Mangabey (*Cercocebus albigena*) Population Density, Group Size, and Ranging: A Twenty-Year Comparison

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Mangabey groups studied in the Kibale Forest Reserve, Uganda, in 1971 were studied again in 1991 using similar data collection protocols. The results were used to assess the effect of group size on activity budgets and travel costs, and to document the effects of habitat changes on mangabey density and demography. Larger mangabey groups traveled longer distances per day than smaller groups. Time budgets were less clearly influenced by group size. Mangabey population density increased over the 20 year period. This increase in population density paralleled habitat changes, particularly an increase in tree density, and was accompanied by increased use of regenerating forest.   © 1994 Wiley-Liss, Inc.

Key words: demography, population density, group size, range use, vegetation change, *Cercocebus*, forest monkeys

INTRODUCTION

Long-term data from natural primate populations are required to assess the effect of habitat alterations on population density and demography, or to investigate variation over time in processes affecting group size and structure. For instance, data from *Papio cynocephalus* and *Cercopithecus aethiops* in Amboseli, Kenya, illustrate dramatic population declines and group size changes as a result of regional ecological changes [Struhsaker, 1973; Cheney et al., 1988; Altmann et al., 1983]. Dittus [1977] describes population changes in *Macaca sinica* and Southwick et al. [1983] provide information on *M. mulatta* populations in agricultural areas. For arboreal forest primates, such data are extremely rare.

The primary objective of this study is to compare density, group size, and demography in a Ugandan population of grey-cheeked mangabeys (*Cercocebus albigena*) first studied in 1971, and then again in 1991. Two social groups of mangabeys have used the study area over this entire 20 year period, but the two 1991 groups differ in size from those studied in 1971. A second objective of this paper is therefore to investigate whether ranging or activity patterns are influ-

enced by group size, and specifically to quantify the travel costs associated with large group size, while partially controlling for the environment by studying groups that differ in size but use the same area.

STUDY AREA AND METHODS

During April–June and August–September of 1991, we studied two groups of mangabeys in the Kibale Forest Reserve, western Uganda. Other, neighboring groups were followed and counted opportunistically. The study area was approximately 5 km², near the Kanyawara Forest Station and the Makerere University Biological Field Station (0° 34' N, 30° 22' E). Groups occupying the same area were first studied in 1971–1974 [Waser, 1974, 1975, 1977; Waser & Floody, 1974]. The Kibale Forest Reserve is a moist evergreen forest, transitional between lowland rain forest and montane forest [Skorupa, 1986; Struhsaker, 1975; Wing & Buss, 1970]. About 50% of the reserve is characterized by tall primary forest with the canopy generally 25–30 m high, some trees exceeding 55 m in height [Butynski, 1990]. The remainder of the reserve is a mosaic of swamp, grassland, thicket, and colonizing forest [Butynski, 1990; Wing & Buss, 1970]. Most of the area used by mangabeys is tall forest, although mangabeys sometimes use colonizing and swamp forest as well as areas of exotic softwoods that have been planted in grassland areas.

Since 1948, the Kanyawara study area has been protected as part of the Kibale Central Forest Reserve and in the mid 1970s it was further protected as a Research Plot. Nevertheless, between 1971 and 1991 the structure of the forest has not remained constant. On the edges of each group's home range, exotic conifer plantations planted in the 1960s have grown to maturity. In the 1970s, these areas were dominated by elephant grass *Pennisetum purpureum* and trees were seedlings and saplings; now, conifers are >25 m high and in some areas have an understory of regenerating native trees. Second, because of programs to prevent encroachment into the forest, there has been considerable regeneration along forest/grassland boundaries, so that the total area of natural forest has probably increased slightly. Third, the northern half of the study area (K14) was selectively felled in the late 1960s; because of this, there were substantial canopy gaps in the early 1970s that have now disappeared. Finally, there have been changes even in the composition of undisturbed forest. For instance, the southern part of the study area (K30) is categorized as *Parinari* forest, but over the last 20 years *Parinari excelsa* has exhibited low rates of recruitment, and there has been a localized dieback of several tree species (J. Kasenene, personal communication) [Struhsaker et al., 1989]. During both time periods there was virtually no hunting pressure (W. Olupot, personal observation) [Struhsaker, 1975], thus hunting likely had little influence on the demography of mangabeys.

