Mangabey (*Cercocebus albigena*) Ranging Patterns in Relation to Fruit Availability and the Risk of Parasite Infection in Kibale National Park, Uganda

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Two opposing hypotheses concerning determinants of mangabey (*Cercocebus albigena*) ranging patterns have been advocated. One hypothesis suggests that ranging patterns of mangabeys are largely a response to fruit availability, while the other hypothesis advocates that concerns of fruit availability are supplemented or overridden by concerns of fecal contamination and that the risk of parasite infection, especially during dry weather, determines their pattern of range use. In this 9 month study of mangabeys in the Kanyawara study area of Kibale National Park, mangabeys moved longer distances during the wet season than during the dry season. There were no seasonal differences in group spread, number of 50 by 50 m quadrats used, or in quadrat overlap between sequential sample periods. Intensity of quadrat use was closely related to the number of fruiting trees/lianas in the quadrats, irrespective of season. These findings are consistent with the hypothesis that fruit availability is a main factor influencing mangabey ranging patterns. The results are not consistent with the hypothesis that mangabey ranging patterns largely reflect differential seasonal risk of parasite infection. Am. J. Primatol. 43:65–78, 1997.   © 1997 Wiley-Liss, Inc.

INTRODUCTION

The most detailed studies of the determinants of primate ranging patterns have been concerned with the distribution and abundance of food resources [Bennett, 1986; Raemakers, 1980]. Such studies have involved interspecific comparisons of ranging patterns [Milton & May, 1976; Clutton-Brock & Harvey, 1977]

or intraspecific comparisons of ranging data from groups occupying different habitats [Crook & Gartlan, 1966] or over time [Chivers, 1974; Struhsaker, 1975; Clutton-Brock, 1975, 1977; Milton, 1980; Raemakers, 1980; Marsh, 1981; Isbell, 1983]. Such studies typically conclude that the frequency with which habitats are used by a primate group is closely related to food abundance. When food abundance changes, both ranging patterns and the diet composition are modified [Rudran, 1978; Bennett, 1986; Hill & Agetsuma, 1995]. For example, Gautier-Hion et al. [1981] found that during the rainy season, when fruit was abundant, there was no correlation between time *Cercopithecus cephus* spent in an area and the number of fruiting trees or the number of fruiting species in the area. Conversely, in the dry season, when fruit was scarce, there was a positive correlation between the time monkeys spent in an area and the number of fruiting trees found there.

Similarly, a study of gray-cheeked mangabeys *(Cercocebus albigena)* conducted by Waser [1974] suggested that fruit availability was a major factor influencing their ranging patterns. Based on a study of five groups in the Kanyawara study area of Kibale Forest, Waser [1975] found that fruits made up the largest single type of food in the mangabey diet, comprising 59% of feeding observations. This closely corresponded to 58% observed by Freeland [1979] and to 61% observed by Wallis [1978] from the Ngogo study area, approximately 10 km away in the same forest. Further, Waser [1977] found that mangabey movement patterns appear to be centered on a large tree in fruit. A group repeatedly visited this tree over periods of days or weeks, while sampling the surrounding area. When fruit from one such tree was exhausted and no others had been located nearby, the group left the area entirely and searched widely until it found a similar large fruiting tree.

However, for some primate species, factors other than food supply have been found to affect ranging patterns. These include such factors as the position of sleeping sites [Crook & Aldrich-Blake, 1968; Tenaza, 1975], location of water holes [Altmann & Altmann, 1970], weather [Chivers, 1974], the need to patrol territorial boundaries [Whitten, 1982], the group's movement on previous days [Fossey & Harcourt, 1977], and intergroup interactions [Struhsaker, 1975; Waser, 1977; Isbell, 1983]. Freeland [1980] and Hausfater and Mead [1982] have suggested that the risk of parasite transmission could also affect primate ranging patterns. Based on a study of two mangabey groups in the Ngogo study area, of Kibale, Freeland [1980] pointed out that relative fruit density in different areas may be important in determining mangabey movements only during wet weather. He observed that mangabeys did not avoid dropping feces on branches and foliage and that extinction rates of intestinal protozoa are higher during the wet weather because rain washed off the feces. He also documented the relationship between weather conditions, mangabey activity, food consumption, movements, and use of space. By surveying areas used by his animals during a 5 day follow compared with areas which were not used, he found that there was no significant difference in fruit availability in the two areas. Freeland concluded that, unlike in wet weather, when range use by mangabeys may be determined by availability of fruit, during dry periods fecal contamination on vegetation and the associated risk of parasite infection may force mangabeys to abandon areas of high fruit density. Such a phenomenon has not been investigated for the mangabeys of the Kanyawara study area of the same park. If it were applicable, one would predict fruit availability to influence ranging patterns only during the wet season. Furthermore, Freeland [1980] hypothesized that during dry weather mangabeys should move longer distances, use more quadrats, and exhibit less day-to-day overlap in quadrat use to avoid reexposure to their own parasites. Freeland's

logic would also lead us to expect mangabeys spread out more during the dry season than during the wet weather. If these hypotheses were generally true, one would expect to see the same seasonal changes in the pattern of range use for other mangabey populations.

While Freeland's [1980] and Waser's [1975] studies agree on the importance of fruit availability as a factor influencing mangabey ranging patterns, they differ on the relative strength of the importance of fruit availability during the wet season. This paper presents data relevant to distinguishing between these two hypotheses.

In this paper, we are indirectly testing Freeland's [1980] ideas by examining changes in ranging patterns. We first show that mangabey ranging patterns did vary among days, months and seasons. We then proceed to test predictions derived from the hypothesis that avoidance of fecal contamination affects ranging patterns independent of changes in food availability. Finally, we examine the relationships between ranging patterns and fruiting tree abundance and diversity to determine whether ranging was equally influenced by fruit availability in the wet and dry seasons.

