

## Densities of Two Frugivorous Primates with Respect to Forest and Fragment Tree Species Composition and Fruit Availability

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Received August 4, 2004; revision January 12, 2005; accepted January 24, 2005;

Published Online March 21, 2006

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*Conservation of wildlife populations requires extensive knowledge of their habitat requirements, efficient methods to evaluate habitat quality, and an understanding of the value of fragments and edges. Kibale National Park, Uganda has areas that differ in the densities of 2 species of frugivorous monkeys—Cercopithecus mitis and Lophocebus albigena—including one on an edge and forest fragments outside the park that lack both species. We compared the basal area densities of important food trees with primate densities. The density of Cercopithecus mitis correlates most strongly with the basal area density of all types of food trees combined. The density of Lophocebus albigena does not correlate with the basal area densities of any category of food trees or with fruit availability. An index of their density—number of groups seen per km walked—correlates to fruit availability but with marginal significance. Lack of a relationship between the basal area densities of food trees and density of Lophocebus albigena may be the result of a mismatch in scale between the forest area measured and their large home ranges. We compared the unused area of forest to the other areas of the forest and the fragments and found it had higher basal area densities in all food tree categories for both species than the fragments and lower basal area densities of*

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*most categories than the other parts of the forest, indicating that the fragments are poor quality and would probably be unused even if dispersal were likely.*

**KEY WORDS:** *Cercopithecus mitis*; Forest edges; Fragments; Habitat assessment; Habitat use; Kibale; *Lophocebus albigena*; Uganda. .

## INTRODUCTION

Primates are currently of great interest to conservation not only because of their potentials to act as flagship species (Karanth, 1992; Vargas *et al.*, 2002), but also because half of the world's primate species are in trouble for a variety of reasons (Chapman and Peres, 2001). Though hunting is an important and widespread threat (Chapman *et al.*, 1999a; Peres, 1990), dependence of most primate species on tropical forests (Mittermeier and Cheney, 1987) and the continuing devastation of forests on a global scale (DeFries *et al.*, 2002) make an understanding of primate habitat requirements, limitations, and flexibilities in both primary and degraded forests paramount for conservation.

Researchers have often viewed forest composition as the major factor determining the abundance and distribution of forest-dwelling primates. Some have conducted studies from this perspective in reference to the changes initiated by logging (Chapman *et al.*, 2000; Fairgrieve and Muhumuza, 2003; Olupot, 2000; Plumptre and Reynolds, 1994; Rao and van Schaik, 1997; Skorupa, 1988; Wilson and Wilson, 1975), or with reference to the unique characters of fragmented forests (Granjon *et al.*, 1996; Marsh and Loiselle, 2003; Medley, 1993; Norconk and Grafton, 2003; Onderdonk and Chapman, 2000; Umaphathy and Kumar, 2000; Woodwell, 2002). In both cases, changes in food availability are often a main driving force behind changes in primate densities. An exception is Onderdonk and Chapman (2000). In fragments, many processes can cause changes in food availability, such as greater windfall, the cutting of firewood, an increase in proportion of unfavorable microclimate, demographic stochasticity, distance from a main forest block, or the extinction of important seed dispersers (Cordeiro and Howe, 2001).

Many previous studies are limited with respect to identifying key habitat requirements because of the time lag between a dramatic disturbance—logging or fragmentation—and a response by the species in question (Brooks *et al.*, 1999; Chapman *et al.*, 2000; Gonzalez and Chaneton, 2002). In fragmentation, the limitation is compounded by the difficulty of separating habitat requirements from dispersal abilities of a species. If a species of interest is absent from fragments, it could be the result of either insufficient resources or the inability of the species to transfer from the main forest or among fragments.

One can use the situation in Kibale National Park, Uganda to address the issue of habitat requirements by relating habitat characteristics and heterogeneity of use in areas of the forest that have not been disturbed, thereby avoiding the time lag issue. One can circumvent the dispersal issue by examining a fragment-like area that the species in question, *Cercopithecus mitis* (blue monkey) and *Lophocebus albigena* (gray-cheeked mangabey), completely avoid but that is contiguous with inhabited forest.

We expected that, within Kibale National Park, the observed densities of *Cercopithecus mitis* and *Lophocebus albigena* would be related to the abundance of their respective food trees. Given that there are forest fragments near Kibale inhabited by the same species of diurnal primates as the avoided area including an absolute lack of *Cercopithecus mitis* and *Lophocebus albigena* (Onderdonk and Chapman, 2000), the question arises as to whether *C. mitis* and *L. albigena* do not use these fragments because of a lack of resources or because of their poor dispersal abilities. By comparing the availability of resources within the fragments with their availability in the used and unused portions of the contiguous forest, one can evaluate the habitat suitability of the fragments. However, if the fragments have poor habitat quality, one cannot reject the hypothesis that distance from the main forest block may limit use of the fragments by *Cercopithecus mitis* and *Lophocebus albigena* yet it is moot from a conservation perspective unless the habitat quality of the fragments increases in the future.

## METHODS

### Study Site

Kibale National Park, Uganda (795 km<sup>2</sup>) is composed mostly of mid-altitude moist tropical forest (elevation: 920–1590 m, rainfall in 1990–2003: 1741 mm/yr, latitude: 0° 13′–0° 41′ N) and has 2 rainy and 2 dry seasons each yr, though the length and severity vary greatly. The fruiting of tree species in Kibale is usually synchronous, though the timing of fruiting can be irregular, subannual, annual, or superannual depending on the species (Chapman *et al.*, 1999b).

Before it became a national park, the area was a forest reserve with the last logging in the natural forest occurring in 1969. Our study took place in an unlogged compartment (K30) and a relatively untouched section of a lightly logged compartment (K14) (Chapman *et al.*, 2000). Outside the national park, community-owned forest fragments provide habitat for many of the forest primates (Onderdonk and Chapman, 2000).

