



Coping with Forest Fragmentation: The Primates of Kibale National Park, Uganda

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*A goal of conservation biology is to determine which types of species are most susceptible to habitat disturbance and which types of disturbed habitats can support particular species. We studied 20 forest fragments outside of Kibale National Park, Uganda, to address this question. At each patch, we determined the presence of primate species, tree species composition, patch size, and distance to nearest patch. We collected demographic, behavioral, and dietary data for Abyssinian black-and-white colobus (*Colobus guereza*). Black-and-white colobus and red-tailed guenons (*Cercopithecus ascanius*) were in almost all fragments; Pennant's red colobus (*Procolobus pennantii*) and chimpanzees (*Pan troglodytes*) were in some fragments; and blue monkeys (*Cercopithecus mitis*) and gray-cheeked mangabeys (*Lophocebus albigena*) were absent from all fragments. No species characteristics—home range, body size, group size, or degree of frugivory—predicted the ability of species to live in patches. No characteristics of patches—area, distance to the nearest patch, distance to Kibale, or number of food trees present—predicted the presence of a particular species in a patch, but distance to Kibale may have influenced presence of red colobus. Black-and-white colobus group size was significantly smaller in the forest patches than in the continuous forest of Kibale. For a group of black-and-white colobus in one patch, food plant species and home range size were very different from those of a group within Kibale. However, their activity budget and plant parts eaten were quite similar to those of the Kibale group. The lack of strong predictive variables as well as differences between other studies of fragmentation and ours*

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caution against making generalizations about primate responses to fragmentation.

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INTRODUCTION

As deforestation and habitat fragmentation continue at alarming rates throughout the world, the survival of many forest species largely depends on their ability to cope with such changes (Marsh *et al.*, 1987; Noss and Csuti, 1994; Robinson and Ramirez, 1982). With only 3.7% of the world's land area officially protected as national parks or forest reserves (McNeely *et al.*, 1990), and many of them only partially protected, most of the area occupied by forest species has been or will be altered in some way by human activity. A common form of humanized landscape is that of remnant forest patches surrounded by agricultural or grazing land. With increasing human population densities, this pattern of land use will increase. It is therefore imperative that research efforts be focused on identifying the types of species that are most susceptible to extinction in forest fragments, and the types of fragments that are most likely to support particular species. Such generalizations allow predictions to be made for areas for which data are not yet available.

Primates are valuable subjects for examining the effects of fragmentation for several reasons. They are relatively easy to census, and primate species in a given community often respond differently to fragmentation (Estrada and Coates-Estrada, 1996; Lovejoy *et al.*, 1986; Tutin *et al.*, 1997). Furthermore, many primate species are endangered or threatened, making it critical that the threats to their survival be better understood.

Several characteristics of primates may influence their ability to live in forest fragments. Home range size is frequently cited as an influencing factor (Estrada and Coates-Estrada, 1996; Lovejoy *et al.*, 1986). A highly frugivorous diet may also limit the ability of species to live in fragments (Estrada and Coates-Estrada, 1996; Lovejoy *et al.*, 1986) because fruit is usually patchily distributed, both spatially and temporally. However, Tutin *et al.* (1997) found that several frugivorous primates were at higher or similar densities in forest fragments than in the intact forest of Lopé. Furthermore, the diet and home range size of some species differ between intact forest and fragments, suggesting that they can be flexible in these parameters (Galetti *et al.*, 1994; Garcia Chiarello, 1993). Clearly, distinct patterns have not yet emerged as to how primates respond to fragmentation.

Outside the boundaries of Kibale National Park in western Uganda, small remnants of forest remain in areas that are difficult to farm, such as swampy valley bottoms and along the steep slopes of hillsides and crater lakes. Many of the forest fragments support primate populations and thus provide an opportunity to address questions relating to primate abilities to cope with fragmentation. Prior studies on Kibale's primate species, which provided an abundance of baseline data for comparison, and the lack of hunting in the area, made it an ideal site for our study.

Our goals were (1) to document which of Kibale's primates are present in forest patches; (2) to determine whether species characteristics can predict their ability to live in patches; (3) to determine whether patch characteristics can predict the presence of primate species; and (4) to examine the mechanisms by which one species, black-and-white colobus (*Colobus guereza*), can persist in forest patches by comparing its group size, diet, and behavior in one forest patch to those in intact forest.

MATERIALS AND METHODS

Study Site

We conducted the study from May to August 1995 in areas neighboring Kibale National Park (766 km²), a mid-altitude moist evergreen tropical forest approximately 24 km east of the Rwenzori Mountains in western Uganda (0°13'-0°41' N and 30°19'-30°32' E; Chapman *et al.*, 1997; Struhsaker, 1997). Elevation in the park ranges from 1590 m in the north to 1110 m in the south. Rainfall in the area is highly variable, but generally bimodal, with peaks occurring in March–May and in August–November. Annual rainfall near the study area averages 178 cm (1977–1998). Because of its relatively high altitude, Kibale's temperatures are fairly cool, with annual means for daily minimum and maximum temperatures of 16.4° and 23.3°C, respectively (1977–1998; Chapman *et al.*, 1997; Struhsaker, 1997).

