home range area (ha) GCA ²	Difference between methods (ha)	Proportion (%) new quads/mo ^ξ	Home range area (ha) MCP ¹	Monthly Proportion (%) of total area used	Home range area (ha) GCA ²	Difference between methods (ha)	Proportion (%) new quads/mo ^ξ
Feb-91	30.7	35.0	19.3	11.4	89.5	46.2	39.6	36.8	9.4	93.6
Mar-91	24.8	28.2	23.8	1.0	77.9	53.7	46.1	52.5	1.2	77.5
Apr-91	27.4	31.2	24.0	3.4	83.5	65.1	55.8	53.5	11.6	83.6
May-91	46.6	53.1	34.5	12.1	64.5	66.1	56.7	47.0	19.1	79.7
Jun-91	41.1	46.8	28.8	12.3	75.2	58.1	49.8	42.0	16.1	80.0
Jul-91	54.9	62.5	37.8	17.1	74.0	66.5	57.0	57.8	8.7	75.0
Aug-91	19.3	22.0	16.3	3.0	59.6	81.2	69.6	52.8	28.4	80.8
Sep-91	14.6	16.7	19.0	4.4	73.1	61.6	52.8	32.0	29.6	79.0
Jul-92	18.6	21.1	19.0	0.4	63.3	38.2	32.7	35.8	2.4	75.3
Aug-92	5.7	6.5	16.0	10.3	59.3	27.8	23.8	29.5	1.7	67.4

MCP¹ = Minimum Convex Polygon method.

GCA² = Grid Cell Analysis.

ξ = Computed as the number of quadrats entered each month that were not previously or subsequently entered in that month.

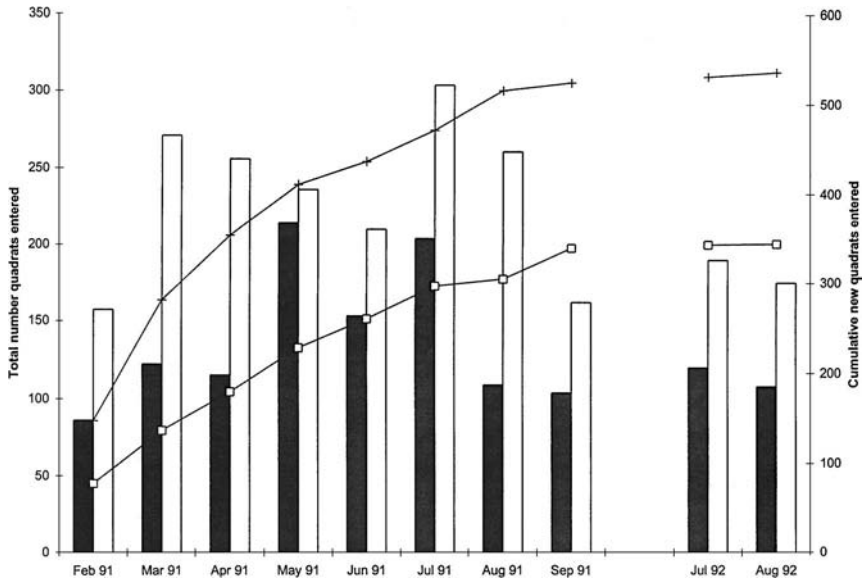


Fig. 2. Monthly total quadrats entered and cumulative quadrats entered by the blue and L'Hoeist's monkey groups. Solid bars = monthly total quadrats entered by the blue monkey group; clear bars = monthly total quadrats entered by the L'Hoeist's monkey group; line with clear square symbols = cumulative new quadrats entered by the blue monkey group; line with cross symbols = cumulative new quadrats entered by the L'Hoeist's monkey group.

6.5–63% of their total home range in any month. Monthly differences between the two methods of estimating home range area are shown in Table II. L'Hoeist's monkey home range areas were greater than those estimated for the blue monkey group in every month sampled, regardless of method used.

Home range area varied across months in both monkey groups (Table II). Figure 2 shows the cumulative new quadrats entered during each monthly sampling period. The blue monkey group appeared to be continually entering new quadrats in the 1991 sample period (Figure 2), though the 1992 sample period indicates site fidelity. Range maps produced by the field assistants for the interim period from October 1991 to June 1992 indicate that the blue monkey group did not shift their home range and moved about within the same quadrats as in the previous sample months. It appears that the L'Hoeist's monkey group home range was adequately sampled by September 1991, and the field assistants' range maps indicate no range shift while I was absent.

Table III. Mean daily travel distance (meters)

	Feb. 91	Mar. 91	Apr. 91	May. 91	Jun. 91	Jul. 91	Aug. 91	Sep. 91	Jul. 92	Aug. 92
Blue monkey										
mean	1207.1	1350.8	1165.6	1577.3	1532.1	1324.5	899.5	1097.3	1419.1	1230.6
s.d	54.3	75.9	238.8	349.0	292.3	278.2	213.8	116.0	135.5	469.9
L'Hoest's monkey										
mean	1907.6	2115.2	1625.6	2251.9	2199.9	2157.5	2439.0	1894.1	2347.1	1706.8
s.d	256.2	171.5	49.0	226.8	196.9	322.1	232.3	437.2	60.3	235.0

Daily Ranging Distance

Daily distances traveled varied widely between days in both groups (L'Hoest's monkeys: $\bar{x} = 2091.5 \text{ m} \pm 333.8$; blue monkeys: $\bar{x} = 1306.7 \text{ m} \pm 335.6$). The mean daily distance traveled by the L'Hoest's monkey group is significantly greater than that of the blue monkey group (Table III; Mann-Whitney, $U_{38,42} = 87.00$, $p = 0.001$, $n = 80$). Daily distances traveled by the blue monkey group are weakly significantly different among seasons (wet season 1991, dry season 1991, dry season 1992; Kruskal-Wallis, $H = 5.66$, $p = 0.059$, $df = 2$); the blue monkeys traveled farther in the wet season than in either dry season. There is no difference between seasons in daily distance traveled by the L'Hoest's monkey group (Kruskal-Wallis, $H = 0.399$, $p = 0.819$, $df = 2$).