## Forest Transects

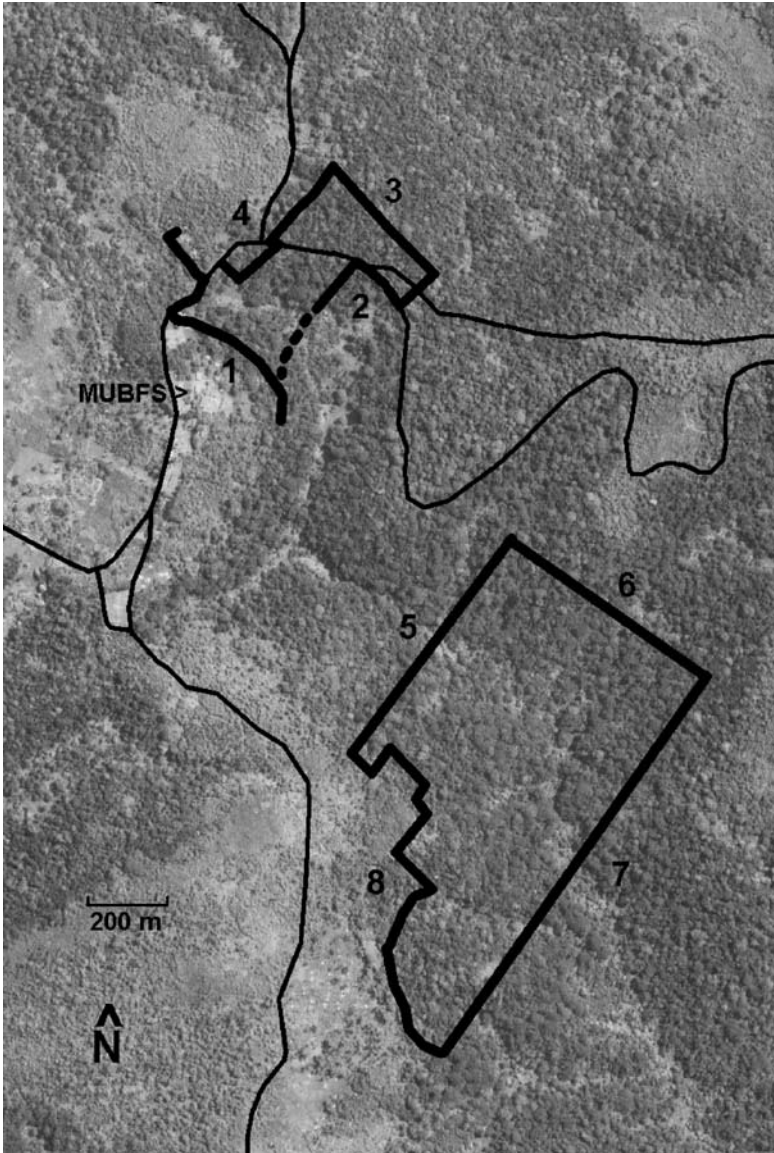
We established a system of transects in the existing research trail grid near the Makerere University Biological Field Station (MUBFS). Because edges are increasingly prevalent sources of habitat heterogeneity, we placed 1 transect (transect 1) along the avoided forest edge and another along an edge that both *Cercopithecus mitis* and *Lophocebus albigena* use (transect 8). We paired both edge transects with a nearby interior transect (transect 1 with transect 3 and 8 with 6) and connected each pair at both ends by 2 transitional transects (transects 2, 4, 5, and 7) (Fig. 1). Because of the lay of the land and limitations of the existing trail system, transects ranged from 453 m to 1205 m long, with a mean of 767 m. Because transect 1 extends beyond the forest, for some analyses we considered only the area in the forest to ensure that any observed difference did not simply result from the open and unique character of parts of that transect. For analysis, we discarded the section of transect 2 that ran through the area avoided by *Cercopithecus mitis* and *Lophocebus albigena*—transect 1—to remove the influence of the avoided area and make transect 2 representative of a utilized forest area. Because of the spatial arrangement of the transects, there is an area of overlap at some of the corners, but it is quite small, accounting for <0.5% of the total area measured; therefore we considered each transect as independent.

## Fragments

The human-dominated matrix outside Kibale National Park consists mainly of small-scale nonindustrialized agriculture, large-scale tea plantations, pastures, and fallow land with forest fragments surviving on agriculturally undesirable land such as steep slopes and swampy lowlands (Chapman *et al.*, 2003). The surrounding people actively use the fragments for fuelwood, poles, livestock fodder, and medicinal and food plants (Chapman *et al.*, 2003). The same primates inhabit many of the fragments as inhabit the national park with the notable exceptions of *Cercopithecus mitis* and *Lophocebus albigena* (Onderdonk and Chapman, 2000).

## Primate Diets

We considered only specific dietary items, i.e., a specific part from a particular species, that constituted  $\geq 4\%$  of the total diet Rudran (1978) and Butynski (1990) reported for *Cercopithecus mitis* or Waser (1975) and Olupot (1994) for *Lophocebus albigena*. We chose the cutoff of 4% because it included specific food items that our team and previous researchers



**Fig. 1.** Locations of the 8 transects in Kibale National Park, Uganda. The transects are shown with thick lines, roads with thin lines, and the discarded area of transect 2 with a dashed line. The Makerere University Biological Field Station (MUBFS) is also labeled. The satellite image is a Quickbird (high resolution, 2.4 m) from Digital-Globe, Inc., Longmont, CO, USA.

**Table I.** Species specific food items constituting  $\geq 4\%$  of the total reported diet of Kanyawara *Cercopithecus mitis* and *Lophocebus albigena* groups

Species	Part	Percentage of total diet	
		<i>Cercopithecus mitis</i>	<i>Lophocebus albigena</i>
<i>Celtis africana</i>	Fruit	4.1 (Butynski 1990) <sup>a</sup> 6.6, 6.8 (Rudran 1978)	— (Olupot 1994) — (Waser 1975)
<i>Celtis durandii</i>	Fruit	— 4.1, 5.2	12.4 6.3
<i>Croton macrostachys</i>	Fruit	— —, —	4.3 —
<i>Diospyros abyssinica</i>	Fruit	— —, —	6.2 22.6
<i>Diospyros abyssinica</i>	Leaves	4.8 —, —	— —
<i>Ficus brachylepis</i>	Fruit	— 4.9, —	4.2 6.1
<i>Ficus exasperata</i>	Fruit	— —, 11.2	4.6 —
<i>Markhamia lutea</i>	Young petioles	8.8 —, —	— —
<i>Pancovia turbinata</i>	Fruit	— 6.6, —	— 4.1
<i>Parinari excelsa</i>	Invertebrates	— —, —	— 5.0
<i>Premna angolensis</i>	Flowers	— 4.3, —	— —
<i>Teclea nobilis</i>	Fruit	— 5.3, —	— —
<i>Uvariopsis congensis</i>	Fruit	— 5.3, 8.5	— —

Note: Butynski's (1990) numbers are the averages of study groups 1–4. Rudran's (1978) numbers are for groups 1 and 2, respectively. Olupot (1994) and Rudran (1978) reported percentages of vegetable diet. We recalculated their numbers as percentages of total diet. The order of sources is constant throughout the table with Butynski and Olupot above and Rudran and Waser below for all foods.

<sup>a</sup>Butynski (1990) reported only foods eaten at Kanyawara and ignored at Ngogo.

studying the species in the same area consistently considered important (Butynski, 1990; Olupot, 1994; Rudran, 1978; Waser, 1975) while avoiding incorporating large numbers of rarely used species. The criterion produced 10 specific dietary items for *Cercopithecus mitis* and 7 for *Lophocebus albigena* (Table I). Though Olupot (1994) reported liana fruits as the second most frequent dietary item for *Lophocebus albigena* (8.34%), he did not differentiate by species so we ignored them because there are a variety of species, liana species in general are poorly known and difficult to identify, and the dominance of lianas measured in basal area is not comparable to that of trees. We aim to show that it is possible to quickly and easily index habitat quality with only a few most important food trees, which

is especially valuable when the diets of populations or species are poorly known

### Primate Densities

We estimated primate group densities via a line transect method, which is appropriate for easily detectable diurnal primates (Chapman *et al.*, 2000; National Research Council, 1981). We surveyed the transects for primates once a fortnight for 1.5 yr (7/01 to 12/02). Observers walked the transects at about 1 km/h in the morning (0730–1030) and recorded the species, the observer to animal distance from the first individual seen, and the perpendicular trail to animal distance. We noted solitary animals, but excluded them from analysis. Trained and practiced field assistants estimated all distances under the supervision of the authors. We checked estimation accuracy against known measurements at the beginning and periodically during the study. We recorded information for groups at transect intersections separately if we saw the group from both transects, or if it was likely we would have seen the group but it moved at the approach of the observers.