The history of land use outside of Kibale is not well known. Pollen diagrams suggest that forest clearing began in Uganda approximately 1000 years B.P., probably due to the introduction of agriculture and iron-making (Hamilton, 1974). Forest clearing throughout the country became extensive in the last 200 years, particularly in the last 50 years (Hamilton, 1984; Howard, 1991). Estimates of forest cover in Uganda have decreased from 12.7% in 1900, to 10.8% in 1926, to 4.6% in 1958 (Hamilton, 1984), to < 3% in 1987 (Struhsaker, 1987). Of the remaining forest, an estimated 2% is further lost each year (Hamilton, 1984). While some of the forest loss is due to illegal encroachment into protected areas, most clearing has taken

place on public lands. Nearly all forest outside of officially protected areas has been converted to farms or grazing areas, with only small pockets of forest remaining. No permit is required to clear public land for agriculture, and while permits are required to cut trees for timber or charcoal, the laws are often not enforced (Struhsaker, 1987).

For the region around Kibale, evidence indicates that, before clearing by people, forest extended west and south from Kibale to the Rwenzori and Virunga Mountains (Osmaston, 1959; Hamilton, 1974). Currently only small remnants of forest remain outside the boundaries of the park. While the precise timing of isolation of these forest remnants is not known, aerial photographs taken in 1959 indicate that most have been isolated from Kibale at least since that time, although many have since decreased in size. An analysis of aerial photographs taken in 1988 shows that 20.3% of the land within 1.5 km of the Kibale boundary consists of forest remnants (Mugisha, 1994). This figure most likely decreases with distance from the park boundary.

Patch Characteristics

We surveyed 20 forest patches outside the western boundary of Kibale (Fig. 1). We sampled patches if they had fairly clearly defined boundaries, were isolated from other patches or tracts of forest by ≥ 50 m, and were small enough for the area to be feasibly measured and all black-and-white colobus groups accounted for (approximately 1–10 ha). We sampled one much larger patch (approximately 130 ha) for comparison to the smaller patches.

We measured the following parameters at each patch: primate species present, tree species composition, area of the patch, and distance to the nearest patch. We determined which primate species were present by observations throughout the 2–4 days in each patch. Since most areas of each patch were sampled while determining tree species composition and area, it is unlikely that any species were missed. Since it is possible that species move between patches, we later revisited several patches. The species present in each patch were confirmed through interviews with people living or farming around the patches. Ideally, species abundance rather than presence/absence would be used as an index of success, but these data were possible to obtain only for black-and-white colobus.

Of Kibale's 12 primate species [chimpanzees (*Pan troglodytes*), gray-cheeked mangabeys (*Lophocebus albigena*), Pennant's red colobus (*Procolobus pennantii*), Abyssinian black-and-white colobus, red-tailed guenons (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), l'Hoest's

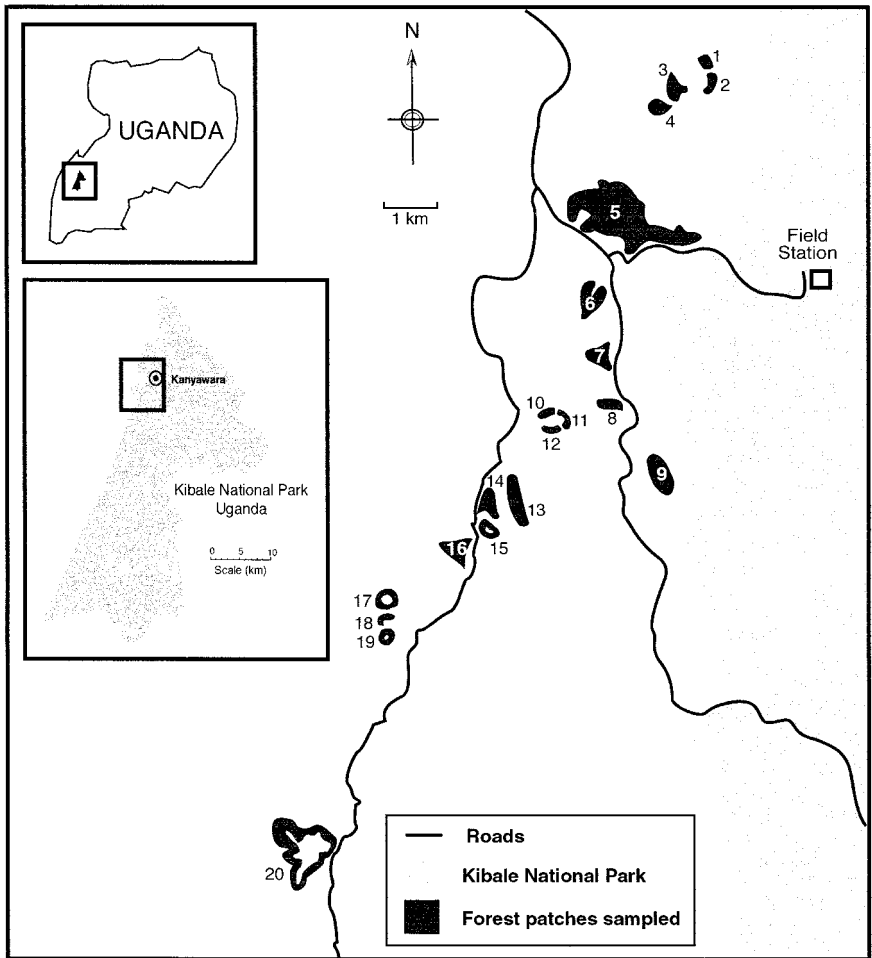


Fig. 1. Twenty forest patches surveyed outside of Kibale National Park, Uganda (note: this does not represent all forest patches in the region). ¹Kiko #3; ²Kiko #4; ³Kiko #2; ⁴Kiko #1; ⁵Kasisi; ⁶Rusenyei; ⁷Kyaibombo; ⁸Durama; ⁹C. K.'s Durama; ¹⁰Rutoma #1; ¹¹Rutoma #4; ¹²Rutoma #3; ¹³Rutoma #2; ¹⁴Nkuruba—fish pond; ¹⁵Nkuruba—lake; ¹⁶Ruihamba; ¹⁷Lake Nyanswiga; ¹⁸Dry Lake; ¹⁹Lake Nyaherya; ²⁰Lake Mwamba.