To evaluate the effect of dietary composition on ranging patterns, I examined the relationship between daily distance traveled and the proportion of fruit in the diet. Fruit was an important component in the diet of the blue monkey group, composing a mean of 47% of the diet, followed by invertebrates (Table IV). Fruit composed a lesser proportion of the L'Hoest's monkey diet (24%), while terrestrial herbs composed the greatest proportion (35%) followed by seeds (Table IV). The 1992 dry season was a period of low fruit abundance for both groups (Figure 3). There are weakly significant differences in the proportions of fruit in the diet of both species between seasons (blue monkeys: Kruskal-Wallis, $H = 5.80$, $p = 0.55$, $df = 2$; L'Hoest's monkeys: Kruskal-Wallis, $H = 5.50$, $p = 0.064$, $df = 2$). Both species ate more seeds during the dry season of 1992 (blue monkeys: Kruskal-Wallis, $H = 5.54$, $p = 0.063$, $df = 2$; L'Hoest's monkeys: Kruskal-Wallis, $H = 5.44$, $p = 0.066$, $df = 2$). The mean daily distance traveled each month by both monkey groups is not correlated with the proportion of fruit in the diet each month

Table IV. Dietary composition of L'Hoest's monkeys and blue monkeys (proportion (%) of scores for each item)

	Fruit	Seeds	Invertebrates	Flowers	Terrestrial Herbs	Other
Mountain monkey						
Mean	24.5	17.8	8.8	4.0	35.2	9.8
St. dev.	9.9	11.7	8.5	3.3	10.2	8.0
	Fruit	Seeds	Invertebrates	Flowers	Tree Leaves	Other
Blue monkey						
Mean	47.4	9.3	24.9	6.2	6.2	6.2
St. dev.	15.8	12.4	9.3	8.9	6.5	6.2

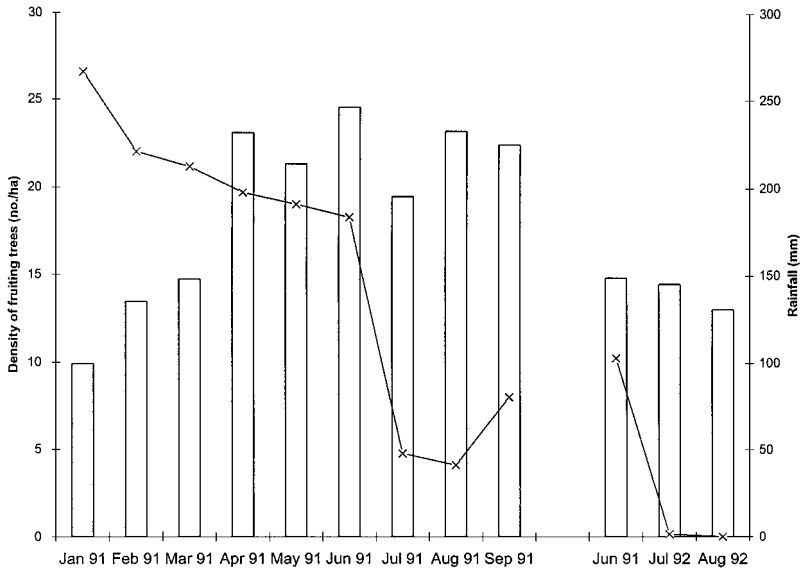


Fig. 3. Monthly rainfall (line) and monthly fruit abundance of 25 species (bars) eaten by the blue and L’Hoest’s monkeys during the study period.

(blue monkeys: $r_s = 0.067$, $p > 0.10$, $n = 10$; L’Hoest’s monkeys: $r_s = 0.367$, $p > 0.10$, $n = 9$). Because terrestrial herbs composed a relatively large component of the L’Hoest’s monkey diet, I looked for a relationship between the monthly proportion of herbs in their diet and daily distance traveled but found no significant relationship ($r_s = 0.383$, $p > 0.10$, $n = 9$). Mean daily distance traveled each month also is not correlated with rainfall in either species (blue monkeys: $r_s = -0.273$, $p > 0.10$, $n = 10$; L’Hoest’s monkeys: $r_s = 0$, $p > 0.10$, $n = 9$).

Home Range Use

I examined patterns of range use using measures of quadrat use. The L’Hoest’s monkeys entered 118–231 new quadrats in any month, while the blue monkey group entered 64–138 new quadrats. The total number of quadrats entered each month is significantly different between seasons (wet season 1991, dry season 1991, dry season 1992) for the blue monkey group (Kruskal-Wallis, $H = 6.12$, $p = 0.047$, $df = 2$), but there is no seasonal difference in the total number of quadrats entered each month by the L’Hoest’s monkey group (Kruskal-Wallis, $H = 0.446$, $p = 0.80$, $df = 2$).

A tendency to reuse quadrats would indicate constancy in home range use, while a low tendency to reuse quadrats indicates constant shifting of the home range. The L'Hoest's monkey group entered significantly more new quadrats each month than the blue monkey group did (Mann-Whitney test, $U_{10,10} = 6.00$, $p = 0.001$). Table II shows the proportion of quadrats entered each month that were new for both groups. The number of new quadrats entered each month is not correlated with fruit abundance in either species (blue monkeys: $r_s = 0.310$, $p > 0.10$, $n = 10$; L'Hoest's monkeys: $r_s = 0.455$, $p > 0.10$, $n = 10$). Both species showed a negative correlation between monthly new quadrat use and the proportion of seeds in the diet, but this relationship is significant for the mountain monkey group ($r_s = -0.683$, $p = 0.05$, $n = 9$; blue monkey group: $r_s = -0.468$, $p > 0.10$, $n = 10$). The proportion of invertebrates in the diet each month and the number of new quadrats entered is negatively correlated in the blue monkey group ($r_s = -0.845$, $p < 0.01$, $n = 10$) but not in the L'Hoest's monkey group ($r_s = -0.083$, $p > 0.10$, $n = 9$).