To quantify differences in tree composition between the 1970s and the 1990s, we replicated the tree enumerations conducted in the early 1970s by Waser [1974, 1977] and Struhsaker [1975]. This involved identifying all trees greater than 10 m tall in 5 m wide transects. We sampled a total of 5.8 hectares (ha), most (4.2 ha) in K30 and the balance in K14. Transects were run along trails cut along compass bearings and did not follow topographic features.

Data from two mangabey groups of 14 (Group I) and 11 individuals (Group II) were recorded systematically between April and September 1991 (558 hours observation of Group I, 310 hours of Group II). These groups occupied home ranges similar to those designated by Waser [1974] as groups S and M. The groups could be followed throughout the day once the observer had made initial contact. This was facilitated by the fact that at Kanyawara there are over 156 km of trails

(nevertheless, Group I sometimes ranged outside of the trail system, as had the S group in the 1970s). In August and September, both groups were followed for five complete days (0700–1900 h) each month. Between April and June, Group I was followed whenever possible between 0715 and 1830 h. Three neighboring groups were observed to obtain group counts and an idea of their movement patterns. Similar observation schedules had been followed with the S and M groups in 1971–1974 (2,259 observation hours in March–April 1971, April 1972–May 1973, and August–October 1974 for the M group; 222 hours in July 1972–April 1973, August–October 1974 for the S group), and three neighboring groups were also counted and followed opportunistically at that time.

For groups with home ranges within the trail system, we estimated population density from observations of home range size, home range overlap, and group size. Home range size was the area of the minimum convex polygon surrounding all sightings, excluding only areas of inappropriate habitat (grassland and swamp). A group's home range overlap was the proportion of its home range that fell within the home range of at least one neighboring group. In the absence of home range overlap, population density would have been the number of individuals in the group divided by its home range size; to correct for home range overlap, we multiplied this estimate by 1 + percent overlap. This procedure yields a crude estimate of population density, but one that we can estimate in a consistent manner across groups and years. Group sizes were determined from counts as groups moved across open valleys or through gaps in the forest canopy. Counts were regarded as complete when two or more counts separated by at least a week gave identical results. Individuals were categorized into age/sex classes according to the characteristics given in Waser [1974].

Data on activity and movement patterns were collected during 5 min sampling periods (scans) centered on the quarter and three quarter hour. During the scans, locations of all individuals sighted were recorded on maps of the study area's trail grid and the position of the group's center of mass was estimated. The activity in which individuals were engaged was scored as foraging, moving, or resting, following Waser [1974].

Daily distance traveled was determined from the maps on which the center of mass was recorded every 30 min, as the sum of the straight line distances between sequential centers of mass. In addition, the study area was divided into 50 by 50 m quadrats. All quadrats in which one or more group members were sighted during the scans for each 5 d study period were counted to determine a group's cumulative quadrat use.

Several of the questions we address concern comparisons of a specific group or population at two points in time (e.g., mangabey population density at Kanyawara in the early 1970s vs. the 1990s); inferential statistics are therefore inappropriate [Hurlbert, 1984]. In comparisons of group size, daily distance, and quadrat use, the hypothesis under test is that our samples are drawn from the same population; we report the results of two-tailed t tests (where the data are normally distributed) or Wilcoxon two-sample tests [SAS, 1985]. We use a sign test to examine patterns of vegetational change, and regression to examine the relationship between daily distance moved and group size.