monkeys (*Cercopithecus lhoesti*), vervets (*Chlorocebus aethiops*), olive baboons (*Papio hamadryas anubis*), pottos (*Perodicticus potto*), Matschie's bush babies (*Galago matschiei*), and Thomas's bush babies (*Galagoides thomasi*), we used only the first 6 in statistical analyses. Patches were only sampled during the day, preventing the three nocturnal prosimians from

being included. Baboons and vervets use the forest habitats within Kibale only occasionally, making them inappropriate for the analyses. L'Hoest's monkeys are uncommon and secretive within Kibale, so very little basic data on their ecology and behavior are available; therefore, they are not included. While we only used the first 6 species in statistical analyses, we report on all diurnal primate species observed in patches.

We assessed tree species composition for each patch by identifying trees along two 50- by 10-m transects, which we placed in areas considered to represent the patch. We recorded tree species and diameter at breast height (DBH) for all trees >10 cm DBH on the transect, giving a sample area of 0.1 ha in each patch. At the 130-ha patch, we sampled four 50- by 10-m transects, for a total area of 0.2 ha. As a measure of recent disturbance, we recorded the number of cut stumps along the transects.

We measured the area of each patch and the distance to the nearest patch either physically with a tape measure or with a range finder or both. We measured one irregularly shaped patch from topographic maps. The distance to the nearest patch could not be determined at the 130-ha patch since the entire perimeter could not be traced. We measured distance to Kibale from topographic maps as the shortest straight line distance from each patch to any part of the National Park.

We performed a forward stepwise logistic regression analysis (Menard, 1995) to determine whether any species characteristics could predict the ability of a primate species to live in patches. Using each species as a data point, we classified them as able or unable to live in patches for the dependent variable. We used as independent variables species characteristics that have been shown to or have been predicted to influence primate responses to disturbance: group size, home range size, body size, and percentage of fruit in the diet (Estrada and Coates-Estrada, 1996; Johns and Skorupa, 1987; Lovejoy *et al.*, 1986; Tutin *et al.*, 1997). We used values for these variables from previous studies on Kibale primate species (Table I). To standardize the values, we first used values from a single study or other studies conducted with the same sampling methods (Struhsaker, 1978; Struhsaker and Leland, 1979). However, the range of values reported for the variables may also be important to consider. Accordingly, we also report the minimum and maximum values from the literature (Table I). As it is the lower limit of these variables that would be most relevant to the ability of a species to live in patches, we conducted a second analysis using the minimum values reported.

For each species that showed some variance in their presence in patches—black-and-white colobus, red colobus, and red-tailed guenons—we used a forced entry logistic regression to determine whether patch characteristics—area of the patch, distance to Kibale, distance to the

Table I. Primate species characteristics used in a logistic regression to predict ability to live in patches

	Group size	Home range (ha)	Degree of frugivory ^a	Body size (kg) ^b
Red-tail	32 ^c (30 ^c –35 ^d)	24 ^c	44 ^d (36 ^c –60 ^e)	3.5 ^c
Blue	24 ^c (15 ^f –25 ^d)	61 ^c (36 ^f –253 ^f)	45 ^d (22 ^f –68 ^g)	4.75 ^c
Red colobus	50 ^c (14 ^h –61 ⁱ)	35 ^c	6 ^d (6 ^d –14 ^e)	8.75 ^c
Black-and-white colobus	9 ^c (6 ^h –11 ⁱ)	16 ^c (15 ^f –16 ^c)	13 ^d (13 ^d –14 ^f)	8.75 ^c
Mangabey	15 ^c (9 ^k –15 ^c)	410 ^c (200 ^l –410 ^c)	59 ^d	8.75 ^c
Chimpanzee	40 ^m	1040 ^m	79 ⁿ	45.25 ^o

Note: Group size, home range, and degree of frugivory values are from data on the species within Kibale National Park, Uganda. Values listed first are from a single study or other studies conducted with the same sampling methods. Minimum and maximum values reported are in parentheses. Where values for several groups were reported in a study, we used the average value within a given site.

^aDegree of frugivory is the percentage of fruit and seeds in a specific diet.

^bValues are the average weights of males and females.

^cStruhsaker and Leland (1979).

^dStruhsaker (1978).

^eChapman and Chapman (2000).

^fButynski (1990).

^gRudran (1978).

^hChapman and Chapman, unpublished data.

ⁱClutton-Brock (1975).

^jOates (1977).

^kOluput *et al.* (1994).

^lOluput, unpublished data.

^mChapman and Wrangham (1993).

ⁿWrangham *et al.* (1996).

^oWrangham *et al.* (1994).

nearest patch, and number of food trees present in the patch—could predict presence or absence of that species, using each patch as a data point. We determined the number of food trees in each patch using data on specific diets within Kibale, as well as information from the vegetation sampling in patches. We determined the top 10 most commonly eaten tree species, in terms of overall frequency of feeding, from the literature for each of the 3 species (Lambert, 1997; Oates, 1977; Struhsaker, 1975, 1978). For red colobus and black-and-white colobus, we also determined the 10 most commonly eaten tree species based on a selection ratio: the frequency of feeding on a tree species relative to its abundance in a group's home range within Kibale (Oates, 1977; Struhsaker, 1975). As there are no data from

Kibale on red-tailed guenon food tree abundance within a group's home range, the 10 most commonly eaten food tree species could not be determined for them based on a selection ratio. We calculated the number of food trees in a patch by extrapolating the number of food trees along the transects to the area of the patch.