To evaluate ranging patterns in both groups of monkeys, I calculated C values from counts of the quadrat use of 34 pairs of sequential day ranges for the blue monkey group and 35 pairs of sequential day ranges for the L'Hoest's monkey group. A higher C value results from more new quadrats entered the second day, suggesting a long-distance ranging pattern. Figure 4 shows the frequency distribution of C values for both groups. The frequency distribution of C values in the L'Hoest's monkey group shows that there were only 4 pairs of days with C values < 0.77 , creating an obvious cutoff between high and low C values (Figure 4). The blue monkey group had 11 pairs of days with C values < 0.77 . Twenty-five pairs of days for the L'Hoest's monkey group had C values computed at ≥ 0.90 , while the blue monkeys had only 10 pairs of days ≥ 0.90 . These findings suggest that the blue monkeys had more concentrated ranging pattern, while the L'Hoest's monkeys had a more long-distance ranging pattern.

C values were < 0.77 for the blue monkeys in June, July, August, and September 1991, and in July and August 1992. The 1991 months with relatively low C values were in a period of relatively high fruit abundance (Figure 3) when the large, fleshy fruits of the primary forest tree species *Beilschmiedia troupinii* composed 41–50% of the blue monkey diet. During the 1992 dates when C values were low, fleshy fruits were not abundant in the home range (Figure 3), and the blue monkey group spent a large proportion of time feeding on seeds of the pioneer species *Macaranga neomildbraediana* (35% and 25% of diet, respectively). In both cases, the low C values are probably associated with the group returning to quadrats where fruit trees of *Beilschmiedia troupinii* or *Macaranga neomildbraediana* were located. The blue monkey group had high C values (≥ 0.90) in February,

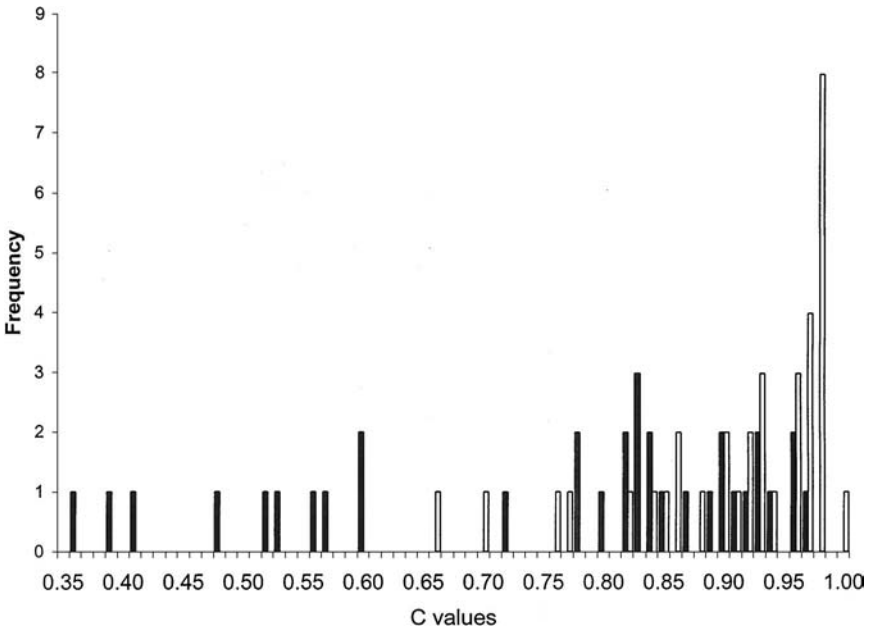


Fig. 4. C values computed for the blue monkey (solid bars) and L'Hoest's monkey (clear bars) groups.

March, and April, coinciding with a period of relatively low fruit availability (Figure 3).

Low C values for L'Hoest's monkeys occurred during May, July and September 1991, and in August 1992, with no clear pattern discernible. High C values were much more common in the L'Hoest's monkeys and were distributed throughout the the study; every month had pairs of days with high C values, suggesting that, unlike blue monkeys, L'Hoest's monkeys tend towards a more long-distance ranging pattern that is stable regardless of season or fruit abundance.

Habitat Use

I evaluated use of forest habitat types by determining the number of times the group entered each of them within their home ranges during complete day follows. Forest habitat types differed in a number of ecological parameters including densities and basal areas of the trees (Table V). The L'Hoest's monkey home range included 21 ha of landslide habitat,

Table V. Parameters of the forest habitat types within the home ranges of blue and L'Hoest's monkey groups and their entry into each habitat type

Forest type	Area (ha)		Entry by L'Hoest's monkey	Area (ha) in mtn. home range	Tree density /ha	Basal area	Mean ht	<i>Ficus</i> density /ha	<i>Beilsch- meidia</i>		<i>Chryso- phyllum</i>		<i>Maca- ranga</i>		Liane & epi- phyte dens./ha
	Entry by blue monkey	home range							<i>trou- pinii</i> density /ha	<i>dense</i> density /ha	<i>neo- mildbrae- dtana</i> dens./ha	Spp. richness	Herb dens. /m2		
a) Wet valleys	249	21.11	497	27.5	118.3	294	11.1	0.0	1.7	0.0	0.0	6.7	71	11.5	198.3
b) Mature forest	42	8.68	360	17.2	458.6	1775	16.0	8.6	4.3	1.4	1.4	90.0	315	2.5	800.0
c) Landslides	0	—	100	4	38.0	61	15.8	0.0	0.0	0.0	0.0	18.0	19	41.5	46.0
d) Open areas	33	0.67	126	4.5	60.0	72	13.4	0.0	0.0	0.0	0.0	25.0	24	9.1	80.0
e) 2° forest	20	0.57	225	8.5	358.0	755	13.8	4.0	4.0	0.0	0.0	132.0	177	5.2	1062.0
f) Steep slopes	51	11.3	360	16.4	224.0	724	17.8	24.0	10.0	0.0	0.0	80.0	100	5.0	332.0
g) Steep slopes	22	2.6	256	9.5	245.0	928	17.1	8.3	8.3	1.7	1.7	128.3	142	3.3	430.0
h) 2° forest	0	—	2137	7.3	396.0	730	14.1	8.0	0.0	0.0	0.0	120.0	194	6.4	1092.0
i) Mature forest	879	32.8	235	11.5	388.3	1306	18.7	28.3	53.3	56.7	56.7	100.0	216	3.3	591.7
j) Mature forest	21	4.76	143	7.3	326.7	1199	18.4	20.0	33.3	1.7	1.7	18.3	184	10.7	536.7
k) 2° forest	11	0.4	14	0.4	433.4	166	14.8	6.8	10.0	3.3	3.3	107.5	128	20.0	766.7
n) Mature forest	103	4.17	0	0	215.0	106	21.0	30.0	50.0	10.0	10.0	65.0	37	4.0	500.0
o) Mature forest	4	0.7	59	2.5	320.0	160	17.1	30.0	50.0	0.0	0.0	115.0	58	3.2	340.0