STUDY AREA AND METHODS

The study group inhabited an area (Fig. 1) which is part of the Kanyawara study area of Kibale National Park, located in western Uganda (0° 34´N, 30 ° 22´E). The forest receives a mean annual rainfall of 1,475 mm, which is relatively well dispersed throughout the year, falling, on average, 166 days per year [Kingston, 1967]. However, there are distinct wet and dry seasons. March–June and September–November are usually wetter months, and July–August and December–February are usually drier months.

A group of 15 individuals occupying the same area as Waser's [1974] groups was studied. Having been a subject of three previous studies [Waser, 1974, 1975, 1977; Waser & Floody, 1974; Olupot et al., 1994] and since researchers were continuously in the area, the study group was well habituated. Mangabeys tolerated the observer walking directly beneath them (less than 10 m away), and it typically was possible to follow this group continuously after initial contact.

Between late October 1992 and the end of June 1993, the group was followed for 10 complete days per month, 5 days during each half of the month. The group was also followed on a partial basis on the other days of the month to maintain a continuous picture of all the areas visited during the study. For all-day follows, contact was established before 0715 and broken after 1845 h. For the partial day follows, duration of contact was variable, ranging from a few hours to almost the entire day. The group was followed for no less than 28 days each month, yielding a total of 970 and 1,712 h of contact for all-day and partial day follows over the entire study.

Data were recorded during 5 min sampling periods (scans) centered on the quarter and three-quarter hours. During these periods, the locations and feeding and foraging activity of as many individuals as possible were recorded. Criteria used to score activity correspond to those of Struhsaker [1975] and Waser and Floody [1974]. Locations of individuals, as well as the trees and liana species from which fruits were taken, were plotted on large scale (1:2,500) maps of the study area.

Centers of "mass" (see Waser, 1975; Olupot et al., 1994) of all individuals sighted were determined. Typically, only a few individuals could be seen from any given location; thus, as large an area as possible was searched during the 5

Home range

Part of home range outside mapped area and through which the group ranged during 3 all-day follows in November and December.
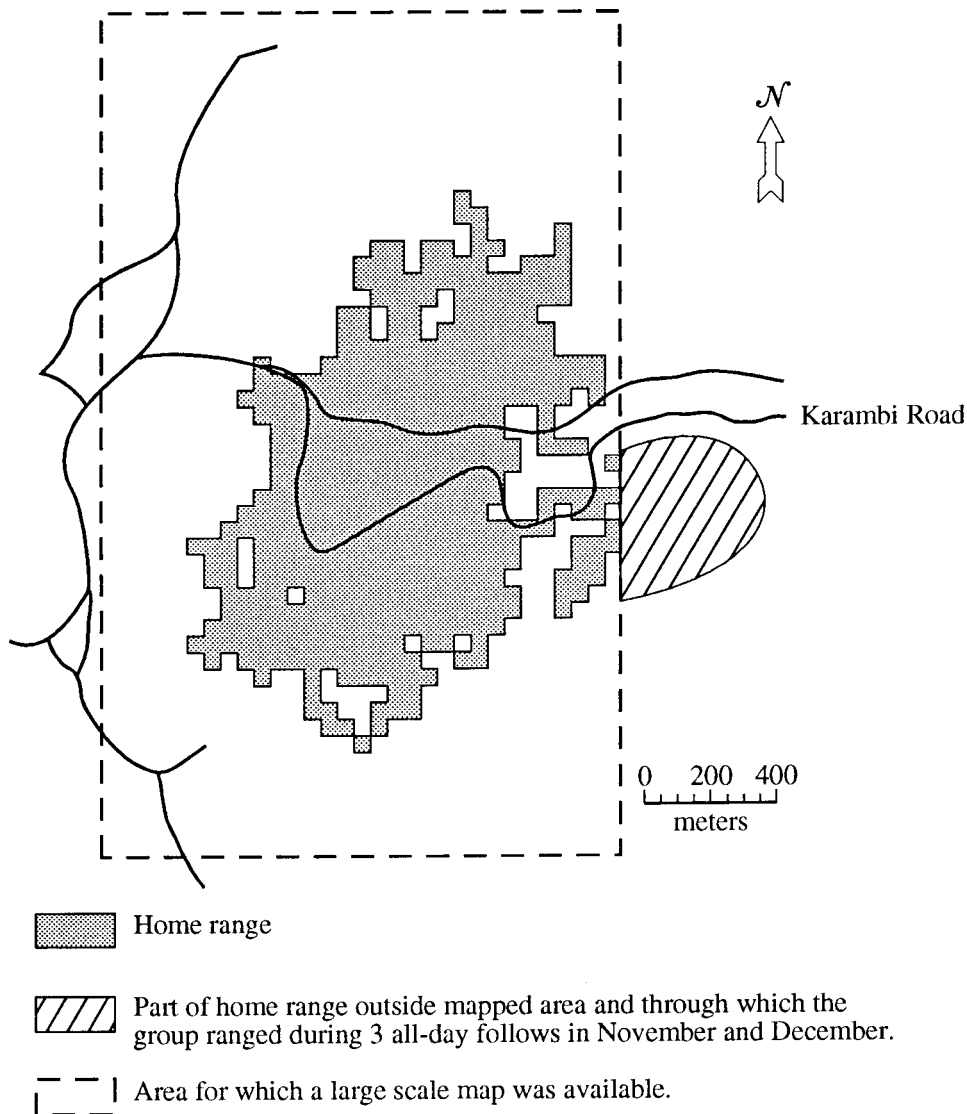
Area for which a large scale map was available.