Black-and-White Colobus Group Size

Black-and-white colobus were common in forest patches, and we studied them in more detail. For each group of black-and-white colobus encountered, we determined group size and composition. All groups were most likely accounted for in all patches except the 130-ha patch. We determined sex and assigned individuals to one of four age classes: infant, juvenile, subadult, or adult per Oates (1974).

We compared group size to those from other studies of black-and-white colobus within Kibale (Clutton-Brock, 1975; Oates, 1977; Teelen, 1994). We excluded solitary individuals from other studies in the comparisons. We compared average group sizes via a Kruskal–Wallis test with associated post hoc tests (Conover, 1980).

We used a forced-entry multiple regression to determine whether patch variables—area of the patch, distance to Kibale, distance to the nearest patch, and both indices of the number of food trees present—could predict the number of black-and-white colobus in a patch. We employed a second forced-entry multiple regression to determine whether variables relating to patch quality—area of the patch and both indices of food trees present—could predict the ratio of immatures—infants and juveniles—to adult females, an index of reproductive success. We used only patches containing black-and-white colobus for this regression. We combined multiple groups within a patch for the analysis, and where the composition of all groups within a patch was not determined, we included only the groups for which the composition was known.

Black-and-White Colobus Behavior and Feeding Observations

At Rutoma #1, we conducted behavior and feeding observations on one group of black-and-white colobus for 5 days during the first 2 weeks of June, July, and August, 1995. We chose this group because it was relatively well habituated and the viewing conditions at the patch were favorable. Rutoma #1 is a thin ring of forest curving around the side of a hill, bordered by papyrus at the bottom and by cropland at the top. The patch

was 1.2 ha, although parts of it were being cleared during our study. Two groups of black-and-white colobus were present in the patch, as well as red-tailed guenons (present most of the time) and an individual red colobus. The study group ($n = 4$) contained an adult male, an adult female, a subadult female, and a juvenile male.

To facilitate comparison with data on black-and-white colobus in the continuous forest of Kibale, observation methods followed those used by Oates (1974, 1977). To obtain an activity budget, we conducted a group scan every half hour between 0800 and 1800 h and recorded the behavior of each individual. We divided behavior into the following categories: inactive sheltered, inactive exposed, feeding, moving, social grooming, self-cleaning, and other per Oates (1974), who included two behaviors that were not applicable to the patch study group: playing and clinging. Playing did not occur in the patch group because there was only one juvenile, and clinging did not occur because there was no infant. For the sake of comparison, we include playing in other behavior and clinging in inactive. During scans, we recorded the plant species and the plant parts eaten by feeding colobus. Plant parts are mature leaves, young leaves, leaf buds, petioles, flowers, fruit, bark, wood, and whole plants.

In the area used by the study group, we identified and measured all trees >10 cm DBH. Following Oates (1977), we calculated a selection ratio (the number of feeding records on a given species/the number of individuals of that species per ha) for each tree species fed on by the study group. As Oates (1977) included only trees >50 cm girth at breast height (≈ 16 cm DBH) in calculations of selection ratios, we also only considered trees this size.

RESULTS

Patch Characteristics

The 20 patches surveyed range from 0.8 ha to 130 ha, but most (18) are <10 ha (mean excluding the 130-ha patch = 4.7 ha, $n = 19$; Table II). The distance to the nearest patch ranged from 50 m (the minimum criterion for patch isolation) to 300 m (mean = 121 m, $n = 19$). The patches are surrounded by farmland, grazing area, papyrus swamp, grassland, and/or tea. The distance from each patch to Kibale ranged from 0.2 km to 7.2 km (mean = 2.8 km, $n = 20$).

There was a consistent pattern as to which primate species were present in the patches (Table II). Black-and-white colobus were in nearly all patches (17 of 20), as were red-tailed guenons (18 of 20). Red colobus were in approxi-

Table II. Characteristics of 20 forest patches sampled outside of Kibale National Park, Uganda

Patch	Area (ha)	Patch type ^a	Distance to Kibale (km)	Distance to nearest patch (m)	No. of cut stumps/ha	Diurnal primate species present ^b						No. of black-and-white colobus individuals				
						Red-tail	Blue	Red colobus	Black-and-white colobus	Mangabey	Chimpanzee		Vervet	Baboon ^{c,d}	I'Hoeist's ^e	
Rutoma #3	0.8	HS	2.2	100	210	1	0	0	0	0	1	0	0	0	0	0
Dry lake	1.2	HS	6.1	155	90	1	0	0	1	0	0	0	0	0	0	2
Rutoma #1	1.2	HS	2.4	80	40	1	0	1 ^h	1	0	0	0	0	0	0	2
Kiko #4 ^f	1.2	VB	7.0	70	20	0	0	1	1	0	0	0	0	0	0	1
Durama	1.4	HS	1.1	60	70	1	0	0	0	0	0	0	0	0	0	0
Kiko #3 ^g	1.7	VB	1.1	70	120	1	0	1	1	0	0	0	0	0	0	2
Rutoma #4	2.0	HS	2.1	80	60	1	0	1 ^h	1	0	0	0	0	0	0	2
Lak Nyanswiga	2.2	CL	6.0	155	90	1	0	0	1	0	1	0	0	0	0	1
Kyabombo	2.3	VB	1.1	162	50	1	0	0	1	0	0	1	0	0	0	1
Ruihamba	2.4	VB	4.1	300	100	0	0	0	1	0	0	1	0	0	0	1
Nkuruba—fish pond	2.8	VB	3.7	70	0 ^g	1	0	1	1	0	1	0	0	0	0	1
Lake Nyaherya	4.6	CL	6.1	300	150	1	0	1 ^h	1	0	0	0	0	0	0	3
Rutoma #2	4.9	HS	3.0	150	170	1	0	0	1	0	1	0	0	0	0	2
Rusenyi	4.9	VB	1.1	50	70	1	0	1 ^h	1	0	0	0	0	0	0	3
Kiko #2 ^g	5.0	VB	1.8	125	100	1	0	1	1	0	0	0	0	0	0	7
Kiko #1 ^g	6.2	VB	2.0	50	130	1	0	1	1	0	0	0	0	0	0	1
Nkuruba—lake	6.4	CL	3.6	70	0 ^g	1	0	0	1	0	1	0	0	0	0	1
C.K. s Durama	8.7	VB/HS	0.2	150	120	1	0	1	1	0	1	0	0	0	0	1
Lake Mwamba	28.7	CL	7.2	100	140	1	0	0	0	0	1	0	0	0	0	11
Kasisi	130	VB/HS	0.9	—	65	1	0	1	1	0	1	0	0	0	0	—