RESULTS
Tree Enumeration

In both regenerating forest (K14) and undisturbed forest (K30), some tree species increased in abundance between 1972 and 1991, while others declined (Table I). Overall tree density increased in both forest compartments, most mark-

TABLE I. Tree Enumerations Conducted in the Kibale Forest Reserve in the Early 1970s and Again in 1992 Along the Same Trails Using the Same Methodology (All Trees >10 m High and Counted Within 2.5 m of the Trail)*

Species	Rank	K14 n/ha 1972	K14 n/ha 1992	K30 n/ha 1972	K30 n/ha 1992
Markhamia platycalyx	13	56.6	66.3	58.0	65.0
Diospyros abyssinica	1	44.3	46.2	65.7	91.7
Celtis durandii	2	38.8	69.5	34.3	46.2
Funtumia latifolia	28	11.7	69.5	14.7	41.3
Teclea nobilis	24	14.8	24.0	21.0	14.7
Uvariopsis congensis	15	18.5	28.3	25.2	54.5
Bosqueia phoberos	43	3.7	33.2	2.8	0.2
Strombosia scheffleri	16	4.9	12.9	14.7	19.6
Millettia dura	12	4.9	11.1	7.6	4.2
Strychnos mitis	44	1.9	2.5	2.1	2.8
Celtis africana	9	8.6	19.1	2.1	2.1
Chaetacme aristata	36	1.2	7.1	8.4	5.6
Dombeya mukole	—	3.7	8.6	4.2	2.1
Parinari excelsa	3	0	2.5	10.5	11.2
Olea welwitschii	8	5.5	4.9	2.8	4.9
Linociera johnsonii	31	5.5	10.5	2.8	0
Premna angolensis	7	1.9	1.2	1.4	2.1
Lovoa swynnertonii	47	0	0	2.8	0
Pancovia turbinata	5	0	0	6.3	5.6
Mimusops bagshawei	40	0.6	0.6	2.1	3.5
Chrysophyllum gorungosanum	34	0.6	0.6	2.1	1.4
Aningeria altissima	29	1.9	1.2	0.7	0.7
Cassipourea ruwensorensis	45	1.2	1.9	3.5	2.1
Trema orientalis	50	6.8	0	0.7	0
Neoboutonia macrocalyx	25	1.2	6.8	3.5	2.1
Fagaropsis angolensis	32	1.9	3.1	2.1	2.1
Ficus brachylepis	4	1.2	3.7	0	1.4
Aphania senegalensis	21	1.2	4.9	2.1	2.1
Cordia millenii	17	0	1.4	1.4	0
Ficus exasperata	6	3.7	6.8	0	0
Leptonychia mildbraedii	—	0.6	2.5	2.1	1.4
Monodora myristica	23	0	0	1.4	3.5
Newtonia buchananii	22	1.9	0.6	1.4	0
Balanites wilsoniana	37	0	0	1.4	1.4
Spathodea campanulata	33	0	0	1.4	2.8
Pseudospondias microcarpa	26	0	0	1.4	1.4
Rauvolfia vomitoria	—	0.6	1.2	0	0
Macaranga schweinfurthii	—	1.2	6.2	0	0
Mitragyna rubrostipulata	—	1.2	0.6	0	0
Sapium ellipticum	—	1.2	0	0	0
Apodites dimidiata	—	1.2	0	0	0
Blighia unijugata	20	1.2	3.1	0	0
Myrianthus arboreus	—	0	6.2	0	0
Kigelia africana	—	0	1.9	0	0
Lymirose sp.	—	0	1.2	0	0
Ilex mitis	—	0	1.9	0	0
Croton sp.	—	0	1.2	0	0
Cordia abyssinica	—	0	2.5	0	0
Unidentified	—	6.8	3.1	0	0

*Species are ordered by their overall relative abundance in 1972. Trail locations are given in Waser [1974; K14] and Struhsaker [1975; K30]. Each species' rank preference indicates the relative amount of time mangabeys spent foraging (for invertebrates) or feeding (on leaves, flowers, or fruits) on this species [Waser, 1977]. K14 had been selectively felled in the 1960s, while K30 was undisturbed.