Fig. 1. Area utilized by the group of gray-cheeked mangabeys studied in Kibale National Park, Uganda, between October 1992 and June, 1993. This is based on data obtained from the quarter and three-quarter of the hour plots of individual sightings during all-day follows.

min of each scan. Emphasis was placed on determining the spatial distribution of group members; thus, the area searched frequently exceeded that occupied by the group. Use of the detailed maps allowed accurate plotting of the location of widely spaced individuals. Two observers simultaneously recorded the individual locations. This allowed accurate determination of distances moved, group spread, and quadrat utilization [Waser, 1975].

Distances traveled were determined as straight line distances between sequential centers of mass or from a sum of these distances on a daily basis (daily distances). Following Waser [1974] we determined group spread as the distance

between the two most spatially separated individuals at each scan. The number of quadrats used was determined by superimposition of a 50 by 50 m grid over areas on the map that the group used. A quadrat was considered used if at least one animal was sighted in it during a scan. This constituted a scan sighting. We quantified sample period to sample period quadrat overlap for the 5 day sample periods as the proportion of quadrats used during a sample period that were used during the preceding sample period.

Fruit availability was quantified as the total number of fruiting trees and liana species occurring in each 50 m × 50 m quadrat used by mangabeys during each 5 day sample period. These data were analyzed by season and for the entire nine months of the study period. Analysis of the influence of fruit availability on ranging patterns was done in two ways.

First, quadrats used in each 5 day sample period were segregated into three categories: lightly used (one to two scan-sightings during the sample period), moderately used (three to four scan-sightings), and heavily used (five or more scan-sightings). Two quadrats were randomly selected from each category and the fruiting trees or lianas seen were counted. Differences in the number of fruiting trees/lianas among the three categories of quadrat were tested for significance using a chi-square. Secondly, to illustrate how fruit availability influenced quadrat use, we constructed ranging maps for each sample period, and the number of fruiting trees occurring in each quadrat was calculated. The number of scan-sightings in each quadrat was then correlated with the number of fruiting trees.

Finally, fruiting trees/lianas were identified by species, and the number of fruiting species in each quadrat for the entire study period was determined. Quadrats were totalled according to the number of trees/lianas as well as the number of fruiting species that they contained. The total number of mangabey scan-sightings in each quadrat was compared to both fruit abundance (number of fruiting trees per quadrat) and species richness (number of fruiting species per quadrat) for each season, and for the entire study.

Parametric tests were conduced where normality and homogenous variance could be verified; otherwise, nonparametric tests were used. Rainfall data were available for 6 of the 9 months of the study; rainfall was significantly greater (mean = 333 mm, SD = 84) during the wet season months of October, November, and March than during the dry season months of December, January, and February (mean = 74 mm, SD = 58). During the other three months of the study, qualitative rainfall patterns were similar to the long-term pattern described by Kingston [1967].

RESULTS
Daily Ranging

Daily distances moved (mean = 1,008 m, SD = 260.2) and group spread (mean = 57 m, SD = 31.2) varied widely between days. Mean distances moved per day (Kruskal-Wallis, H = 47.3; $P < 0.001$) and group spread (H = 33.9; $P < 0.001$) varied significantly between months. Five day sample plots of quadrats used suggested a low tendency to reuse most individual quadrats and therefore a general tendency for constant home range shift (Fig. 2).

Seasonal Ranging

Mean daily distances moved were greater in wetter sample periods than in drier sample periods (t = 3.11; $P < 0.01$). In contrast, group spread (t = 1.244; $P > 0.2$) and the number of quadrats used (Mann-Whitney U-test, U = 25, $P > 0.2$)
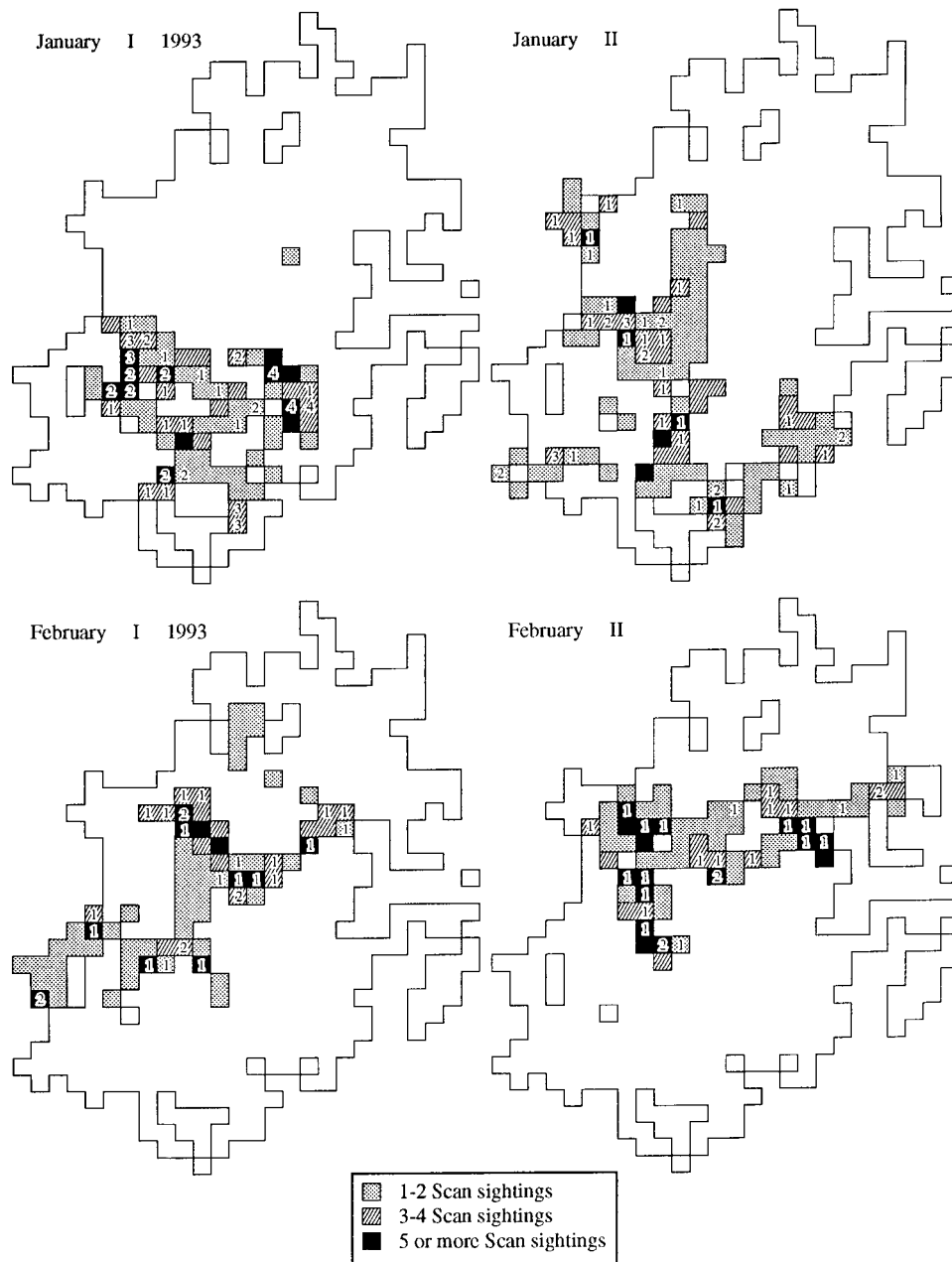
A   Dry Months