^aPatch types: HS = hillside, VB = valley bottom, and CL = crater lake.

^bFor primate species present, 1 = present, 0 = absent.

^cThese species were not included in statistical analyses (see Methods).

^dWhile no baboon was in the 20 patches sampled, we observed them in two patches not included in the study.

^eThese patches were in the middle of a tea plantation.

^fThe distance to nearest patch could not be determined for this patch since the entire perimeter could not be traced.

^gThese patches are part of a conservation and development project, and so tree clearing is prohibited.

^hIndicates that red colobus was present in these patches only as single individuals.

ⁱAll black-and-white colobus groups could not be accounted for in this patch.

mately half of the patches (11 of 20), but not always as entire groups. In 4 of the 11 patches with red colobus, we saw only solitary individuals, often in association with a black-and-white colobus group. Chimpanzees were seen in only one patch, but evidence of chimpanzees, such as nests, dung, and/or wadges of pith, was found in 9 patches, including the smallest one.

Blue monkeys and gray-cheeked mangabeys were absent from all patches, including the 130-ha patch. While it was not feasible to survey the entire large patch, we asked people living nearby if they had ever seen or heard blue monkeys or mangabeys, both of which have very loud, distinct calls. None of those interviewed had seen or heard them. In fact, while there are Rutoro names for most of Kibale's primate species, there is no local name for blue monkeys or mangabeys. This suggests that people in the area around Kibale have very little contact with them relative to Kibale's other primates.

We observed vervets in three of the forest patches. While we saw no baboon in the sample patches, they were in two forest patches that we did not study. L'Hoest's monkeys were not in any of the forest patches, and we saw no large mammal other than primates. However, farmers reported that bushpigs (*Potamochoerus porcus*) come occasionally to one patch and porcupines (*Hystrix* sp.) live in another (Onderdonk, 1998).

Black-and-white colobus groups appeared to be resident in a given patch; we never saw them moving between patches, and the presence or absence of black-and-white colobus groups was consistent whenever we revisited patches. Conversely, we saw red-tailed guenons moving between patches on three occasions. We saw no red colobus moving between patches, and their presence or absence in a patch did not vary among repeat visits. However, discrepancies between direct observations and reports by local farmers of red colobus in several patches (Onderdonk, 1998) suggest they might move between patches. The fact that there was recent evidence of chimpanzees in several patches, while we actually saw them in only one patch, suggests that they move between patches where they forage for short periods.

For the logistic regressions predicting ability of species to live in patches, black-and-white colobus, red-tailed guenons and chimpanzees were classified as able to live in patches, while blue monkeys and gray-cheeked mangabeys were classified as unable to live in patches. It was ambiguous whether red colobus should be classified as able or unable to live in patches since they were present in approximately half the patches; thus we conducted separate analyses classifying them both as able and unable to live in patches. We ran the regressions both including and excluding chimpanzees, since they are markedly different from the other species in most parameters considered. None of the independent variables, using

either standard values or minimum values (Table I), is a significant predictor of ability of species to live in patches (classifying red colobus as able or unable to live in patches, and including or excluding chimpanzees).

Since red colobus, black-and-white colobus, and red-tailed guenons showed some variance in their presence in patches, we employed each of them in the logistic regressions using patch characteristics to predict presence or absence of particular species. Although chimpanzees were evidenced in approximately half of the patches, the data suggest that they are capable of stopping briefly at almost any kind of patch. Therefore, we did not conduct this analysis with chimpanzees. For the analysis predicting presence or absence of red colobus, we ran two regressions (1) considering only the presence of groups and (2) considering the presence of groups or individuals. The values of the patch characteristics used for these regressions are in Table II (patch area, distance to Kibale, distance to nearest patch) and Table III (number of food trees present).

Table III. The number of stems of the top 10 most commonly eaten food trees for red colobus, black-and-white colobus, and red-tailed guenons in 20 forest patches sampled outside of Kibale National Park, Uganda

Patch	Red colobus		Black-and-white colobus		Red-tail
	Overall frequency	Selection ratio	Overall frequency	Selection ratio	Overall frequency
Rutoma #3	88	80	48	40	64
Dry lake	72	60	72	60	96
Rutoma #1	120	120	96	72	96
Kiko #4	0	0	0	0	0
Durama	140	140	84	42	84
Kiko #3	0	0	0	0	0
Rutoma #4	200	200	80	20	100
Lake Nyanswiga	44	0	22	22	66
Kyaibombo	0	0	0	0	0
Ruihamba	0	0	0	0	0
Nkuruba—fish pond	56	56	56	56	56
Lake Nyaherya	184	138	138	92	276
Rutoma #2	490	343	539	490	490
Rusenyi	98	98	49	49	49
Kiko #2	0	0	0	0	0
Kiko #1	248	248	62	62	62
Nkuruba—lake	448	384	256	64	512
C.K.'s Durama	435	435	348	261	609
Lake Mwamba	1148	861	861	287	2296
Kasisi	6500	6500	1950	1950	1300

Note: For red colobus and black-and-white colobus, the top ten most commonly eaten tree species are from both the overall frequency of feeding and from a selection ratio (see text). For red-tailed guenons, the top 10 most commonly eaten tree species was determined only from overall frequency of feeding.