TABLE II. Mangabey Group Sizes Within the Kanyawara Study Area

	S/I[a]	N/V[a]	BT[a]	M/II	WR/III	IV
1971				17		
1972	5			15		
1973	6			16		
1974	7	10	10	16	9	
1977[b]	10			15		
1991	14	13		11	11	24

[a]Groups that primarily use K14, regenerating forest. Other groups use primarily K30, undisturbed forest. Groups whose names are separated by a slash (e.g., S/I) used similar home ranges and may have been the same group.
[b]S. Wallis, personal communication.

edly in regenerating forest (K14). In K14, overall tree density increased 88%, from 256 trees/ha in 1972 to 481 trees/ha in 1992. Sixty-seven percent of the identified species increased in abundance, 15% decreased, and 18% remained unchanged ($z = 3.53, P < 0.001$). In undisturbed forest (K30), overall tree density increased 27%, from 315 trees/ha in 1972 to 400 trees/ha in 1992. Twenty-seven percent of the identified species increased in abundance, 33% decreased, and 40% remained unchanged ($z = 0.38, P = 0.35$).

Of the ten species most preferred as food sources by mangabeys, there was a 48% increase in abundance in regenerating forest, and a 34% increase in undisturbed forest. Six of these ten species, including *Diospyros abyssinica* (rank 1 in the mangabey diet) [Waser, 1977], *Celtis durandii* (rank 2), and *Ficus* spp., increased in number in both undisturbed and regenerating forest (Table I).

Population Density

Mangabey population density has substantially increased over the past 20 years, from $6–7/km^2$ in 1971–1974, to $13–14/km^2$ in 1991.

In 1974, the median size of five completely counted Kanyawara groups was 10 animals; in 1991, it was 13 ($z = -1.68, P = 0.09$).

Increases in group size were more common in regenerating forest; group sizes in K14 were unusually small in 1971–74 and the S group in 1972 was the smallest mangabey group ever recorded (Table II). K14 groups in 1974 were significantly smaller than 11 groups counted by Waser [1974] and Wallis [1978] in other, undisturbed parts of Kibale forests (median size 10 vs. 15, $z = -2.19, P = 0.03$). By 1991, K14 groups had grown to be indistinguishable in size from these reference groups ($z = -0.50, P = 0.62$).

In contrast, group sizes in undisturbed forest have remained essentially constant (Table II). Groups counted in K30 had a median size of 12.5 in 1974, 11 in 1991. Groups in both of these samples were similar in size to the reference groups mentioned above ($z = -0.49, P = 0.62; z = -0.47, P = 0.64$, respectively).

It is difficult to assess whether increases in density have been accompanied by changes in home range size or overlap. In 1991, the cumulative areas used by Group II over two months (86 ha) and by Group I over five months (160 ha) were similar to the cumulative area used by the M group (80 and 150 ha) during comparable periods in 1972–1973 [Waser, 1977]. However, it is clear that there have been changes in habitat use. The most striking of these is that 13% of 1991 Group I mangabey sightings were in regenerating forest and exotic softwood plantations, habitats that were unavailable or unused in 1974. In these areas, mangabeys fed on *Diospyros abyssinica* fruit, flowers and young leaves of *Erythrina abyssinica*,

TABLE III. Age/Sex Composition of Mangabey Populations

	Adult males	Adult females	Subadult males	Juveniles	Infants
1974[a]	4	8	3	4	3
1991[b]	5	12	2	13	5

[a]Sum of S and M groups.
[b]Sum of Groups I, II, and III.

and seeds of *Albizia grandibracteata* as well as reproductive parts and bark of introduced *Cupressus* sp. In addition, they foraged for invertebrates in both introduced softwoods and regenerating native trees.