Fig. 2. Examples of utilization of 50 by 50 m quadrats by gray-cheeked mangabeys studied between October 1992 and June 1993 in Kibale National Park, Uganda. Values in the quadrats represents the number of fruiting trees/lianas present during each sample period. January and February (**A**) represent drier months, while April and May (**B**) represent wetter months. The symbols I and II refer to samples from the first and second half of each month, respectively.

B

Wet Months

April I 1993

April II

May I

May II

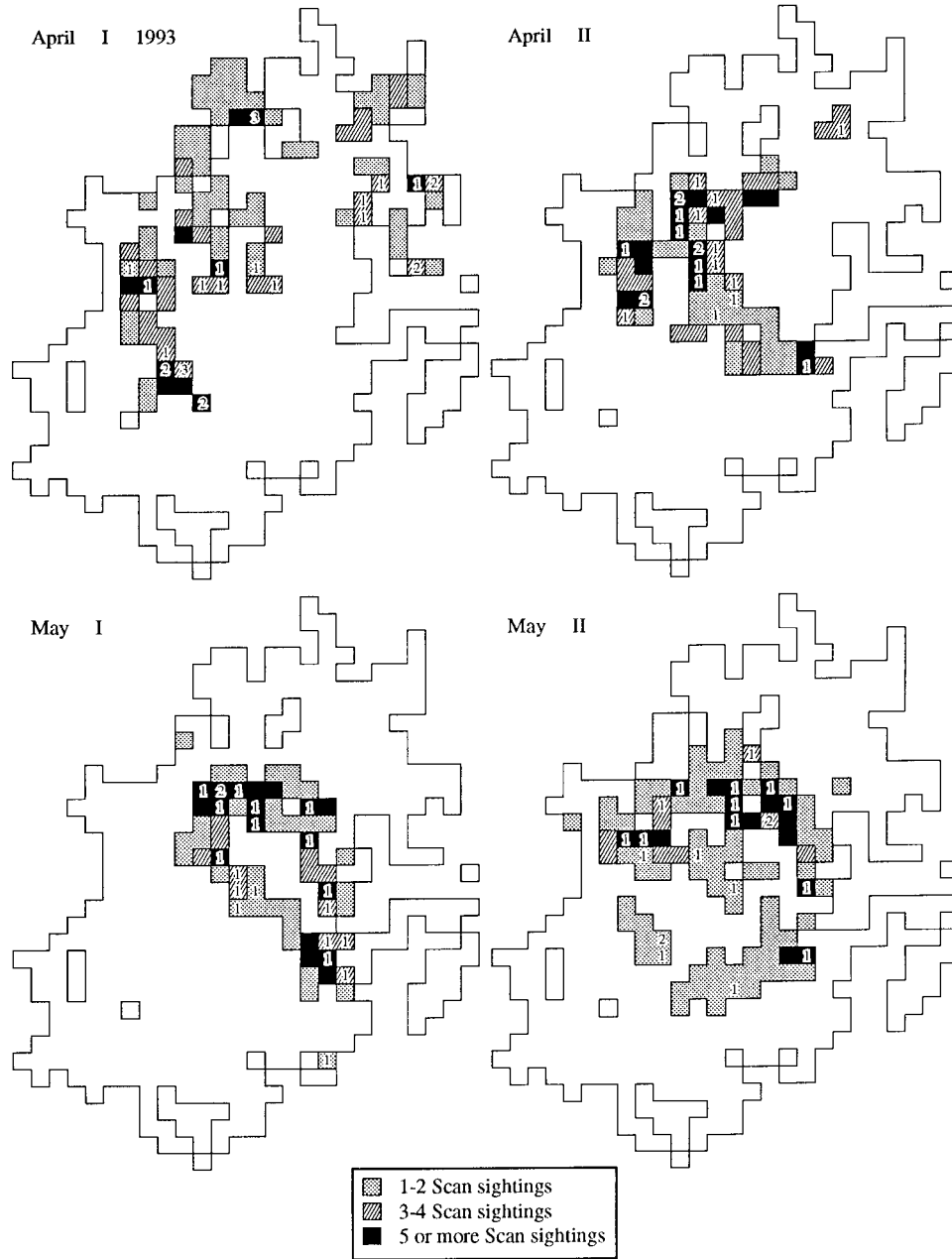| | 1-2 Scan sightings |
| | 3-4 Scan sightings |
| | 5 or more Scan sightings |

Figure 2B.