Unfortunately, we did not see enough groups of *Cercopithecus mitis* or *Lophocebus albigena* to use density estimating computer programs such as Distance (Buckland *et al.*, 1993), and there is debate over the most appropriate method of estimating densities from line transect counts for primates (Chapman *et al.*, 2000). Unlike the landscape available for travel by large ungulates, that of arboreal primates is fully three-dimensional, which can lead to unusual sighting-distance histogram profiles which in turn are thought to overestimate group densities (National Research Council, 1981). To control for this difficulty, observer to animal distance is often used instead of perpendicular distance (National Research Council, 1981), a method that overestimates the area sampled and can exclude observations of groups seen in the sampled area but from a long distance, therefore lowering density estimates. However, the histogram we generated via perpendicular distance and 5-m intervals is a classic Kelker histogram with a plateau extending from 0 to a distinct shoulder and subsequent steep decline in sightings. Therefore we used perpendicular distances to estimate densities.

Because of the very few sightings of *Cercopithecus mitis* or *Lophocebus albigena*, we used all primate sightings to produce the Kelker histogram with the assumption that all species are equally visible. Even when we excluded unusual species, i.e., ground dwellers such as *Papio anubis* (olive baboon) and *Cercopithecus lhoesti* (L'Hoest's monkey) and species normally found in small quiet groups such as *Colobus guereza* (black-and-white

colobus) and *Pan troglodytes* (chimpanzee), which often exhibits both characters, the location of the histogram shoulder did not change.

The Kelker method assumes that 100% of the animals or groups within a certain distance are detected, and one uses the distance, multiplied by the transect length, to delineate the area sampled for density calculations. Ideally, one determines the cutoff distance by the sharp drop-off of observations after an initial plateau in the sighting distance histogram. It is assumed that the animals are distributed randomly in space—at least with respect to the transect—so a drop-off in the probability of detection causes the drop-off in observations. Previous studies often used an objective method for determining the cutoff distance (Chapman *et al.*, 2000), but the method assumes a sudden decline in the probability of being seen with distance from transect instead of a slow, consistent drop. Using the same objective criteria as Chapman *et al.* (2000), our cut-off would be 44 m, which is almost twice the subjectively determined cutoff of 24 m and seems unreasonable for this area of forest. The violation of the assumption that no groups within the cutoff are missed underestimates densities. There is no correlation between distance from transect and number of groups within the 24-m cutoff (1-tailed Pearson's  $r = -0.157$ ,  $p = 0.227$ ,  $N = 25$ ), indicating that the assumption is not significantly violated. However,  $\leq 44$  m, there is a significant negative correlation between distance from transect and number of groups seen (1-tailed Pearson's  $r = -0.296$ ,  $p = 0.024$ ,  $N = 25$ ), indicating that 100% detectability cannot be assumed if a cutoff of 44 m is used.

We did not take group spread into account because the assumption that group spread is circular is often violated (Struhsaker, 1997) and the reported group spread from Kibale varies tremendously (for *Cercopithecus mitis*, 0–120 m; for *Lophocebus albigena*, 5–480 m; Struhsaker and Leland, 1979). Group spread also changes seasonally and by time of day and according to Plumptre (2000) one should not incorporate it in density estimations. Not accounting for group spread overestimates densities because groups with centers outside the cutoff distance are still included if the first individual seen was inside limits (the probability of being seen is greater for peripheral than for center individuals; Fashing and Cords, 2000).

We used Pearson's correlations to detect relationships between densities of *Cercopithecus mitis* and *Lophocebus albigena* on each transect and the average summed standardized fruiting intensity (Fruit Availability below) for species-specific fruit trees, and the basal area density of all trees, species-specific food trees, species-specific fruit trees, arthropod trees (tree species used as invertebrate foraging substrate; *Lophocebus albigena* only), leaf trees (*Cercopithecus mitis* only), and flower trees (*Cercopithecus mitis* only) on each transect. In the analyses, we used 1-tailed probabilities



because we had made clear predictions *a priori*. We used only the forest area to represent transect 1 for the analyses.

One can compare a relative index of density—groups sighted/km walked during the surveys—to the density estimations for each species to strengthen confidence in the density estimations (Chapman *et al.*, 2000). The small numbers of sightings may make density estimates particularly susceptible to the influence of a single sighting and its inclusion or exclusion due to distance from the transect; therefore we recalculated the Pearson's correlations via the index of relative density for both primate species. We considered checking the results in this manner more important for *Lophoceros albigena* because the relative index of density correlated less strongly with calculated density for *L. albigena* ( $r = 0.736$ , 1-tailed  $p = 0.019$ ,  $N = 8$ ) than for *Cercopithecus mitis* ( $r = 0.986$ , 1-tailed  $p < 0.001$ ,  $N = 8$ ).

Though invertebrates generally form an important part of the diet of *Cercopithecus mitis* (Twinomugisha *et al.*, in press), we did not use invertebrates as a dietary category because the subjects did not use any particular species of tree enough for invertebrate foraging to qualify as an important food species. Therefore one should not take the lack of an invertebrate foraging substrate category in food trees to mean that invertebrates are unimportant, but as an indication that *Cercopithecus mitis* may not be as selective about the species of tree in which they forage for invertebrates as they are about the species of trees in which they forage for fruit, leaves, or flowers.

We do not give the results for the *Pan troglodytes*, *Cercopithecus lhoesti*, and *Papio anubis* because they have more terrestrial habits, making line transect surveys less appropriate, and we rarely saw them during surveys, despite frequent observation of them or sign of them at other times.

### Forest Composition

We identified the species and measured the diameter at breast height (dbh) of all free-standing woody plants, including strangler figs, with a dbh  $\geq 10$  cm and  $\leq 10$  m of either side of a transect. Trees with a dbh  $\geq 10$  cm were large enough for both species to forage in, 10 cm dbh was the smallest tree fruiting during the study, and researchers have commonly used the criterion to describe primate resources. We excluded snags from the analyses. If a plant was in an area of overlap between transects, we counted it in each separately. We attempted to measure above any pronounced buttressing, and, though it was not always feasible to measure above large buttresses, only a few of the largest trees of rarer species presented this sort of problem. We treated multiple stemmed plants as if each stem were a separate individual.

A *Ficus* with a diameter of  $>10$  cm 3 m up on the host and with a substantial crown could be supported by only small roots at breast height, making dbh an inappropriate measure. If multiple roots converged into a single trunk before the trunk started branching, we measured or estimated the diameter of the single trunk. If the fig had large roots connecting above the branching point—essentially multiple trunks but with a single crown—we measured the main trunk and several of the large roots and combined them to give a single dbh estimate. These huge figs are widely spaced and rare. Most of the fig trees measured presented no unusual difficulties.

We converted the dbh of each plant to basal area and summed each species to produce the total basal area by species for each transect. We divided the total species basal area by the total area covered by a given transect, producing a basal area density ( $\text{cm}^2/\text{m}^2$ ) for each species for each transect.