Table VI. Number of entries into each forest type during full day follows compared to expected values based on distribution of forest types in the home ranges

Forest type	Blue monkey Number entries		χ^2	L'Hoest' monkey Number entries		χ^2
	Observed	Expected		Observed	Expected	
a	249	345.18	26.80	497	1064.2	302.27
b	42	141.93	70.36	360	665.6	140.3
c	0	0.00	—	100	154.8	19.39
d	33	10.96	44.32	126	174.1	13.31
e	20	9.32	12.24	225	328.9	32.83
f	51	184.77	96.85	360	634.6	118.84
g	22	42.51	9.90	256	367.6	33.89
h	0	0.00	—	2137	282.5	12175
i	879	536.33	218.94	235	445	99.11
j	21	77.83	41.50	143	282.5	68.87
k	11	6.54	3.04	14	15.5	0.14
n	103	68.19	17.77	0	0	—
o	4	11.45	4.85	59	96.74	14.72
Total	1435	1435.01	546.552			13018.6
			$p < 0.001$			$p < 0.0001$

which they used in 17.4% of the habitat-type entries recorded, while the blue monkeys are absent from landslide habitat records. I used χ^2 tests to evaluate the hypothesis that the groups used habitat types randomly in relation to their availability within each of their home ranges. Results of these tests showed that the groups did not use habitat types randomly, but instead selected certain types over others (blue monkeys: $\chi^2 = 546.55$, $p < 0.001$, $df = 12$; L'Hoest's monkeys: $\chi^2 = 13018.64$, $p < 0.001$, $df = 12$; Table VI). The L'Hoest's monkey group entered all habitat types in their home range less than expected except for two secondary forest types, k and h; they entered habitat h (secondary forest) most frequently (47.4% of all entries). The blue monkey group used wet valleys (habitat type a) and steep, open slopes (habitat types f and g) less than expected. They used mature forest (habitat type i) most frequently and more than expected (61.3% of entries).

I examined the effects of habitat structure and resource abundance as measured by specific parameters in Table V on ranging patterns in both groups via forward stepwise multiple regression analyses; I used a square root transformation on the dependent variables. I analyzed the frequency of entry by the blue monkey group into quadrats of each habitat type as a function of: overall tree basal area, density, and species richness per habitat type; density of lianes, epiphytes, and terrestrial herbs per habitat type; basal area and density of trees producing fruits known to be consumed by the blue monkey group; and individual densities of four fruit tree species important

in the groups' diets: *Ficus oreodryadum*, *Beilschmiedia troupinii*, *Macaranga neomildbraediana*, and *Chrysophyllum rwandense*.

After controlling for the effects of differing areas of each habitat type in the home range, the density of *Chrysophyllum rwandense* had a significant positive effect on frequency of entry by the blue monkey group (partial slope = 11.05, $T = 19.91$, $p < 0.0001$, $df = 4$). The density of figs, *Ficus oreodryadum* (partial slope = -2.53 , $T = -4.47$, $p = 0.01$), the basal area of trees with fruits consumed by the blue monkeys (partial slope = -0.16 , $T = -2.96$, $p = 0.04$), and the density of terrestrial herbs (partial slope = -5.84 , $T = -3.04$, $p = .038$), all had a significant negative effect on entry by the blue monkey group. I included the following parameters in the L'Hoest's monkey regression model: overall tree density and basal area per habitat type, tree species richness, density of lianes and epiphytes, terrestrial herb density, density and basal area of trees producing fruits eaten by L'Hoest's monkeys, and the densities of the same four fruit tree species. The area of each habitat type was not a predictor in the regression model for the L'Hoest's monkey group. Furthermore, no parameter had a significant effect on frequency of entry by them.

Although certain habitat types may have high densities of tree species that have the potential to produce fruits consumed by the monkeys, previous phenological studies have demonstrated that fruits fluctuate in abundance and are not continuously available (Figure 3). I examined the relationship between the density of tree species in fruit each month in each habitat type and entry by each monkey group via Spearman rank correlations. The density of trees in fruit in each habitat each month and entry into the habitat each month are not correlated in either group (Figures 5a and b; blue monkeys: $r_s = -0.058$, $p > 0.10$, $n = 130$; L'Hoest's monkeys: $r_s = -0.095$, $p > 0.10$, $n = 130$).

I classified the 13 habitat types into 6 broad ecological forest types and found that the blue monkey group used mature forest habitats most frequently (Table VII). The L'Hoest's monkey group used mature forest, secondary forest, and wet valleys in nearly equal proportions (Table VII). On a monthly basis, the blue monkeys consistently used mature forest at a higher frequency compared with the other broad forest type categories (Figure 6a). Wet valleys were the second most frequently used forest type each month by the blue monkeys, always $<50\%$ of mature forest use. L'Hoest's monkeys showed a different pattern of monthly forest type use: they used mature forest, secondary forest, wet valleys, and steep slopes in relatively equal frequencies each month until August 1992, a dry season month (Figure 6b), when they spent a large proportion of time in secondary forest.