TABLE I. Seasonal and Daily Ranging: Distances Moved, Group Spread, and Number of Quadrats Used*

	Wet season	Dry season	Wet + dry season
Daily distances (m)	1,108	885	1,008
SD	304	144	260
Daily spread (m)	61	50	57
SD	19	8	31
Number of quadrats	82	87	83
SD	14	18	14

*n = 84 days for daily distances and spread; 17 sample periods for number of quadrats

did not show any significant difference between seasons (Fig. 2; Table I). Also, quadrat overlaps between sequential sample periods in the wet season and the dry season were not significantly different (U = 14.5; $P > 0.05$).

Fruit Availability and Quadrat Utilization

During this study, fruit was an important component of the mangabey diet, constituting 59% of feeding observations (when invertebrate foraging scores are included among feeding observations). The distribution of fruit abundance between quadrats was heterogeneous during both wet and dry seasons (wet season χ^2 = 12.83, $P < 0.001$; range = 0–8 trees/lianas; dry season χ^2 = 12.68, $P < 0.001$, range: 0–6 trees/lianas). The number of fruiting trees/lianas per quadrat (wet season: n = 349 quadrats, median = 0, range = 0–9 trees/lianas; dry season: n = 300 quadrats, median = 0, range = 0–6 trees/lianas) was not different between the wet and dry season (Mann-Whitney U-test, U = 51823.5, $P = 0.93$; n wet = 349 quadrats, n dry = 300 quadrats). Similarly, there were no significant seasonal differences in the total number of fruiting species in each quadrat (wet season: n = 349 quadrats, median = 0, range = 0–4 species; dry season: n = 300 quadrats, median = 0, range = 0–9 species) (U = 51360, $P = 0.78$). Seasonal differences in the type and amount of fruit available reflect the tendency by the monkeys to utilize different proportions of each food type between seasons (Table II).

An analysis of the number of fruiting trees in two randomly selected quadrats of each category per sample period revealed that the intensity of quadrat use was significantly related to the number of fruiting trees in the quadrat (H = 12.70, $P < 0.01$) (Table III). Additionally, there was a significant relationship between the total number of individual fruiting trees/lianas in a quadrat and the number of mangabey scan-sightings in the quadrat (Spearman's rank correlation coefficient, r_s = 0.702, $P < 0.0001$, n = 444 quadrats) (Fig. 3). The same was true when the analysis was

TABLE II. Seasonal Changes in Dietary Composition in the Study Group of Gray-Cheeked Mangabeys

	Food item					Total number of
	% fruit[a]	% leaf	% bark	% flowers[a]	% invertebrates	feeding observations[b]
Dry season	85.41	5.63	4.79	2.55	1.60	3,443
Wet season	80.78	4.88	4.79	7.51	2.02	3,461

[a]Significant differences in the proportions of feeding observations of each type of food item between the two seasons as tested by the Z test for proportions (CI$\alpha_{0.05}$; fruit = 0.043 ± 0.018; flowers = −0.05 ± 0.009).
[b]Scores for searching for invertebrates (foraging) are not included.

TABLE III. Number of Fruiting Trees in Two Randomly Selected Quadrats of Those Used During Each 5-Day Sample Period by a Group of Gray-Cheeked Mangabeys in the Kanyawara Study Area of Kibale National Park Between October 1992 and June 1993, Inclusive

Sample period	Number of fruiting trees in heavily used quadrats ($\geq$5 scan-sightings)	Number of fruiting trees in moderately used quadrats (3–4 scan-sightings)	Number of fruiting trees in lightly used quadrats (1–2 scan-sightings)
Oct II	2	1	0
Nov I	3	4	0
Nov II	2	0	0
Dec I	1	0	1
Dec II	4	2	0
Jan I	6	2	2
Jan II	1	1	2
Feb I	1	1	0
Feb II	2	2	0
Mar I	3	0	1
Mar II	1	5	0
Apr I	3	0	0
Apr II	1	0	0
May I	0	1	0
May II	2	2	1
June I	4	2	0
June II	3	1	3
Mean	2.29	1.41	0.59
SD	1.49	1.42	0.94
Range	0–6	0–5	0–3

*The quadrats are categorized according to the number of times mangabeys were sighted in them during sampling. The symbols I and II refer to the first and second samples of the month, respectively.

carried out separately for the wet (r_s = 0.656, P < 0.0001, n = 349 quadrats) and the dry (r_s = 0.610, P < 0.0001, n = 300 quadrats) seasons (Figs. 4, 5).

When quadrat use was analyzed in terms of species richness rather than fruit abundance, there was a significant relationship between the total number of fruiting species in each quadrat and the number of scan-sightings in the quadrat (r_s = 0.697, P < 0.0001, n = 444 quadrats). This relationship held both for the wet (r_s = 0.649, P < 0.0001, n = 349 quadrats) and the dry (r_s = 0.610, P < 0.0001, n = 300) seasons.

DISCUSSION

There was a pronounced temporal variation in mangabey *(Cercocebus albigena)* ranging patterns. Mean daily distances varied between days, between months, and between seasons and the number of quadrats used varied from month to month. This variation could reflect changing food availability [e.g., Waser, 1977; Wallis, 1978; Gautier-Hion et al., 1981; Hill & Agetsuma, 1995] or changes in some other environmental factor unrelated to food [e.g., Struhsaker, 1975; Waser, 1974; Freeland, 1980; Whitten, 1982].