For each of the three species, none of the independent variables is a significant predictor of specific presence or absence in a patch. However, for red colobus, the distance to Kibale showed a trend toward predicting their presence, both considering individuals and groups ($p = 0.07$) and considering only groups ($p = 0.06$).

Black-and-White Colobus Group Size

We encountered 29 groups of black-and-white colobus in the 20 forest patches. Four groups were seen in the 130-ha patch, and they undoubtedly represent a small fraction of the total number of groups. We found 25 groups in the other 19 patches, for an average of 1.3 groups/patch (range = 0–3; Table II). We determined group size for all 29 groups, and group composition for 26 of them (Table IV). The number of black-and-white colobus in a patch ranged from 0 to 19 (overall mean = 8.5; mean when present = 10.1; Table II), while their density ranged from 0 to 12.5 individuals/ha (overall mean = 3.5, mean when present = 4.2). The mean group size of all black-and-white colobus groups is 6.2 (range = 3–11, s.d. = 2.4, $n = 29$; Table IV). Group size in forest patches is significantly smaller than those from 3 studies of black-and-white colobus in Kibale National Park [Clutton-Brock (1975): 9.3; Oates (1977): 10.7; Teelen (1994): 8.0; $H = 17.06$, $df = 3$, $p = 0.001$].

The multiple regression analysis shows that no patch characteristic—area of the patch, distance to Kibale, distance to nearest patch, and both indices of food tree abundance—is a significant predictor of the number of black-and-white colobus in a patch ($r^2 = 0.33$, $p = 0.26$). Furthermore, the variables relating to patch quality—area of the patch, and both indices of food tree abundance—did not predict the ratio of immatures to adult females ($r^2 = 0.092$, $p = 0.75$).

Black-and-White Colobus Behavior and Feeding Observations

The observation group used approximately 2/3 of the forest patch, an area of 0.8 ha. Their home range did not appear to overlap with that of the other black-and-white colobus group in the patch, although home ranges of black-and-white colobus groups in other patches overlapped. On several occasions, the group descended the hill until they were out of sight, presumably in the swamp below.

From the group scans, we collected 1173 behavior records, which show that they spent 68.9% of time inactive, 16.5% feeding, 6.4% moving, 6.1%

Table IV. Group size and composition of 29 black-and-white colobus groups in forest patches outside of Kibale National Park, Uganda

Patch	Group size	Adult male	Adult female	Subadult male	Subadult female	Juvenile	Black-and-White infant	White infant
Dry Lake (A)	6	1	2	0	1	1	1	0
Dry Lake (B)	9	—	—	—	—	—	—	—
Rutoma #1 (A)	4	1	1	0	1	1	0	0
Rutoma #1 (B)	6	1	3	0	0	0	0	2
Kiko #4	6	1	1	2	1	0	0	0
Kilo #3 (A)	9	2	2	1	1	3	0	0
Kiko #3 (B)	9	1	4	1	1	0	0	2
Rutoma #4 (A)	3	1	1	0	0	0	1	0
Rutoma #4 (B)	5	1	2	0	0	0	2	0
Lake Nyanswiga	8	1	4	1	1	0	0	1
Kyaibombo	8	1	2	1	1	1	0	2
Ruihamba	8	1	2	1	0	3	0	1
Nkuruba—fish pond	5	1	1	1	1	1	0	0
Lake Nyaherya (A)	4	1	2	0	1	1	0	0
Lake Nyaherya (B)	5	1	1	2	0	1	0	0
Lake Nyaherya (C)	10	—	—	—	—	—	—	—
Rutoma #2 (A)	5	1	2	0	1	0	1	0
Rutoma #2 (B)	9	—	—	—	—	—	—	—
Rusenyei (A)	3	1	1	0	1	0	0	0
Rusenyei (B)	3	1	1	0	1	0	0	0
Rusenyei (B)	5	1	1	2	0	0	1	0
Rusenyei (C)	4	1	1	0	1	1	0	0
Kiko #2	7	2	2	1	0	1	1	0
Kiko #1	8	2	2	2	1	1	0	0
Nkuruba—lake	5	2	2	0	1	0	0	0
C.K.'s Durama	11	1	2	2	2	2	2	0
Kasisi (A)	3	1	1	0	1	0	0	0
Kasisi (B)	3	1	1	0	0	1	0	0
Kasisi (C)	9	1	2	1	0	3	2	0
Kasisi (D)	4	1	2	0	0	1	0	0
Means	6.2	1.2	1.8	0.7	0.6	0.9	0.5	0.3

Note: For patches containing more than one group, groups are differentiated by letters in parentheses. Dashes indicate that composition could not be determined for these groups.

social grooming, 0.7% self-cleaning, and 1.4% in other activities. Their activity budget is quite similar to an activity budget of black-and-white colobus inside Kibale: 63.1% of time inactive, 19.9% feeding, 5.4% moving, 6.2% social grooming, 0.7% self-cleaning, and 4.7% in other activities (Oates, 1974).