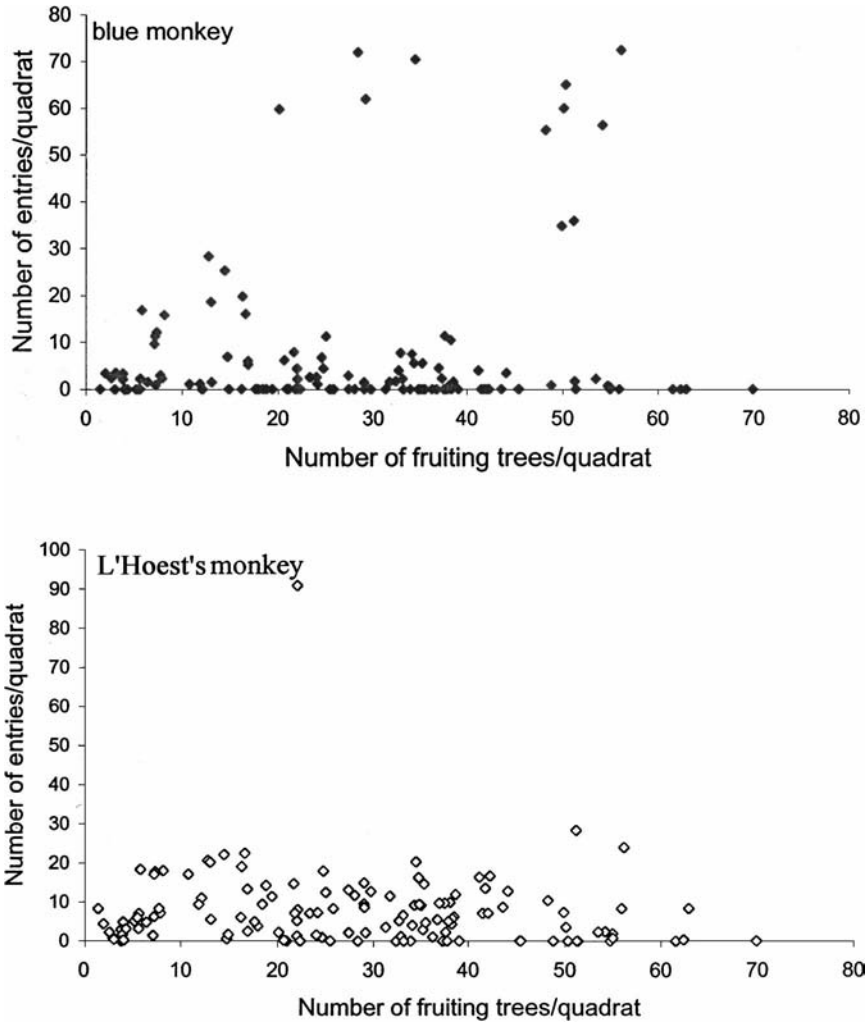


Fig. 5. Relationship between the number of fruiting trees in a quadrat and the number of blue monkey group (top) and L'Hoest's monkey group (bottom) entries in that quadrat across the sample period.

Sleep Sites

Both species climbed into trees at the end of the day to sleep. The blue monkey group used only 6 of the 11 forest habitat types in their home range

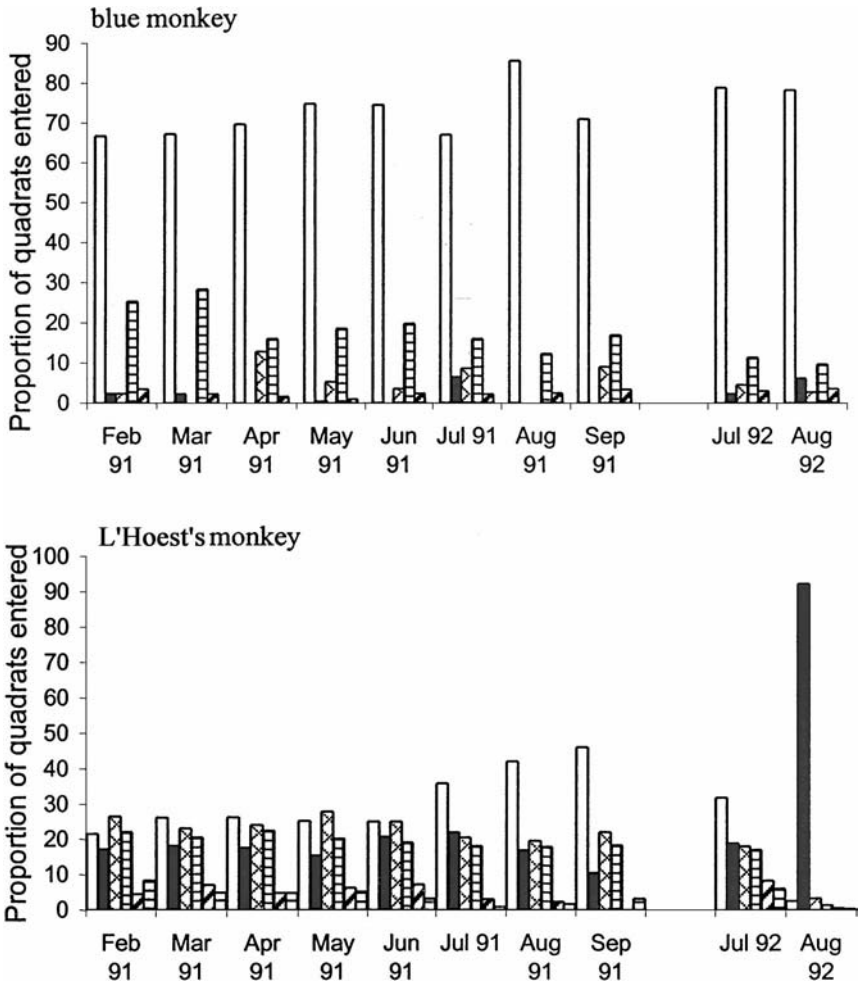


Fig. 6. Monthly use of the five different forest types by the blue monkey (top) and the L'Hoest's monkey (bottom). Clear bars = mature forest, solid bars = secondary forest, cross-hatched bars = steep slopes, gridded bars = wet valleys, single slashed bars = openings, and horizontal lined bars = landslides.

for sleeping sites ($n = 57$); they used mature forest in 71.9% of the sleep site locations (Table VIII). The L'Hoest's monkey group used 10 of 12 habitat types for sleep sites ($n = 69$; Table VIII).