A logical extension of Freeland's [1980] hypothesis that range use is influenced by seasonal changes in the risk of parasite infection would be that mangabeys should move longer distances, use more quadrats, and spread out more during the dry season than during the wet season and that there should be
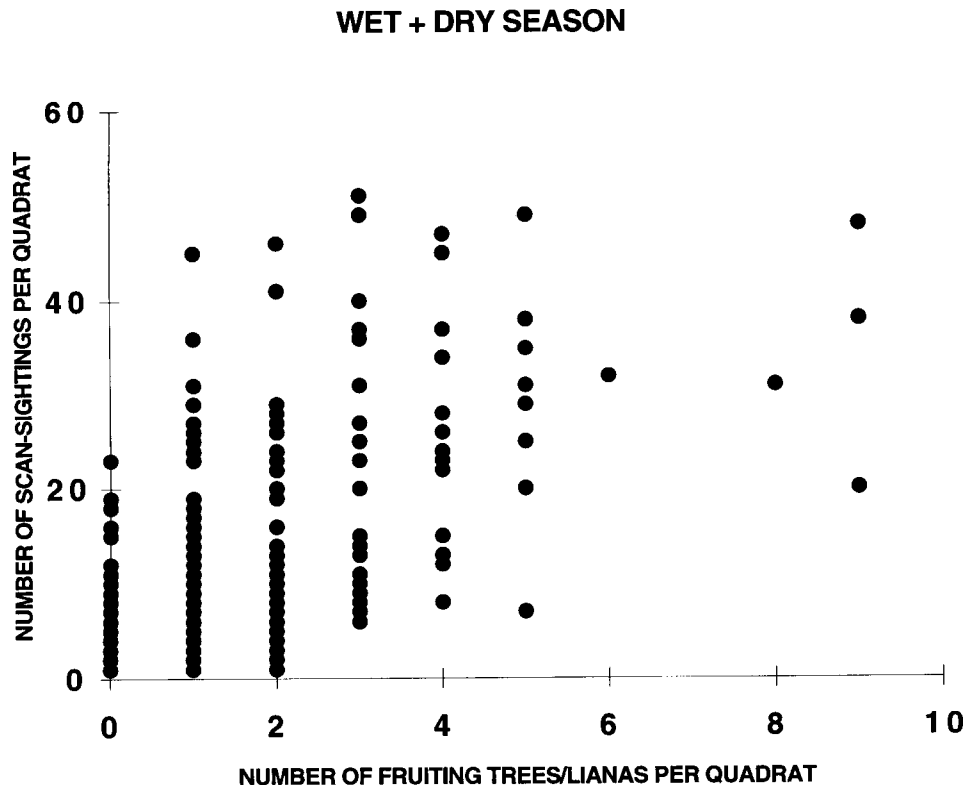
WET + DRY SEASON

Fig. 3. Relationship between the total number of fruiting trees/lianas in a quadrat and the number of mangabey scan-sightings in that quadrat in the Kanyawara study area of Kibale National Park, Uganda.

more quadrat overlaps between sample periods during the wet than during the dry season. However, counter to this hypothesis, we documented that mangabeys moved significantly longer distances during the wet than the dry season and that there were no significant seasonal differences in quadrat overlap, in the number of quadrats used, or in group spread.

This suggests that at least for the mangabey group studied, avoidance of fecal contamination was either not a factor influencing movements, or if it was, it was not a major one. In the sense that mangabeys moved significantly longer distances during the wet season, these results are consistent with the findings of Struhsaker [1975] who found that, for unknown reasons, the folivorous *Colobus badius tephrosceles* moved further on days with rain than on days without.

The numbers of fruiting trees/lianas per quadrat were highly heterogeneously distributed among quadrats during both the wet and dry season, suggesting that fruit was not equally distributed in the used and unused parts of the home range. These results are not consistent with Freeland's [1979] findings that fruit availability in used and unused areas of the home range was equal.

Although the differences from Freeland's [1979] results could reflect differences in sampling methodology, the results may be a true representation of differences in food availability between the two areas. Intensity of quadrat use was significantly related to the number of fruiting trees/lianas in the quadrat. The significant relationship between length of time the monkeys spent in different quadrats and the number of fruiting trees/lianas overall and for both the wet
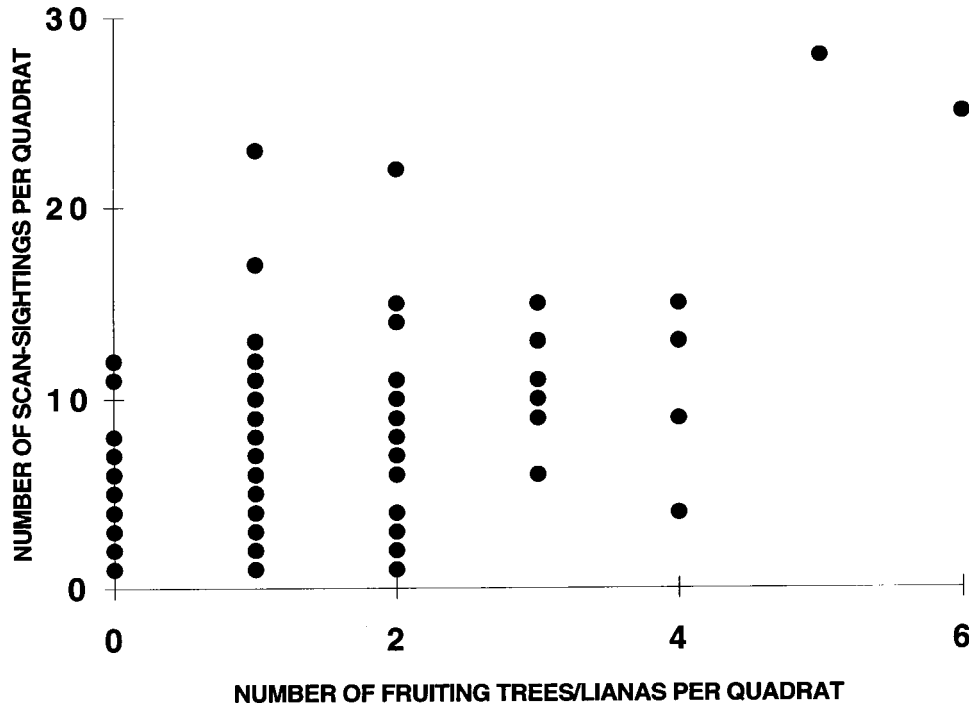
DRY SEASON