In the fragments, we did a complete census of every tree  $\geq 10$  cm dbh. We compared the forest fragments and transects via bootstrapping analysis to see if the forest composition of the unused transect was more similar to that of the fragments or the rest of the forest. The variables we used to characterize the transects and fragments for *Cercopithecus mitis* are the basal area densities of all trees, all food trees of *C. mitis*, fruit trees, leaf trees, and flower trees. Variables for *Lophocebus albigena* are the basal area densities of all trees, all food trees of *L. albigena*, fruit trees, and arthropod foraging trees. We assumed that the values for transect 1 would fall between those of the fragments and the forest so we calculated the upper 97.5% confidence limit for the fragment characters and the lower 97.5% confidence limit for the transect characters and compared to transect 1 and transect 1 forest only. For each variable, we created a sample population equal in size to the original population by sampling the original population with replacement 10,000 times. We calculated the 97.5% confidence limits for each variable from the distributions of the means of the sample populations.

To determine if the habitat of the fragments mirrored that of the main block of forest, we classed the top 10 trees by basal area density for each fragment and transect as edge/savanna if they occurred as only, primarily, or commonly in forest edges or savannas as described in Hamilton (1991); otherwise we classed them as forest trees. *Eucalyptus* sp. was the only exotic in the top 10 lists and we treated it as an edge species because either humans plant it or it disperses from the human-dominated matrix outside the fragments. We did  $\chi^2$  analyses on the frequency of edge/savanna or exotic species or both in the 10 most dominant species in the fragments vs. the transects. To be as conservative as possible, we included all of transect 1 in the transect group. One species, *Markhamia lutea*, formerly *Markhamia platycalyx*, which Hamilton (1991) defined as “[a] very common forest edge

species, sometimes found within forests, either where the canopy is fairly open or where there has been a large gap,” is characterized by Struhsaker (1997) as a late successional or old growth forest species. The disparity may be the result of site-specific conditions so we did a second set of  $\chi^2$  analyses with *Markhamia lutea* defined as a forest interior tree.

### Fruit and Flower Availability

Researchers commonly used fruit availability as an index of habitat quality or productivity despite the inherent problems of combining species that differ in the quality or quantity of fruit produced and the amount of time required to assess patterns of phenology accurately (Basabose, 2004; Butynski, 1990; Chapman *et al.*, 1994; Doran-Sheehy *et al.*, 2004; Felton *et al.*, 2003; Poulsen *et al.*, 2001). We include an estimate of fruit availability to compare its usefulness as an index of habitat quality with the quicker, easier, and more stable basal area density measures.

Each mo for 6 mo (June, 2002–November, 2002), we collected phenological data—presence of ripe and unripe fruit and fruiting/flowering intensity—from all transects, including the dbh of the fruiting trees ( $\geq 5$  cm dbh) important in the diet of either species within 10 m of either side of the transects. We determined the fruiting intensity by assigning each tree to a numerical class (1–5) based on the fruit density in the crown, with each class indicating about twice the density as the next lower class and 3 being the average fruit density of the species while in full fruit. Because basal area correlates strongly with crown size (Anderson *et al.*, 2000) and fruit production (Chapman *et al.*, 1992), we multiplied the basal area of each tree by a factor ( $1/4, 1/2, 1, 2, \text{ or } 4$ , respectively) based on the fruit density class to obtain an index of the total fruit load on each tree. We summed the fruit loads, considering trees having both ripe and unripe fruits to have  $1/2$  ripe and  $1/2$  unripe fruit, and divided them by the total area sampled to produce a standardized monthly fruiting intensity for each species and transect for both ripe and unripe fruit. The only flowering species the subjects ate frequently, *Premna angolensis*, flowered during the study, but synchronously for a short duration and our surveys missed it.

## RESULTS

### Primate Densities

*Lophocebus albigena* had the lowest average density over all the transects and *Cercopithecus mitis* had the next lowest; however, densities

**Table II.** Group densities of the arboreal monkeys of Kanyawara by transect

Transects	Group densities (groups/km <sup>2</sup> )				
	<i>Cercopithecus mitis</i>	<i>Lophocebus albigena</i>	<i>Cercopithecus ascanius</i>	<i>Colobus guereza</i>	<i>Ptilocolobus tephrosceles</i>
1	0.0	0.0	4.1	11.6	15.8
1 Field station	0.0	0.0	6.8	25.5	15.3
1 Forest	0.0	0.0	2.3	2.3	16.1
2	5.9	0.0 <sup>a</sup>	24.8	10.6	16.5
3	5.3	3.9	14.4	3.9	7.9
4	5.2	2.1	8.3	8.3	8.3
5	3.4	0.9	7.7	4.3	6.8
6	0.0 <sup>b</sup>	1.6	3.9	0.8	2.3
7	1.1	1.1	2.8	1.7	7.2
8	0.5	0.0 <sup>b</sup>	6.4	3.5	4.4
Mean	2.7	1.2	9.1	5.6	8.7

*Note.* 1 Field station is the portion of transect 1 running through the Makerere University Biological Field Station. 1 Forest is the portion of transect 1 that is in the forested area. Transect 1 is the entirety of the transect. We calculated the means with all of transect 1.

<sup>a</sup>Presence noted with opportunistic observations.

<sup>b</sup>Presence noted during surveys but at distances of >24 m.

varied between transects. *Cercopithecus ascanius* (red-tailed monkey) and *Ptilocolobus tephrosceles* (red colobus) had the highest overall group densities (Table II). The index of density—groups observed/km walked (Table III)—showed the same pattern.

The density of *Cercopithecus mitis* on the transects correlated most strongly with total food tree basal area density, but also correlated positively with fruit tree basal area density and leaf tree basal area density. Density of *Cercopithecus mitis* does not correlate positively with average summed standardized fruiting intensity, total tree basal area density, or with flowering tree basal area density (Table IV). The *Cercopithecus mitis* index of relative density—groups observed/km walked—also correlates positively with total food tree basal area density, fruit tree basal area density, and leaf tree basal area density but not with average summed standardized fruiting intensity, total tree basal area density, or with flowering tree basal area density (Table IV).

Density of *Lophocebus albigena* does not correlate positively with average summed standardized fruiting intensity, total tree basal area density, total food tree basal area density, fruit tree basal area density, or with invertebrate foraging tree basal area density (Table IV). Similarly, the *Lophocebus albigena* relative index of density—groups observed/km walked—do not correlate positively with total tree basal area density, total food tree basal area density, fruit tree basal area density, or with invertebrate foraging tree basal area density. However, there is a marginally significant

**Table III I.** Groups of the arboreal monkeys of Kanyawara sighted/km walked by transect during the monkey

Transects	Relative group density index (groups sighted/km walked)				
	<i>Cercopithecus mitis</i>	<i>Lophocebus albigena</i>	<i>Cercopithecus ascanius</i>	<i>Colobus guereza</i>	<i>Ptilocolobus tephrosceles</i>
1	0.0	0.0	0.36	0.92	1.18
1 Field station	0.0	0.0	0.57	1.63	1.31
1 Forest	0.0	0.0	0.22	0.44	1.10
2	0.34	0.0 <sup>a</sup>	1.25	0.85	1.30
3	0.25	0.19	0.76	0.32	0.76
4	0.30	0.10	0.60	0.60	0.60
5	0.16	0.12	0.57	0.29	0.70
6	0.04	0.11	0.37	0.04	0.22
7	0.08	0.19	0.29	0.16	0.59
8	0.05	0.07	0.40	0.24	0.36
Mean	0.15	0.10	0.58	0.43	0.71

Note. Transects are labeled as in Table II. We calculated means with all of transect 1.