Table VII. Area covered by forest types and mean proportion of observations in each type for blue and L'Hoeest's monkeys

	Mature forest		Secondary forest		Steep slopes		Wet valleys		Openings		Landslides	
	% use	Area (ha)	% use	Area (ha)	% use	Area (ha)	% use	Area (ha)	% use	Area (ha)	% use	Area (ha)
Blue Monkey	Mean (s.d.)	51.1	2.0 (2.4)	1.0	4.9 (3.9)	13.9	17.4 (5.6)	21.1	2.5 (0.8)	0.7	0	0
L'Hoeest's Monkey	Mean (s.d.)	38.5	24.9 (22.6)	16.2	17.7 (5.7)	25.9	21.0 (6.6)	27.5	4.4 (2.7)	4.5	3.8 (2.4)	4

Table VIII. Sleep site locations and proportion used for blue and L'Hoest's monkeys

Blue monkey group		L'Hoest's monkey group	
Habitat type	% Use	Habitat type	% Use
a	12.3	a	14.5
b	5.2	b	11.6
d	1.8	d	10.1
f	5.3	e	8.7
i	71.9	f	23.2
j	3.5	g	5.8
		h	13
		i	7.3
		j	2.9
		o	2.9

DISCUSSION

Determinants of Ranging Behavior

The L'Hoest's monkey group altered ranging patterns in response to changes in specific fruit resources, demonstrating an overall tendency towards a long-distance ranging pattern relative to the blue monkey group. Monthly home range areas were smaller during the 1992 dry season, when fruits were scarce and the L'Hoest's monkeys focused on the seeds of the pioneer *Macaranga neomildbraediana*, which had the highest density in their home range (Kaplin and Moermond, 2000). The group altered movements typical in previous months from a far ranging transitory pattern to a more concentrated ranging pattern in this season. However, the overall disproportionately high frequency of high C values suggests that they tended towards a long-distance ranging pattern compared to that of the blue monkey group. The L'Hoest's monkeys did not rely as heavily on single fruit or seed species as the blue monkeys did; the distribution of terrestrial herbaceous vegetation may have influenced their movement patterns. Malenky and Stiles (1991) found that bonobos feeding on terrestrial herbs are highly selective of the plant parts they consume. They concluded that terrestrial herbs are distributed in discrete patches, much like fruit. Although there are no data concerning the selectivity of L'Hoest's monkeys on terrestrial herbs, if they are selective, a group foraging in a patch of herbs may be required to move more frequently and over greater distances to locate patches of herbs suitable for consumption.

The blue monkey group also showed both a concentrated and a widely-ranging pattern in response to fruit scarcity; the response depended on the

availability of specific resources and dietary diversity. The group traveled farther and exhibited a more widely-ranging pattern when the density of trees in fruit was relatively low (the 1991 wet season) and the diversity of items in their diet was relatively high (Kaplin *et al.*, 1998). Similarly, Struhsaker (1978) found that the ranging diversity of red-tailed guenons (*Cercopithecus ascanius*) increased with plant food diversity. A more widely-ranging or diverse pattern would allow the group to monitor the environment for resource availability (Gautier-Hion, 1988; Garber, 1993) and to encounter a greater diversity of resources necessary during periods of fruit scarcity. The group exhibited a more concentrated ranging pattern when preferred fruits were plentiful (the 1991 dry season), and during a period of fruit scarcity (1992 dry season); their dietary diversity was lower during both of these seasons. The blue monkeys spent a large proportion of time feeding on one of two species: fruits of *Beilschmiedia troupinii* in the 1991 dry season (41%–50% of diet), and seeds of *Macaranga neomildbraediana* (25% to 35% of diet) in the 1992 dry season (Kaplin *et al.*, 1998). When suitable fruit tree species are relatively plentiful in the home range, the group can apparently economize on the time and energy requirements of travel by remaining within the portion of its home range that provides the greatest concentration of resources (Terborgh, 1983). Several other anthropoid studies showed that the availability of more concentrated or large food patches affects daily movement patterns, causing less diversified ranging (Rudran, 1978; Gautier-Hion *et al.*, 1981; Strier, 1987; Garber, 1993).

I initially predicted that L'Hoest's monkeys would have smaller home ranges and daily range distances than those of blue monkeys for two reasons. First, the proportion of foliage in the diet has been negatively related to day range length and home range size in primates (Clutton-Brock and Harvey, 1977). This relationship, based on tree leaf foliage, has been explained by the distribution of foliage, which is believed to be a dense and relatively predictable food supply. The L'Hoest's monkey group might be expected to have smaller day range lengths and home range areas than the more frugivorous blue monkeys, assuming that terrestrial herbs are distributed similarly to arboreal foliage. Secondly, it has been argued that invertebrate and fruit foraging are predictors of habitat use and ranging behavior: home ranges should be large enough to supply adequate space for invertebrate foraging, since invertebrates are believed to be widely distributed throughout the habitat, and home ranges should be large enough to accommodate a fluctuating fruit resource base (Terborgh, 1983; Robinson, 1986; O'Brien and Kinnaird, 1997). Again, the blue monkey group, which consumed more fruit and invertebrates, would be expected to have a greater home range area and ranging pattern than the L'Hoest's monkey group. My findings suggest that if ranging behavior is linked to food availability in the L'Hoest's monkeys,

terrestrial herbs may indeed not be densely and predictably distributed, as Malenky and Stiles (1991) found for the bonobos, or some other variable is influencing ranging behavior in this group, such as intergroup encounters and the need to monitor home range boundaries.