We collected a total of 192 feeding records on the patch group. In all but one of them (soil), they fed on plant material. Leaf parts composed the majority of their diet (83.2%), while the remaining portion consisted of fruit (15.2%) and lichens (1.6%; Table Va). The proportions of plant parts eaten by black-and-white colobus inside Kibale (Oates, 1977) are quite similar to those of the patch group (Table Va). Oates (1977) observed Kibale black-and-white colobus eating three plant parts for which we have no record in the forest patch: flowers, bark, and whole plants (mostly aquatic swamp plants). They constitute a small percentage of the feeding observations, so we may have missed them in the patch because of the shorter duration of our study.

The black-and-white colobus patch group ate items from 7 tree species; 2 species of shrubs; vines, which we did not identify to species; lichens; one crop species (beans, *Phaseolus vulgaris*); and soil (Table Vb). The top 4 most commonly eaten foods (combining all vines) composed 79.7% of their diet. The tree species that they ate most commonly in the forest patch were not important components of the Kibale group's diet (Oates, 1977; Table Vb), despite the fact that they were present in the study area (Oates, 1974). Because this difference might be a result of comparing a 3-month sample with a full-year sample, we compared the dietary data from our study with the dietary data from the same 3 months (June, July, and August) of Oates' study (1974). This could only be done for 3 of the 7 species eaten by the patch group (*Celtis africana*, *Olea welwitschii*, and *Ficus sansibarica*) because Oates (1974) reported the dietary composition data by month for only the top 10 most commonly eaten tree species (Table Vb). For two of the three species, the differences between the patch group's diet and the Kibale group's diet are even more striking when only the summer months are compared. In Kibale, three tree species comprised 69% of black-and-white colobus diet: *Celtis durandii*, *Markhamia platycalyx*, and *Ficus exasperata*. They were almost entirely absent from the observation patch (1 *Celtis durandii* <10 cm DBH, 2 *Markhamia platycalyx* <15 cm DBH, and 2 *M. platycalyx* cut stumps were present).

The tree species eaten in the forest patch were fairly low-ranking, in terms of the selection ratio, in the diets of the Kibale group (Oates, 1977). The highest selection rank in Kibale for a tree species eaten by the patch group is six (*Ficus sansibarica*). *Diospyros abyssinica*, one of the species eaten in the patch, ranked 25th out of 25 species eaten in Kibale. The patch

Table V. (a) Plant parts eaten by black-and-white colobus in a forest patch outside of Kibale National Park and inside Kibale, and (b) foods eaten by black-and-white colobus in a forest patch outside of Kibale, and the contributions of those species to the diet of black-and-white colobus inside Kibale

Plant part	Records (%)	
	Forest patch	Kibale ^a
Leaf parts	83.2	76.9
Mature leaves		12.4
Young leaves	55.5	57.7
Leaf buds	5.8	4.0
Leaf petioles	0.0	0.4
Undetermined leaves	17.8	2.5
Fruit	15.2	13.6
Lichens	1.6	0.2
Flowers	0.0	2.1
Wood/bark	0.0	1.1
Whole plants	0.0	0.6

^aSource: Oates (1977).

(b)

Species/category ^a	Feeding records (%)		
	Patch	Kibale (all year) ^b	Kibale (June, July, August) ^b
<i>Celtis africana</i>	33.9	3.0	0.0
Vines	17.7	3.3	
<i>Olea welwitschii</i>	14.6	3.6	5.6
<i>Ficus sansibarica</i> ^c	13.5	3.3	2.5
<i>Vernonia amygdalina</i> ^d	7.3	0.0	
<i>Fagara angolensis</i>	4.7	0.3	
<i>Polyscias fulva</i>	2.6	0.04	
<i>Aningeria altissima</i>	1.6	0.1	
Lichens	1.6	0.2	
<i>Diospyros abyssinica</i>	1.0	0.2	
<i>Acanthus pubescens</i> ^d	0.5	0.0	
Beans (<i>Phaseolus vulgaris</i>)	0.5	0.0	
Soil	0.5	0.0	

^aSpecies listed are trees unless otherwise indicated.

^bSource: Oates (1974). Percentage of feeding records for June, July, and August could not be determined for all species, as Oates (1974) reports only the top 10 most commonly eaten species by month. Numbers listed for June, July, and August are the mean percentages for those 3 months.

^cFormerly *Ficus brachylepis*.

^dShrubs.

black-and-white colobus were eating species low on the selection list of Kibale black-and-white colobus.

DISCUSSION

Primate Characteristics

The consistent pattern as to which of Kibale's primate species were in forest patches suggests that certain characteristics of the primates allow them to persist in patches. However, none of the traits used in the logistic regression could predict ability of species to live in patches. Of course, long-term detailed demographic data are needed to determine whether species presence in patches is stable or not, but the consistent pattern of species presence, except perhaps for red colobus, suggests that presence/absence is a reasonable indicator of success.

While home range size is not a significant predictor, the two species that were absent from the patches—blue monkeys and mangabeys—have the largest home ranges, excluding chimpanzees. To be able to live in forest fragments, perhaps a primate species must have either a small home range or, if they have a large home range, the ability to move between patches. Chimpanzees in Kibale and mandrills (*Mandrillus sphinx*) of the Lopé Reserve, Gabon, have very large home ranges (>10.4 km², Chapman and Wrangham, 1993; and 36–45 km², Harrison, 1988, respectively) and are able to use forest fragments by moving between them. If home range size is a limiting factor for blue monkeys and mangabeys, it is unclear why they cannot move between patches; both species come to the ground in the continuous forest of Kibale (Gebo and Chapman, 1995). Furthermore, gray-cheeked mangabeys live in forest fragments at Lopé, where they move between patches (Tutin *et al.*, 1997).