<sup>a</sup>Presence noted with opportunistic observations.

positive correlation between the relative index of mangabey density and average summed standardized fruiting intensity (Table IV).

### Forest Composition

The 97.5% basal area density confidence intervals of the tree types— all trees; *Cercopithecus mitis* fruit, leaf, flower, and total food trees; and

**Table IV.** Correlations between primate densities and relative densities and the basal area densities of various tree categories and fruit availability (average summed standardized fruiting intensity)

Basal area density and fruit availability	<i>Cercopithecus mitis</i> density		<i>Cercopithecus mitis</i> relative density		<i>Lophocebus albigena</i> density		<i>Lophocebus albigena</i> relative density	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>r</i>	<i>p</i>
	Total tree	0.306	0.231	0.371	0.183	0.032	0.470	0.042
Food tree	<b>0.745</b>	<b>0.017</b>	<b>0.824</b>	<b>0.006</b>	-0.159	0.353	-0.126	0.383
Fruit tree	<b>0.662</b>	<b>0.037</b>	<b>0.741</b>	<b>0.018</b>	0.212	0.307	0.134	0.376
Leaf tree	<b>0.630</b>	<b>0.047</b>	<b>0.685</b>	<b>0.031</b>	—	—	—	—
Flower tree	-0.519	0.094	-0.572	0.069	—	—	—	—
Invert. tree	—	—	—	—	-0.441	0.137	-0.304	0.232
Fruit availability	0.239	0.285	0.237	0.289	0.399	0.164	<u>0.596</u>	<u>0.060</u>

Positive correlations significant at  $\alpha = 0.05$  are in bold font. Positive correlations significant at  $\alpha = 0.10$  are underlined. We did not adjust significance for multiple tests as each test was a planned comparison and addresses an independent hypothesis. Instead, we report all results. In all cases  $N = 8$

**Table V.** The basal area densities (cm<sup>2</sup> tree basal area/m<sup>2</sup> land) of trees  $\geq 10$  cm dbh in transect 1 and the forest section of transect 1 compared to the 97.5% confidence limits of the fragments and the other transects

	Fragments: (mean) upper 97.5% confidence limit	Transect 1	Transect 1 forest only	Transects 2–8: lower 97.5% confidence limit (mean)
All trees	(10.4) 14.9	22.0	30.4	30.8 (36.7)
Total food trees of	(0.6) 0.8	2.2	3.6	10.7 (14.5)
<i>Cercopithecus mitis</i>				
fruit trees of	(0.3) 0.6	0.9	1.4	6.0 (8.4)
<i>Cercopithecus mitis</i>				
leaf trees of	(0.2) 0.3	0.9	1.5	3.6 (5.7)
<i>Cercopithecus mitis</i>				
flower trees of	(0.001) 0.002	0.4	0.7	0.1 (0.4)
<i>Cercopithecus mitis</i>				
Total food trees of	(1.1) 2.8	6.1	10.2	8.7 (10.8)
<i>Lophocebus</i>				
<i>albigena</i>				
fruit trees of	(0.2) 0.3	1.4	2.2	6.5 (8.7)
<i>Lophocebus</i>				
<i>albigena</i>				
invertebrate foraging	(0.9) 2.5	4.8	8.0	0.6 (2.1)
trees of				
<i>Lophocebus</i>				
<i>albigena</i>				

*Lophocebus albigena* fruit, invertebrate foraging, and total food trees—of the fragments and the forest transects never overlapped and were separated by large gaps, except in the case of *Lophocebus albigena* invertebrate foraging trees. Transect 1 and the forest part of transect 1 had higher basal area densities than the fragments in every category. They had lower basal area densities than the other transects in every category except *Cercopithecus mitis* flower trees, *Lophocebus albigena* total food trees, and *L. albigena* invertebrate foraging trees (Table V).

The 10 species with the highest basal area densities were more often exotic (*Eucalyptus* sp.) (df = 1,  $\chi^2 = 5.6$ ,  $p \leq 0.025$ ), edge/savanna species (excluding *Eucalyptus* sp.) (df = 1,  $\chi^2 = 5.1$ ,  $p \leq 0.025$ ), or both (df = 1,  $\chi^2 = 6.0$ ,  $p \leq 0.025$ ) in the fragments than in the forest even with the inclusion of all of transects 1 and 8. A second set of analyses with *Markhamia lutea* defined as an interior species confirmed the differences between the fragments and transects (edge/savanna species excluding *Eucalyptus* sp.: df = 1,  $\chi^2 = 6.8$ ,  $p \leq 0.01$ ; edge/savanna/exotic species: df = 1,  $\chi^2 = 10.2$ ,  $p \leq 0.01$ ).

### Fruit Availability

Transect 1 had some species fruit during the study, e.g., one small *Monodora myristica*, several large *Parinari excelsa*, and 2 individuals in a grove of *Diospyros abyssinica*, but none of the important dietary species for *Cercopithecus mitis* fruited on these. For *Lophocebus albigena*, the only important tree species to fruit was *D. abyssinica*, which fruited from July until at least November, leaving May and June with no available fruit from important species. For both primate species, transects 3 and 7 had the highest fruiting intensity overall, transect 2 having a large pulse from a single *Ficus exasperata* in November. *Celtis durandii* was the only fruit available in every mo in all transects, except for transect 1.

## DISCUSSION

### Primate Densities

We never observed or heard reports of the presence of *Cercopithecus mitis* or *Lophocebus albigena* groups in the field station or the adjoining forest, despite the constant presence of potential observers over many years. Researchers regularly see other primates the area. Correlations between density of *Cercopithecus mitis* and food tree basal area density, fruit tree basal area density, and leaf tree basal area density suggest that, in the case of the species, and potentially others, habitat quality might be indexed dependably and quickly with a knowledge of local diet and corresponding basal area measurements of only a few important food species (Siex and Struhsaker, 1999). It is notable that total food tree basal area density correlates more highly with monkey density than that of any dietary component alone, which is not surprising considering the diverse diet of *Cercopithecus mitis*.

Several factors may contribute to the lack of correlations between the basal area densities of the tree categories and density of *Lophocebus albigena*. All liana fruit combined was the second most important mangabey food item of Olupot's (1994) study, but is not accounted for here, weakening the predictive power of the food plant index. Certain species of lianas, or lianas in general, may be important to understand mangabey habitat use and should be a larger component of dietary studies than they have been in the past. In addition, *Lophocebus albigena* home ranges are large (410 ha), an order of magnitude larger than those of *Cercopithecus mitis* (61 ha; Struhsaker and Leland, 1979), and the scale of the system of transects is probably not large enough to match the scale at which the mangabeys for-

age. One of the reasons for such wide ranging in *Lophocebus albigena* is their exploitation of rare, intense fruiting events including those produced by widely separated large *Ficus* spp. (Waser, 1975). The area of the transects is most likely insufficient to accurately represent the occurrence of large, widely spaced, and important figs. Increasing the size of the area studied to include multiple home ranges could alleviate this problem. It is also possible that the diet of *Lophocebus albigena* changes substantially depending on the level of production of various tree species from season to season, so a long study spanning several years or several short studies might be necessary to get an accurate picture of the mangabey diet.