There is an inverse relationship between the proportion of invertebrates in the diet of the blue monkeys and both home range area and the number of new quadrats entered each sample period, suggesting a more confined movement pattern when invertebrate feeding was high. In contrast, Rudran (1978) found that blue monkeys in Kibale Forest, Uganda, used highly transitory movements, rarely reusing quadrats within a day, and he suggested that this was related to the need to continually exploit new areas as invertebrates are readily depleted in the environment. Similarly, Cords (1987), in a study of blue monkeys and red-tail monkeys (*Cercopithecus ascanius*) in Kakamega Forest, Kenya, hypothesized that they avoid reuse of quadrats within a day because of a decrease in invertebrate prey abundance in quadrats recently used. However, a study of Sulawesi macaques demonstrated that the frequency of entry into quadrats is highly correlated with invertebrate foraging, but the time spent foraging on invertebrates is unrelated to home range size (O'Brien and Kinnaird, 1997). None of the researchers examined invertebrate distribution and abundance. Estimates of invertebrate availability both on a daily basis and seasonally are needed to understand this relationship, particularly because invertebrates provide an important protein component in the diets of fruit-eating primates.

Parasite avoidance has been hypothesized as a determinant of travel distance and quadrat use in mangabeys (Freeland, 1980), though a recent study of mangabey ranging behavior discounted the role of parasites in ranging behavior (Olupot *et al.*, 1997). Freeland (1980) argued that during dry seasons parasite infested fecal material posed a threat to mangabey populations so that groups would travel farther and avoid returning to quadrats already visited, whereas during wet seasons the fecal material would be washed away and parasites would experience high mortality rates. I believe parasite avoidance was not a determinant of ranging behavior in the focal blue and L'Hoest's monkey groups. Rainfall was not related to travel distance. Furthermore, the groups showed a reduced ranging pattern (increase in reuse of quadrats) during the second dry season (1992), most likely related to the composition of their diets.

Intergroup conflict can also affect ranging behavior in primates (Struhsaker, 1974; Isbell, 1983). I never observed the focal blue monkey group encounter a conspecific group, and their ranging pattern did not indicate border-monitoring behavior. Conversely, encounters with other L'Hoest's monkey groups was relatively common during follows of the focal group (unpublished data). These encounters could last ≥ 1 h and involved

chases and vocalizing. Accordingly, intergroup conflicts and the threat of conflict (border-monitoring) may determine ranging behavior in L'Hoest's monkeys. I believe that intergroup encounters with conspecifics did not determine blue monkey ranging behavior during my study. However, it cannot be discounted as a factor influencing ranging behavior in either species.

Forest Use

The blue monkeys selected mature forest above all other forest types within their home range. The density of *Chrysophyllum rwandense* had a positive effect on entry into forest habitat types by the blue monkey group. *Chrysophyllum rwandense* produce relatively large (13.2 mm) fleshy fruits, which were among the top 5 food items from June 1991 through the end of the study (Kaplin *et al.*, 1998). Mature forest habitats had the highest densities of *Chrysophyllum rwandense* and *Beilchmiedia troupinii*, another large fleshy fruit that ranked first in the diet during 6 months of the study. The presence of these two tree species is positively correlated in the habitat types ($r^2 = 0.682$, $p < 0.01$). Terrestrial herbaceous vegetation may be an indicator of the degree of canopy closure. There is an inverse relationship between the density of terrestrial herbs in a habitat and entry into that habitat by the blue monkey group, suggesting that they selected habitats with more closed, continuous canopy. The blue monkeys moved most frequently at heights >12 m, and they rarely traveled on the ground, versus L'Hoest's monkeys, which spent about 38% of their time on the ground (Kaplin and Moermond, 2000). In the Kibale Forest, Rudran (1978) found that the lack of continuous canopy produced bottlenecks which served as pathways for movement from one part of the home range to another by blue monkeys. Similarly, Naughton-Treves (1998) suggested that the movements of red-tailed monkeys (*Cercopithecus ascanius*) may be limited by arboreal travel routes.

In contrast, the L'Hoest's monkey group used a broader range of habitat types than the blue monkeys did, and they included disturbed habitats such as landslides and road edges where they foraged for terrestrial herbs (Kaplin and Moermond, 2000). They used secondary forest most frequently within their home range and this was also reflected in their selection of sleep sites. Measures of fruit abundance did not have an influence on habitat use by L'Hoest's monkeys, nor did the structural characters that I measured. Although there is no relationship between the density of terrestrial herbaceous vegetation and use of habitat types by the L'Hoest's monkeys, herbs cannot be ruled out as a determinant. If they forage selectively, the scale of measurement of terrestrial herbs may not have been fine enough to detect changes evident to them.

Overall, the L'Hoest's monkeys tended to be generalists in the use of habitat types compared with the blue monkey group. Factors that may allow L'Hoest's monkeys to be more flexible in use of habitats include: unlike many other arboreal primates, they travel on the ground and are not restricted to specific arboreal structural characteristics and they eat more fruits and seeds from shrubs and secondary tree species than blue monkeys do, which may bring them into contact with ecotones and secondary forest more frequently. The blue monkeys showed a preference for mature forest habitats, which may be linked to both fruit resource availability and structural characteristics such as larger fruit patches (Leighton, 1993) or a closed canopy for arboreal travel.