Demography

Adult sex ratios have changed little in the two main study groups (0.5 adult male/adult female in 1974, 0.4 in 1991). Age structures suggest equal or greater rates of reproduction in 1991 than in 1974. The number of infants/adult female was 0.4 in both 1974 and 1991, but the ratio of young animals (infants, juveniles, and subadults) per adult had increased from 0.8 to 1.2. This change is due primarily to an increase in the number of juveniles (Table III).

Ranging Patterns

During 1971–1974, the daily distance traveled by the S group was 900 ± 50 m (mean $\pm$ SE, n = 21 complete observation days), while its mean size was six animals. The much larger M group (mean size 15 animals) traveled significantly longer daily distances ($1,230 \pm 30$ m, n = 117 d, $t = 4.06, P = 0.0001$). In 1991 Groups I and II moved similar distances (Group I, 14 animals, 960 ± 70 m, n = 10 d; Group II, 11 animals, 980 ± 50 m, n = 10 d; $t = 0.29, P = 0.77$).

Comparisons across time also suggest that larger groups may move farther. Group II used much of what had been the M group's home range but was smaller (11 vs. 16 animals) and traveled 250 m/d less ($t = 2.10, P = 0.04$). Group I used nearly the same home range in 1991 as had the S group in 1971–1974, was larger (14 vs. 6 animals), and traveled 80 m/day farther ($t = 0.71, P = 0.49$).

Mangabey foraging distances vary substantially from day to day and month to month, and only the M group has been followed year-round [Waser, 1975]. To control for time of year and location, we compared the distances moved by Group I in August 1991 to those moved by the M group in August 1972; during these months, both used the same part of K14. Similarly, we compared distances moved by Group II in September 1991 with distances moved in the same part of K30 by the M group in September 1972.

The results show that the larger group, using the same area at the same time of year, moved greater distances than did the smaller groups. In K14 the M group (16 animals, $1,465 \pm 100$ m, n = 6 d) moved farther than Group I (14 animals, $1,030 \pm 105$ m, n = 5 d, $t = 3.01, P = 0.01$); in K30 the M group (15 animals, $1,305 \pm 85$ m, n = 9 d) moved farther than Group II (11 animals, $1,035 \pm 90$ m, n = 5 d, $t = 2.04, P = 0.06$).

In all four pairwise comparisons, we found that larger groups used larger areas, but perhaps because of the relatively small numbers of 5 d periods in our samples, the differences were not significant. In 1974, the larger M group used 111 $\pm$ 6 quarter-ha quadrats (n = 12 months), while the smaller S group used 89 $\pm$ 13 (n = 2 months; $t = 1.33, P = 0.21$). In 1991, the larger Group I used 139 $\pm$ 8

quadrats (n = 2 months) while the smaller Group II used 105 ± 12 (n = 2 months, $t = 3.31$, $P = 0.09$). Comparing within areas, the smaller S group used smaller areas than Group I (89 vs. 139 ha, $t = 3.49$, $P = 0.07$), while the M group and Group II used similar areas (111 vs. 105 ha, $t = 0.40$, $P = 0.70$).

Activity Pattern

Time budgets were less clearly influenced by group size. During the years 1971–1974, S group members foraged during 44.6% of scan samples (n = 902) while members of the much larger M group foraged during 42.7% (n = 18,673). Proportions of time spent foraging by the two groups observed in 1991 were virtually identical (Group I, 41.5%, n = 544; Group II, 40.7%, n = 404).

The proportion of time individuals spent moving was apparently higher in both 1991 groups (Group I: 28%; Group II: 27%) than for the 1971–1974 samples (M group: 21%; S group: 21%). The data suggest no relationship between group size and percent time moving.