Fig. 4. Relationship between the number of fruiting trees/lianas in a quadrat and the number of mangabey scan-sightings in that quadrat during the dry season.

and dry seasons suggests that fruit availability is a factor influencing mangabey ranging patterns irrespective of season. This is consistent with Waser's [1974] observation that overall, fruiting trees form the main focus of all mangabey movements and with Freeland's [1980] suggestion that fruit may determine mangabey ranging patterns during the wet weather. It is likely that in parts of the home range mangabeys did not use in a given period, fruit availability was comparatively lower. As suggested by the lack of differences in fruit availability between quadrats used during the wet and dry seasons, tracking the availability of fruit is likely to have been the main cause for the constant home range shifts. These results are, however, not consistent with Freeland's [1980] suggestion that fruit availability may not be a factor influencing mangabey ranging patterns during the dry weather.

Mangabeys shifted their diet between the two seasons. For instance, a decrease in fruit consumption during the dry season was accompanied by a corresponding increase in flower consumption. This appeared to affect the relationship between fruit availability and the degree of quadrat use, which was slightly weaker during the dry than wet season.

The calculated r_s values are likely to be underestimates of the real relationship between ranging patterns and fruit availability. This is for two reasons. First, each quadrat was assumed to have been visited independently. The common occurrence of intensively used quadrats with no fruit in them near quadrats
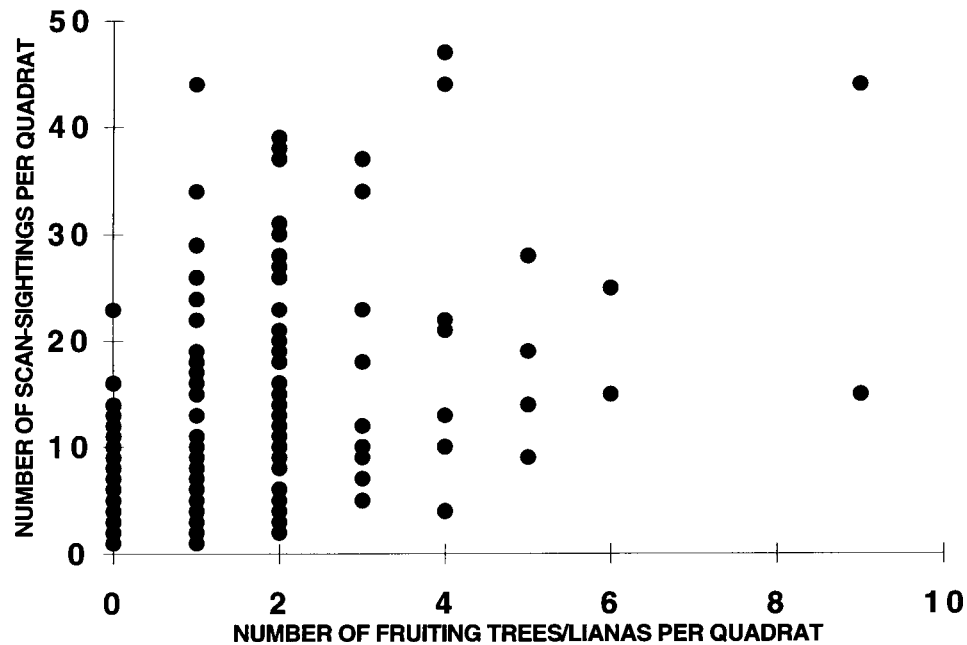
WET SEASON

Fig. 5. Relationship between the total number of fruiting trees/lianas in a quadrat and the number of mangabey scan-sightings in that quadrat during the wet season.

with fruiting trees suggests that use of quadrats without fruiting trees may at least have partly depended on availability of fruit in the neighboring quadrats. Second, using the number of fruiting plants rather than the actual amount of fruit utilized by mangabeys as a measure of fruit availability would inherently provide a crude estimate of the degree to which fruit availability would determine range use. The reason is that use of the number of fruiting trees/lianas makes the following implicit assumptions: 1) all individual fruiting plants (of the same and of different species) provided the same amount of utilizable fruit; 2) different types of fruit are equally preferred; and 3) mangabeys do not have a preference for quadrats with a high diversity of food types. The potential effect of violating any of these assumptions is to increase variance and therefore lower any estimates of the actual relationship.

While it is clear that individual fruit plants bear different amounts of fruit and that mangabeys have a preference for certain fruit types over others [Waser, 1977; Olupot, personal observation], previous work has not examined whether mangabey ranging decisions reflect fruit species diversity as opposed to simple abundance. In this study, the number of scan-sightings in a quadrat was related to number of fruiting species found in a quadrat overall and for each season. This reflects the importance of dietetic diversity to primates [Struhsaker, 1975; Clutton-Brock, 1975; Gautier-Hion et al., 1981; Bennett, 1986] and reinforces the view that foraging concerns influence ranging patterns independent of season.