ACKNOWLEDGMENTS

The study was supported by grants from U.S.A.I.D. Program for Science & Technology Cooperation (DHR-5542-G-SS-9033-00), U.S.A.I.D. Mission to Rwanda, the Davis Fund Summer Fellowships from the Dept. of Zoology, Univ. of Wisconsin-Madison, and a P.E.O. Scholar Award. I am thankful to the host institutions O.R.T.P.N. and I.R.S.T. for facilitating the research. P.C.F.N./WCS provided logistical support in the field. Field work was made possible through the assistance and dedication of J.-B. Gakima, K. Kristensen, G. Kamarapaka, F. Manirafasha, J. Mvukiyumwami, G. Ndirayime, E. Ngabonziza, F. Ngayabahiga, F. Nkurunziza, I. Semahoro, and C. Sun. I am indebted to T.C. Moermond for support throughout the study, J.W. Jordan for his mapping skills, E. Neufeld for scanning and digitizing assistance, and B. Feeny for his artwork. Discussions of home range analysis with John Cary and Linde T. Ostro were most insightful. I thank M. Schultz for assistance with statistical analyses, and P. Arcese, T.C. Moermond, C.T. Snowdon, K.B. Strier, M.G. Turner, and two anonymous reviewers for helpful comments on earlier versions of this manuscript.

REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behavior* 49: 227–267.
- Altmann, S. A., and Altmann, J. (1970). *Baboon ecology: African field research*. Chicago: University of Chicago Press.
- Bennett, E. L. (1986). Environmental correlates of ranging behavior in the banded langur, *Presbytis melalophos*. *Folia Primatologica* 47: 26–38.
- Boinski, S. (1987). Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia primatologica* 49: 151–167.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammology* 24: 346–352.

- Butynski, T. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecological Monographs* 60: 1–26.
- Chapman, C.A., Wrangham, R., and Chapman, L. J. (1994). Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160–171.
- 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, London, pp. 557–584.
- Conover, W. J. (1980). *Practical nonparametric statistics*. Wiley & Sons, New York.
- Cords, M. (1987). *Mixed-species association of Cercopithecus monkeys in the Kakamega Forest, Kenya*. Vol. 117, University of California Press, Berkeley, California.
- De Solla, S., Bonduriansky, R., and Brooks, R. J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology* 68: 221–234.
- Deneba Software. (1992). *CANVAS 3.0*. Miami, Florida.
- Freeland, W. J. (1980). Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. *Ecology* 61: 1297–1303.
- Garber, P. A. (1993). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology* 14: 145–166.
- Gautier-Hion, A. (1988). The diet and dietary habits of forest guenons. In Gautier-Hion, A., Bourlière, F. and Gautier, J.-P. (eds.), *A primate radiation: evolutionary biology of the African guenons*, Cambridge University Press, Cambridge, pp.257–283.
- Gautier-Hion, A., Gautier, J.-P., and Quris, R. (1981). Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Revue Ecologie (Terre et Vie)* 35: 511–536.
- Isbell, L. A. (1983). Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest Uganda. *Folia Primatologica* 41: 34–48.
- Kaplin, B. A. and Moermond, T. C. (2000). Foraging ecology of the mountain monkey (*Cercopithecus lhoesti*): implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology* 50:227–246.
- Kaplin, B. A., Munyaligoga, V., and Moermond, T. C. (1998). The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica* 30:56–71.
- Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica* 24: 187–194.
- Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* 14: 257–313.
- Lemos de Sá, R. M., and Strier, K. B. (1992). A preliminary comparison of forest structure and use by two isolated groups of woolly spider monkeys, *Brachyteles arachnoides*. *Biotropica* 24: 455–459.
- Malenky, R.K., and Stiles, E. W. (1991). Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. *American Journal of Primatology* 23: 153–169.
- Martin, P., and Bateson, P. (1986). *Measuring Behavior*. Cambridge University Press, New York.
- Medway, L. (1972). Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society* 4: 117–146.
- Naughton-Treves, L. (1998). Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology* 12: 156–168.
- O'Brien, T. G., and Kinnaird, M. F. (1997). Behavior, diet, and movements of the Sulawesi Crested Black Macaque (*Macaca nigra*). *International Journal of Primatology* 18: 321–351.
- Olupot, W., Chapman, C.A., Waser, P.M., and Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology* 43: 65–78.
- Ostro, L. E. T., Young, T. P., Silver, S. C., and Koontz, F. W. (1999). A geographic information system (GIS) method for estimating home range size. *The Journal of Wildlife Management* 63: 748–755.

- Raemakers, J. J. (1980). Causes of variation between months in distance traveled by gibbons. *Folia Primatologica* 34: 46–60.
- Robertson, P. A., Aebischer, N. J., Kenwood, R. E., Hanski, I. K., and Williams, N. P. (1998). Simulation and jack-knifing assessment of home-range indices based on underlying trajectories. *Journal of Applied Ecology* 35: 928–940.
- Robinson, J. G. (1986). Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. *Smithsonian Contributions to Zoology* 431: 1–60.
- Rudran, R. (1978). *Socioecology of blue monkeys (Cercopithecus mitis stuhlmanni) of the Kibale Forest, Uganda*. Smithsonian Institution Press, Washington, D.C.
- Strier, K. B. (1987). Ranging behavior of Woolly Spider Monkeys, or Muriquis, *Brachyteles arachnoides*. *International Journal of Primatology* 8: 575–591.
- Struhsaker, T. T. (1974). Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *American Zoologist* 14: 177–184.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*. Chicago: University of Chicago Press.
- Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In Chivers, D. J. and Herbert, J. (eds.), *Recent advances in primatology*, Academic Press, New York, pp. 225–248.
- Sun, C., Kaplin, B. A., Kristensen, K. A., Munyaligoga, V., Mvukiyumwami, J., Kajonda, K., and Moermond, T. C. (1996). Tree phenology in a tropical montane forest of Rwanda. *Biotropica* 28: 668–681.
- Terborgh, J. (1983). *Five New World Primates*. Princeton University Press, Princeton, N.J.
- Troupin, G. (1982). *Flores des plantes ligneuses du Rwanda*. Publication no. 21. Institut National de Recherche Scientifique, Butare, Rwanda.
- White, G. C., and Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data*. Academic Press, Inc., New York.
- Wu, H.-Y., and Lin, Y.-S. (1993). Seasonal variation of the activity and range use patterns of a wild troop of Formosan macaque in Kenting, Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 32: 242–252.