We did not anticipate a strong relationship with the average summed standardized fruiting and the densities of either monkey species because of the assumptions inherent in calculating a fruit availability index for each transect over a long period. By summing all fruiting species, we necessarily assumed that to the frugivores the normal fruit load on individual trees of a species is equivalent in value to that of any other species. We also assumed that the value of the fruit does not change from one mo to the next. Given that the assumption of normal fruit load interchangeability is almost certainly violated and that the assumption of unchanging monthly fruit value is violated (Worman and Chapman, 2005), the near significance of the correlation between number of mangabey groups seen per km walked during the primate surveys and average summed standardized fruiting intensity may be as much as can be expected. In view of the specialization of *Lophocebus albigena* on concentrated fruiting events compared with the more diverse diet of *Cercopithecus mitis*, it is logical that use of habitat by *L. albigena* would be more easily related to fruit availability and use of habitat by *C. mitis* would be more related to the occurrence of all types of food trees (Beeson, 1989). Fruit availability might be an acceptable indicator of habitat quality for fruit specialists such as *Lophocebus albigena*, but given the temporal variation in fruit load, long-term studies are necessary.

### **Transect 1: A Primate Perspective**

The area represented by transect 1 is a low-quality habitat for both *Cercopithecus mitis* and *Lophocebus albigena* but low quality does not automatically exclude incidental use of or travel through the area by either. To understand the absolute lack of use by troops of the monkeys, it is important to take a deeper look at their natural history.

Researchers have noted that home ranges of *Cercopithecus mitis* tend to have obvious visual landmarks as boundaries, such as exotic plantations,

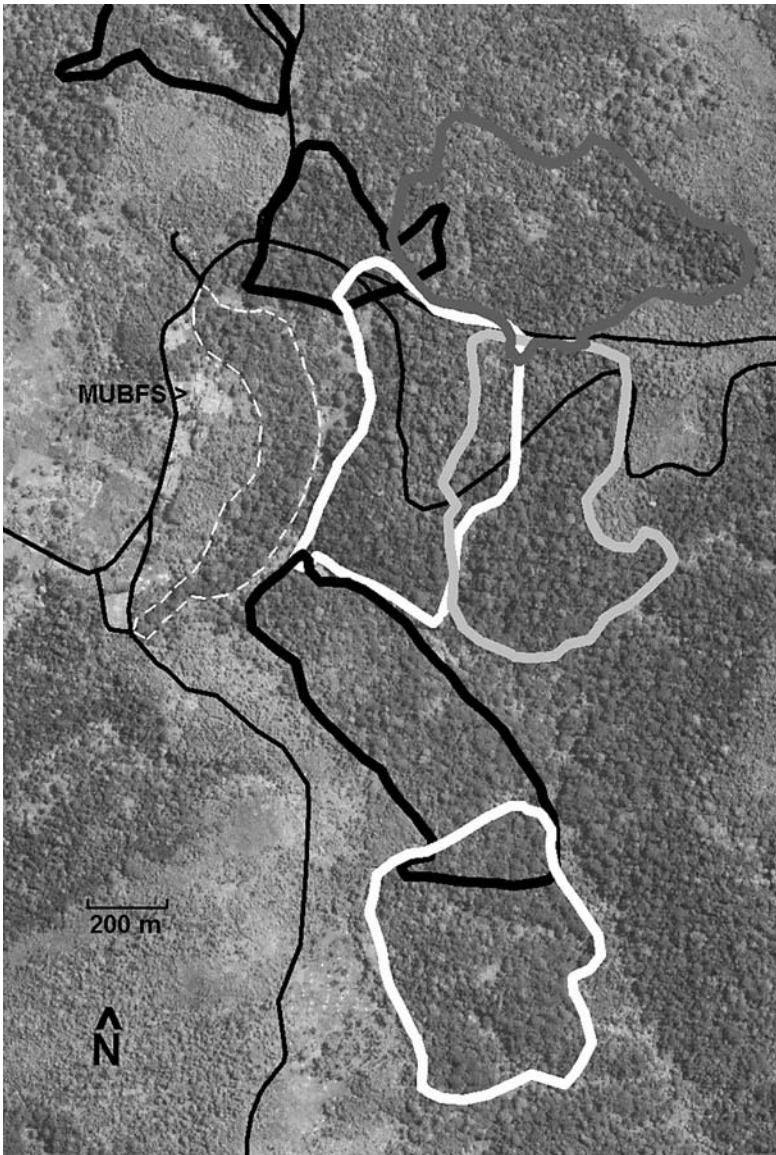


swamps, roads, streams, and, of course, forest edges (Aldrich-Blake, 1970; Butynski, 1990; Rudran, 1978). It not surprising that visually oriented primates, which probably do not mark boundaries with scent, might use natural, easily seen habitat changes and features for boundaries. The area around transect 1 is cut off from the rest of the forest by a belt of swamp-marsh that delineates the unused area and is the limit for *Cercopithecus mitis* territories given by Butynski (1990) and our sightings of *C. mitis* (Fig. 2). Thus, from the perspective of *Cercopithecus mitis*, the area of transect 1 might not be simply an area of low food, but an area of low food cut off from the rest of the forest by a distinct boundary.

The case for *Lophocebus albigena* is less conclusive. They commonly use marshes and swamps in other areas (Poulsen *et al.*, 2001) and we saw them in the middle of the swamp-marsh belt. One of their major fruit trees (*Diospyros abyssinica*) fruited on transect 1, and their most important invertebrate foraging tree (*Parinari excelsa*) has an extremely high basal area density there. It is possible that *Diospyros abyssinica* rarely fruits in the area, rarely did so in the past, or that the fruiting intensity is not worth the trip considering how common fruiting trees of the species are throughout the forest. However, given the use of fragments by *Lophocebus albigena* in other areas (Tutin *et al.*, 1997), the presence of at least some important fruit, and their willingness to use swamps and marshes in this and other areas, *L. albigena* is probably the more likely of the 2 frugivores to incorporate the area of transect 1 into a home range.

### Forest Composition

The fragments have lower basal area densities of trees and higher proportions of edge/savanna trees in their 10 most important species than Kibale forest, making the fragments different in more ways than just being physically isolated. Isolation in itself does not imply that the fragments are unsuitable habitat for resident or transient groups of *Cercopithecus mitis* or *Lophocebus albigena*, because both are found widely through equatorial Africa in diverse habitats (Kingdon, 1997). Similarly, the fact that the fragments are much smaller in area than home ranges of *Cercopithecus mitis* and *Lophocebus albigena* at Kanyawara does not automatically exclude them because other primates—*Cercopithecus ascanius* and *Pan troglodytes*—are able to move among fragments to meet their needs (Chapman *et al.*, 2003). While the necessity of traveling among fragments to gather enough food may have an impact on the use of the fragments by *Cercopithecus mitis*, which rarely descends to the ground (Beeson, 1989; Kingdon, 1974; Rudran, 1978) or crosses open areas (Devos and Omar, 1971; Fairgrieve, 1995;



**Fig. 2.** Territories of *Cercopithecus mitis* from the 1980s in relation to the unused area of forest. Territories are outlined in thick lines (redrawn from Butynski, 1990). The unused area of forest is outlined with a white dashed line. Note that it is separated from surrounding territories by a band of swamps. Roads are shown with thin lines. The Makerere University Biological Field Station (MUBFS) is labeled. The satellite image is a Quickbird (high resolution, 2.4 m) from DigitalGlobe, Inc., Longmont, CO, USA.