DISCUSSION

The 1974 study occurred when the northern half of the study area (K14) had recently been selectively logged. Logging may have resulted in the reduction of mangabey food trees relative to prelogging levels [Skorupa, 1986]. By 1991, regeneration of K14 had resulted in a substantial increase in mangabey food tree densities (Table I). In addition, it is conceivable that mangabey populations have responded to less direct effects of regeneration. Following logging, the forest canopy was discontinuous; the re-establishment of a closed canopy may have influenced mangabey density by influencing their vulnerability to aerial predators, or by eliminating the necessity of crossing or traveling around large canopy gaps.

Increase in mangabey density may also reflect use of regenerating forest edge and softwood plantations. In 1971–1974, exotic softwoods were young and mangabeys were not seen to use grassland areas. By 1991, exotic softwoods had grown to maturity and the former grassland areas were used by Group I. Anecdotal observations indicate that Group II also used former grassland areas, though perhaps less often. If proposed logging of softwoods is conducted without care to preserve regenerating natural forest, we anticipate a negative impact on mangabey populations.

Mangabey density has responded less clearly to vegetational change in undisturbed forest (K30). Natural processes such as those that caused the decline of *Parinari* might have had a negative influence on the diversity or density of mangabey food species. However, two species that are known to have suffered a dieback in parts of K30 adjacent to softwood plantations, *Newtonia buchananii* and *Lovoa swynnertonii* [Struhsaker et al., 1989], are not heavily used by mangabeys.

Mangabey group size has also responded to vegetational changes; the fact that group sizes have increased primarily in K14 suggests that forest regeneration there is partially responsible.

The age structure of the 1991 mangabey population suggests healthy reproduction, probably better than in 1974. Younger age classes, and particularly juveniles, are better represented in 1991 than in 1974, suggesting higher rates of reproduction or of juvenile survival, at least in the late 1980s. This observation is consistent with the supposition that forest regeneration during the last two decades has increased the carrying capacity for mangabeys.

While population density and group size (at least in K14) have been increasing, it appears that increases in group size are not without cost to mangabeys. Five day quadrat use appears to be higher for larger groups, and ranging data indicate
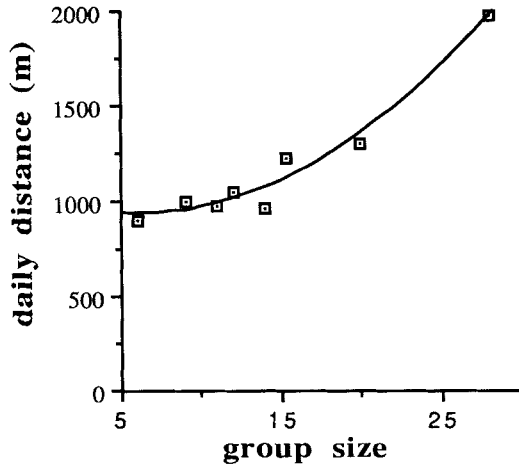
Fig. 1. Mean daily distances moved as a function of mean group size for eight Kibale mangabey groups. Data include the four groups discussed in this paper, as well as groups in other undisturbed parts of the Kibale Forest Reserve [Waser, 1977; Freeland, 1979]. Movement costs increase with increasing group size, and the relationship is concave upwards.

that larger groups move greater distances per day, presumably with attendant increases in caloric costs for each group member.

Models of primate group size [Terborgh, 1983; Terborgh & Janson, 1986] have generally assumed a nonlinear relationship between group size and costs of group membership. Intragroup competition is assumed to increase with group size [Dunbar, 1988; Isbell, 1992; van Schaik, 1983], and to increase disproportionately as group size exceeds a threshold determined by the size of the usual foraging "patch." Waser [1977] suggested just such a relationship for Kibale forest mangabeys based on observations of daily travel distances: locomotory costs of group membership increased with group size. The suggestion was speculative, based on data from five groups, not equally habituated, from various parts of Kibale forest that differed vegetationally. However, data from Groups I and II, as well as from other groups studied in Kibale [Freeland, 1979], now reinforce the original conclusion. Mean daily distance moved increases significantly with group size (distance = 485 + 48 * group size, $P = 0.001$, $R^2 = 0.88$). A quadratic regression (distance = 1,009 − 25 * group size + 2.1 * group size^2, $P = 0.005$, $R^2 = 0.96$) explains even more of the variance; as predicted by most models of optimal group size, the cost curve is concave upwards (Fig. 1).