The importance of dietetic diversity may lie with obtaining sufficient nutrients of a variety of types as well as a variety of species [Milton, 1980; Gautier-Hion et al., 1981] and may go beyond simple fruit diversity. Our impression was that quadrats with fruiting trees/lianas and plants with other parts like leaves, flowers, and bark that were eaten by mangabeys were visited more often than quadrats without. Because fruit is the largest component of mangabey diet, however, the potentially most critical factor during leaner periods could be low species diversity of fruiting trees and climbers. In such situations, the monkeys have a small number of fruit sources at their disposal, and they may run the risk of not obtaining a balanced diet [Gautier-Hion et al., 1981]. The findings of this study and other findings [Waser, 1974; Wallis, 1978] strongly argue for the suggestion that foraging concerns rather than risk of parasite infection always affect mangabey ranging patterns.

CONCLUSIONS

1. Mangabey ranging patterns vary on daily, monthly and seasonal bases. Mangabeys moved significantly longer distances during the wetter than during the drier months, but there were no significant seasonal differences in the number of quadrats used, in group spread, or in quadrat overlap between sequential sample periods.

2. Intensity of use of a quadrat was closely related to the number of fruiting trees/lianas in the quadrat during both the wet and dry seasons.

3. Evidence presented here suggests that variation in mangabey ranging patterns can better be explained in terms of responses to fruit availability (or in general terms, food availability) rather than in terms of responses to differential risks of parasite infection.

ACKNOWLEDGMENTS

REFERENCES

Altmann, S.A.; Altmann, J., eds. BABOON ECOLOGY. Chicago, University of Chicago Press, 1970.

Bennett, E.L. Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos.* FOLIA PRIMATOLOGICA 47:26–38, 1986.

Chivers, D.J. The siamang in Malaya: A field study of a primate in a tropical rain forest. CONTRIBUTIONS TO PRIMATOLOGY, 4:1–335, 1974.

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

Clutton-Brock, T.H. PRIMATE ECOLOGY. London, Academic Press, 1977.

Clutton-Brock, T.H.; Harvey, P.H. Primate ecology and social organisation. JOURNAL OF ZOOLOGY 183:1–39, 1977.

Crook, J.H.; Aldrich-Blake, F.P.G. Ecological and behavioural contrasts between sympatric ground dwelling primates in Ethiopia. FOLIA PRIMATOLOGICA 8:192–227, 1968.

Crook, J.H.; Gartlan, J.S. Evolution of primate societies. NATURE 210:1200–1203, 1966.

Fossey, D.; Harcourt, A.H. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). Pp. 415–447 in PRIMATE

ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Freeland, W.J. Mangabey (*Cercocebus albigena*) Social organisation and population density in relation to food use and availability. FOLIA PRIMATOLOGICA 32:108–124, 1979.

Freeland, W.J. Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. ECOLOGY 61:1297–1303, 1980.

Gautier-Hion, A.; Gautier, J.P.; Quris, R. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). TERRE ET VIE), 35, 1981.

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

Hill, D.A.; Agetsuma, N. Supra-annual variation in the influence of *Myrica ruba* fruit on the behavior of a troop of Japanese macaques in Yakushima. AMERICAN JOURNAL OF PRIMATOLOGY 35:241–250, 1995.

Isbell, L.A. Daily ranging behaviour of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. FOLIA PRIMATOLOGICA 41:34–48, 1983.

Kingston, A., ed. A WORKING PLAN FOR KIBALE AND ITWARA CENTRAL FOREST RESERVES. Entebee, Uganda, Forest Department and Government Printer, 1967.

Marsh, C.W. Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratus*). JOURNAL OF THE ZOOLOGICAL SOCIETY, LONDON. 195:473–492, 1981.

Milton, K. THE FORAGING STRATEGY OF HOWLER MONKEYS. New York, Columbia University Press, 1980.

Milton, K.; May, M.L. Body weight, diet and home range area in primates. NATURE 259:459–462, 1976.

Olupot, W.; Chapman, C.A.; Brown, C.H.; Waser, P.M. Mangabey (*Cercocebus albigena*). Population in density size and ranging: A twenty year comparison. AMERICAN JOURNAL OF PRIMATOLOGY 32:194–205, 1994.

Raemakers, J.J. Causes of variation between months in distance travelled by gibbons. FOLIA PRIMATOLOGICA 34:46–60, 1980.

Rudran, R. Sociobiology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY 249:1–88, 1978.

Struhsaker, T.T., ed. THE RED COLOBUS MONKEY. Chicago, The University of Chicago Press, 1975.

Tenaza, R.R. Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia, FOLIA PRIMATOLOGICA 24:68–80, 1975.

Wallis, S.J. THE SOCIOLOGY OF *CERCOCEBUS ALBIGENA JOHNSTONI* (Lyddeker), AN ARBOREAL, RAINFOREST MONKEY. Ph.D. Thesis, University of London, 1978.

Waser, P.M. INTERGROUP INTERACTION IN A FOREST MONKEY: THE MANGABEY *CERCOCEBUS ALBIGENA.* Ph.D. Thesis, The Rockefeller University, New York, 1974.

Waser, P.M. Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena.* EAST AFRICAN WILDLIFE JOURNAL 13:249–263, 1975.

Waser, P.M. Feeding, ranging and group size in the mangabey *Cercocebus albigena.* Pp. 183–222 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Waser, P.M.; Floody, O. Ranging patterns of the mangabey *Cercocebus albigena,* in the Kibale Forest, Uganda. ZEITSCHRIFT FUR TIERPSYCHOLOGIE 35:2–101, 1974.

Whitte, P.L. Female reproductive strategies among vervet monkeys. Ph.D. dissertation, Harvard University, Cambridge, 1982.