Lawes, 2002), researchers have reported that *Lophocebus albigena* travels among fragments and reaches densities in fragments similar to densities in neighboring contiguous forest (Tutin *et al.*, 1997). In addition, there are larger fragments not available for the analysis of forest composition—Kasisi (130 ha) and Lake Mwamba (28.7 ha)—that also lack both species (Onderdonk and Chapman, 2000) despite being large enough to contain the home range of  $\geq 1$  group of *Cercopithecus mitis* (25–44 ha; Butynski, 1990), though not the entire home range of a group of *Lophocebus albigena* (441 ha; Waser, 1984). In any case, neither differences in forest structure nor size apply to the area of transect 1 because a group from the adjoining areas could easily use it. The fact that groups could use the unused area in concert with populated adjacent areas and therefore would not be required to derive all their resources from the unused area suggests that the unused area does not produce resources at high enough levels to attract even casual use.

If one examines the basal area densities of the important food trees for both *Cercopithecus mitis* and *Lophocebus albigena*, it becomes clear how different the fragments are from the inhabited forest. The area of transect 1 generally falls between the 2. The only exceptions to this pattern are given by minor, though not necessarily unimportant, dietary components. In the case of *Cercopithecus mitis*, transect 1 has the same basal area density of flower-producing species as the mean of the other transects. Excluding the field station simply increases the flower-producing basal area density. This finding suggests that lack of flower-producing trees can be ruled out as a possible reason *Cercopithecus mitis* avoids the area.

Likewise, the total *Lophocebus albigena* food tree basal area density is different from the other transects only when one includes the field station. The forest alone fits in well with the rest of the transects in this characteristic and actually had a higher basal area density of invertebrate foraging species than any other transect. However, the extremely high basal area density of *Parinari excelsa*—the 1 important invertebrate foraging species for *Lophocebus albigena*—in the area of transect 1 seems to drive the results. The high density of *Parinari excelsa* in one of the fragments also drives the overlap of the fragment and transect confidence intervals for invertebrate foraging trees. The high density of invertebrate foraging trees in unused areas suggests that invertebrate foraging substrate is, in this case, not limiting the range of *Lophocebus albigena*.

Our findings support the hypotheses that the basal area density of fruit-producing trees or, in the case of *Cercopithecus mitis*, leaf-producing trees or a combination of the 2, drive the pattern of *C. mitis* and *Lophocebus albigena* occurrence. It is not possible to rule out that the basal area density of all tree species drives the pattern, but it seems unlikely given that both

species use logged areas around Kanyawara that lack a closed canopy (the transect 1 forest has a closed canopy).

The low fruiting basal area in the fragments is probably not the result of a lack of fruit dispersers, as Cordeiro and Howe (2001) suggested, because large-bodied frugivores are still present (Onderdonk and Chapman, 2000), and almost certainly not the result of a lack of dispersers in the area of transect 1. Here, it is the lack of fruiting trees that leads to a lack of frugivores and not the other way around.

Ample evidence indicates that the fragments are a poor habitat and do not contain enough food trees to support their use by *Cercopithecus mitis* or *Lophocebus albigena*. That transect 1 has higher food tree basal areas than the fragments and yet is completely unused by either species though they inhabit the adjoining forest indicates how poor the fragments really are. This suggests that even if the matrix between the fragments and the forest were conducive to dispersal by *Cercopithecus mitis* and *Lophocebus albigena*, the fragments would likely still be unused. That *Eucalyptus* spp. is 1 of the top 10 trees in 8 of the 12 fragments indicates the importance of human impacts on the fragments. If native trees important to frugivores were found to be suitable alternatives to *Eucalyptus* spp. for human use and planted instead, the habitat value of the fragments might increase greatly even with no change in extraction practices. Though managing the smaller fragments for *Cercopithecus mitis* or *Lophocebus albigena* would be overly optimistic, wildlife species that currently depend on the fragments could benefit from management aimed at increasing native forest trees at the expense of *Eucalyptus* spp. and edge/savanna trees that are common in the surrounding matrix.

In this case, it appears that forest composition has a major impact on use of forest areas and fragments by *Cercopithecus mitis* and *Lophocebus albigena*. Though it is currently unclear why the area of transect 1 differs from the rest of the forest and how dispersal limited *Cercopithecus mitis* and *Lophocebus albigena* are, human use of the fragments is probably the main agent of change and could potentially degrade the fragments until they are empty of the primates that still inhabit them.

## ACKNOWLEDGMENTS

We are grateful to Amooti Katusabe Swaibu for providing invaluable assistance with fieldwork and John Poulsen for his help. The Wildlife Conservation Society, the National Science Foundation (grant no. SBR-9617664, SBR-990899), and an Alumni Fellowship from the University of Florida provided funding for this research. Makerere University

Biological Field Station, Uganda Wildlife Authority, and the National Council on Science and Technology granted permission to conduct research in Kibale National Park.

## REFERENCES

- Aldrich-Blake, F. P. G. (1970). *The Ecology and Behavior of the Blue Monkey Cercopithecus mitis stuhlmanni*, PhD Thesis, University of Bristol, Bristol.
- Anderson, S. C., Kupfer, J. A., Wilson, R. R., and Cooper, R. J. (2000). Estimating forest crown area removed by selection cutting: A linked regression-GIS approach based on stump diameters. *Forest Ecol. Manage.* 137: 171–177.
- Basabose, A. K. (2004). Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. *Primates* 45: 211–219.
- Beeson, M. (1989). Seasonal dietary stress in a forest monkey (*Cercopithecus mitis*). *Oecologia* 78: 565–570.
- Brooks, T. M., Pimm, S. L., and Oyugi, J. O. (1999). Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 13: 1140–1150.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993). *Distance Sampling: Estimating Abundance of Biological Populations*, Chapman and Hall, London.
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density and low-density subpopulations. *Ecol. Monogr.* 60: 1–26.
- Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., and Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: A 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14: 207–217.
- Chapman, C. A., Chapman, L. J., Wrangham, R. W., Hunt, K. D., Gebo, D., and Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527–531.
- Chapman, C. A., Gautier-Hion, A., Oates, J. F., and Onderdonk, D. A. (1999a). African primate communities: Determinants of structure and threats to survival. In Fleagle, J. G., Janson, C. H., and Reed, K. E. (eds.), *Primate Communities*, Cambridge University Press, Cambridge, UK, pp. 1–37.
- Chapman, C. A., Lawes, M. J., Naughton-Treves, L., and Gillespie, T. R. (2003). Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use? In Marsh, L. K. (ed.), *Primates in Fragments*, Kluwer Academic/Plenum Publishers, New York, p. 404.
- Chapman, C. A., and Peres, C. A. (2001). Primate conservation in the new millennium: The role of scientists. *Evol. Anthropol.* 10: 16–33.
- Chapman, C. A., Wrangham, R. W., and Chapman, L. J. (1994). Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160–171.
- Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., and Zanne, A. E. (1999b). Fruit and flower phenology at two sites in Kibale National Park. *J. Trop. Ecol.* 15: 189–211.
- Cordeiro, N. J., and Howe, H. F. (2001). Low recruitment of trees dispersed by animals in African forest fragments. *Conserv. Biol.* 15: 1733–1741.
- DeFries, R. S., Houghton, R. A., Hansen, M. C., Field, C. B., Skole, D., and Townshend, J. (2002). Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980's and 1990's. *Proc. Natl. Acad. Sci. USA* 99: 14256–14261.
- Devos, A., and Omar, A. (1971). Territories and movements of Sykes monkeys (*Cercopithecus mitis kolbi* Neuman) in Kenya. *Folia Primatol.* 16: 196.
- Doran-Sheehy, D. M., Greer, D., Mongo, P., and Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *Am. J. Primatol.* 64: 207–222.
- Fairgrieve, C. (1995). *The Comparative Ecology of Blue Monkeys (Cercopithecus mitis stuhlmannii) in Logged and Unlogged Forest, Budongo Forest Reserve, Uganda: The*