CONCLUSIONS

1. Mangabey densities in the Kibale Forest, Uganda, have increased over the past 20 years. The increase has been accompanied by a net increase in group size and by increased representation of young animals in the population.

2. The increase in mangabey density reflects regeneration of selectively felled forest, as well as increased use by mangabeys of native trees regenerating within exotic conifer plantations adjacent to natural forest.

3. Larger groups in the same area move farther each day, suggesting that there is a cost to group membership. Consistent with several models of primate group size, the cost curve is concave upwards.

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REFERENCES

Altmann, J.; Hausfater, G.; Altmann, S.A. Demography of Amboseli baboons, 1963–1983. AMERICAN JOURNAL OF PRIMATOLOGY 8:113–125, 1985.

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

Cheney, D.L.; Seyfarth, R.M.; Andelman, S.J.; Lee, P.C. Reproductive success in vervet monkeys. Pp. 384–402 in REPRODUCTIVE SUCCESS. T.H. Clutton-Brock, ed. Chicago, University of Chicago Press, 1988.

Dittus, W.P.J. The social regulation of population density and age–sex distribution in the Toque monkey. BEHAVIOUR 63:281–322, 1977.

Dunbar, R.I.M. PRIMATE SOCIAL SYSTEMS. Ithaca, NY, Cornell University Press, 1988.

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

Hurlbert, S.H. Pseudoreplication and the design of ecological field experiments. ECOLOGICAL MONOGRAPHS 54:187–211, 1984.

Isbell, L. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. BEHAVIORAL ECOLOGY 2:143–155, 1992.

SAS. SAS/STAT guide for personal computers, version 6 edition. Cary, NC, SAS Institute Inc., 1985.

Skorupa, J.P. Responses of rainforest primates to selective logging in Kibale forest, Uganda: A summary report. Pp. 57–70 in PRIMATES: THE ROAD TO SELF-SUSTAINING POPULATIONS. K. Benirschke, ed. New York, Springer-Verlag, 1986.

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

Struhsaker, T.T. A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. ECOLOGY 54:930–932, 1973.

Struhsaker, T.T.; Kasenene, J.M.; Gaither J.C.; Larsen, N.; Musango, S.; Bancroft, R. Tree mortality in the Kibale forest, Uganda: A case study of dieback in a tropical rain forest adjacent to exotic conifer plantations. FOREST ECOLOGY AND MANAGEMENT 29:165–185, 1989.

Terborgh, J. FIVE NEW WORLD PRIMATES. Princeton, Princeton University Press, 1983.

Terborgh, J.; Janson, C.H. The socioecology of primate groups. ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS 17:111–135, 1986.

van Schaik, C.P. Why are diurnal primates living in groups? BEHAVIOUR 87:120–143, 1983.

Southwick, C.H.; Siddiqi, M.F.; Oppenheimer, J.A. Twenty-year changes in rhesus monkey populations in agricultural areas of northern India. ECOLOGY 64:434–439, 1983.

Wallis, S.J. The sociology of Cercocebus albigena johnstoni (Lyddeker), an arboreal rain forest monkey. Unpublished PhD thesis, University of London, 1978.

Waser, P.M. Intergroup interaction in a forest monkey: The mangabey Cercocebus albigena. Unpublished PhD thesis, Rockefeller University, 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 35:85–101, 1974.

Wing, L.D.; Buss, I.O. Elephants and forests. WILDLIFE MONOGRAPHS 19:1–92, 1970.