- Effects of Logging on Habitat and Population Density*, PhD Thesis, University of Edinburgh, Edinburgh.
- Fairgrieve, C., and Muhumuza, G. (2003). Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 41: 141–149.
- Fashing, P. J., and Cords, M. (2000). Diurnal primate densities and biomass in the Kakamega Forest: An evaluation of census methods and a comparison with other forests. *Am. J. Primatol.* 50: 139–152.
- Felton, A. M., Engstrom, L. M., Fleton, A., and Knott, C. D. (2003). Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol. Conserv.* 114: 91–101.
- Gonzalez, A., and Chaneton, E. J. (2002). Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* 71: 594–602.
- Granjon, L., Cosson, J. F., Judas, J., and Ringueut, S. (1996). Influence of tropical rainforest fragmentation on mammal communities in French Guiana: Short-term effects. *Acta Oecol. Int. J. Ecol.* 17: 673–684.
- Hamilton, A. (1991). *A Field Guide to Ugandan Forest Trees*, Makerere University Printery, Kampala.
- Karanth, K. U. (1992). Conservation prospects for lion-tailed macaques in Karnataka, India. *Zoo Biol.* 11: 33–41.
- Kingdon, J. (1974). *East African Mammals: An Atlas of Evolution in Africa*, The University of Chicago Press, Chicago.
- Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals*, Academic Press, London.
- Lawes, M. J. (2002). Conservation of fragmented populations of *Cercopithecus mitis* in South Africa: The role of reintroduction, corridors and metapopulation ecology. In Glenn, M. E., and Cords, M. (eds.), *The Guenons: Diversity and Adaptation in African Monkeys*, Kluwer Academic/Plenum Press, New York, pp. 375–392.
- Marsh, L. K., and Loiselle, B. A. (2003). Recruitment of black howler fruit trees in fragmented forests of Northern Belize. *Int. J. Primatol.* 24: 65–86.
- Medley, K. E. (1993). Primate conservation along the Tana River, Kenya—An examination of the forest habitat. *Conserv. Biol.* 7: 109–121.
- Mittermeier, R. A., and Cheney, D. L. (1987). Conservation of primates and their habitats. In Smuts, B. B., Cheney, D. L., Seyfarth, R., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, Chicago University Press, Chicago, pp. 477–490.
- National Research Council (1981). *Techniques for the Study of Primate Population Ecology*, National Academy Press, Washington, DC.
- Norconk, M. A., and Grafton, B. W. (2003). Changes in forest composition and potential feeding tree availability on a small land-bridge island in Lago Guri, Venezuela. In Marsh, L. K. (ed.), *Primates in Fragments: Ecology and Conservation*, Kluwer Academic/Plenum Press, New York, pp. 211–225.
- Olupot, W. (1994). *Ranging Patterns of the Grey-Cheeked Mangabey Cercopithecus albigena with Special Reference to Food Finding and Food Availability in Kibale National Park*, M.Sc. Thesis, Makerere University, Kampala.
- Olupot, W. (2000). Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conserv. Biol.* 14: 833–843.
- Onderdonk, D. A., and Chapman, C. A. (2000). Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *Int. J. Primatol.* 21: 587–611.
- Peres, C. A. (1990). Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* 54: 47–59.
- Plumptre, A. J. (2000). Monitoring mammal populations with line transect techniques in African forests. *J. Appl. Ecol.* 37: 356–368.
- Plumptre, A. J., and Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol.* 31: 631–641.

- Poulsen, J. R., Clark, C. J., and Smith, T. B. (2001). Seasonal variation in the feeding ecology of the Grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *Am. J. Primatol.* 54: 91–105.
- Rao, M., and van Schaik, C. P. (1997). The behavioral ecology of Sumatran orangutans in logged and unlogged forest. *Trop. Biodiver.* 4: 173–185.
- Rudran, R. (1978). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contrib. Zool.* 249: 88.
- Six, K. S., and Struhsaker, T. T. (1999). Ecology of the Zanzibar red colobus monkey: Demographic variability and habitat stability. *Int. J. Primatol.* 20: 163–192.
- Skorupa, J. P. (1988). *The Effect of Selective Timber Harvesting on Rainforest Primates in Kibale Forest, Uganda*, PhD Thesis, University of California, Davis.
- Struhsaker, T. T. (1997). *Ecology of an African Rainforest*, University of Florida Press, Gainesville.
- Struhsaker, T. T., and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In Rosenblatt, J., Hinde, R. A., Beer, C. and Busnel, M. C. (eds.), *Advances in the Study of Behavior*, Academic Press, New York, pp. 158–228.
- Tutin, C. E. G., White, L. J. T., and Machanga-Missandzou, A. (1997). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conserv. Biol.* 11: 1190–1203.
- Twinomugisha, D., Chapman, C. A., Lawes, M. J., Worman, C. O., and Danish, L. M. (in press). How does the golden monkey of the Virungas cope in a fruit scarce environment? In Newton-Fisher, N., Notman, H., Renolds, V., and Paterson, J.D. (eds.), *Primates of Western Uganda*, Springer.
- Umapathy, G., and Kumar, A. (2000). The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. *Biol. Conserv.* 92: 311–319.
- Vargas, A., Jimenez, I., Palomares, F., and Palacios, M. J. (2002). Distribution, status, and conservation needs of the golden-crowned sifaka (*Propithecus tattersalli*). *Biol. Conserv.* 108: 325–334.
- Waser, P. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercopithecus albigena* (Lydekker). *East Afr. Wildlife J.* 13: 249–263.
- Waser, P. (1984). Ecological differences and behavioral contrasts between two mangabey species. In Rodman, P. S., and Cant, J. G. H. (eds.), *Adaptations for Foraging in Non-Human Primates*, Columbia University Press, New York, pp. 195–216.
- Wilson, C. C., and Wilson, W. L. (1975). The influence of selective logging on primates and some other animals in East Kalimantan. *Folia Primatol.* 23: 245–274.
- Woodwell, G. M. (2002). On purpose in science, conservation and government—The functional integrity of the Earth is at issue not biodiversity. *Ambio* 31: 432–436.
- Worman, C. O., and Chapman, C. A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *J. Trop. Ecol.* 21: 689–697.