Lovejoy *et al.* (1986) suggested that large home ranges limit the ability of primates to live in forest patches in Brazil. Of 6 species originally present in the area, the 3 with the largest home ranges (*Ateles paniscus*, *Chiropotes satanus*, and *Cebus apella*) were unable to persist in fragments of 100 and 10 ha, although *Ateles* and *Chiropotes* were absent from the 100-ha fragment at the time of isolation. The relatively recent clearing of land surrounding the patches may be a factor deterring them from moving between patches.

While degree of frugivory did not predict ability of species to live in patches, another dietary factor that might influence this ability is dietary diversity. In a comparison of black-and-white colobus and red colobus, Struh-saker and Oates (1975) found that red colobus have a more diverse diet than black-and-white colobus. It might be expected that the species with the

broader diet would be better able to persist under varying conditions. However, if dietary breadth is consistently required over relatively short periods of time, then a patch might not be able to provide the necessary diversity of plant species and parts. The idea that red colobus require a consistently diverse diet over short periods of time is supported by the fact that red colobus in Kibale have a greater index of dietary diversity when calculated on a monthly basis than those of blue monkeys and red-tailed guenons, which both have higher indices of dietary diversity when calculated on a yearly basis (Struhsaker, 1978). In contrast, black-and-white colobus dietary diversity is lower than Kibale's other common monkeys, both on a monthly and a yearly basis (Struhsaker, 1978). Black-and-white colobus, with their relatively monotonous diet, might not be expected to succeed in habitats with a limited number of food species if the right food species were not available. However, if they can be monotonous on whatever is available, then their dietary strategy may be beneficial in a species-poor forest fragment. This appeared to be the case for the Rutoma #1 group of black-and-white colobus.

For the primates of Kibale, ability to live in patches may be related to an ability to live on the edge of forest. The species that live in patches outside of Kibale are also ones that occur on the edge of the continuous forest, while the species absent from patches are not typically on the forest edge (personal observations). As forest patches have a much higher ratio of edge to area than continuous forest, ability to live on edges is a logical requirement for living in patches.

For the colobines, there is evidence that ability to live on edges may be related to a dietary preference for secondary growth. Coley (1983) demonstrated that fast-growing trees and vines of forest gaps have leaves with higher protein and lower fiber and phenolic levels than those of mature forest. Colobine biomass correlates with the ratio of protein to fiber in mature foliage at several sites across Africa and Asia (Oates *et al.*, 1990) and among sites within Kibale (Chapman *et al.*, unpublished data). Therefore, areas with colonizing plants, such as edges or disturbed areas, might support a higher abundance of colobines. This nutritional effect (Oates, 1996) is consistent with Struhsaker's (1975) and Skorupa's (1986) findings that black-and-white colobus in Kibale are at higher densities in logged areas than in unlogged areas, and with Plumptre and Reynolds' (1994) finding that black-and-white colobus densities in different logging compartments at Budongo correlate negatively with time since logging.

Patch Characteristics

We have defined forest patches in a way that is logical to how we perceive them, but this may be different from how monkeys perceive forest

patches. They may be using patches on a different spatial scale, preventing patch characteristics used here from correlating with presence or abundance of primate species. Furthermore, the fragmentation process is a dynamic and ongoing one, so present characteristics of patches may not be strong predictors of primate response.

The number of food trees in a given patch (based on the top 10 most commonly eaten species in Kibale) did not predict the presence or absence of the three primate species that showed variation in their presence in patches. This is not entirely unexpected, since tree species composition varied greatly among patches, while the presence or absence of primate species was fairly consistent. The index of food tree abundance was based on data from inside Kibale, since that is where the diets of these species are known, but it is clear that dietary composition can vary with availability.

Food tree abundance also was not a significant predictor of the number of black-and-white colobus in patches. This is consistent with the findings of Skorupa (1986), who found no relationship between abundance of black-and-white colobus and abundance of their food trees in five sites impacted to differing degrees by logging. Food tree abundance does not seem to be an accurate measure of overall food availability for the species (Davies, 1994), perhaps due to their reliance on nontree food items such as vines (Dasilva, 1994; this study).

Primates living in forest patches probably do not subsist on food from forest trees alone, but supplement their diets by raiding crops in neighboring farmlands (Naughton-Treves, 1996). We observed 6 instances of crop raiding by 4 species of primates from forest patches: black-and-white colobus, red-tailed guenons, vervets, and chimpanzees. We need more data to determine whether the patch primates are raiding crops because the food available in the patches is insufficient to sustain them or because they merely prefer crop foods. Given the small size of some of the patches and the temporally uneven availability of most foods, it is likely that in at least some of the patches, the food available from trees within the patch is inadequate to maintain primate populations. Reliance on crops helps to explain the lack of relationships between food tree abundance or patch area and the presence of primate species.

The fact that distance to Kibale tends to predict the presence or absence of red colobus suggests that they are colonizing from Kibale rather than existing as remnant populations. This relationship is consistent with island biogeography theory (MacArthur and Wilson, 1967), in that red colobus are less likely to be found in a given patch the farther the patch is from a source of colonization. The lack of relationship between distance to Kibale and the presence of red-tailed guenons and black-and-white colobus could be due to the fact that they are not colonizing from Kibale, but instead

existing as remnant populations, although the low variation in their presence or absence makes this relationship difficult to test. The relationship between presence or absence and the distance to Kibale could be further obscured for all species by the relatively recent presence of other potential sources of colonization, the Miranga and Kasenda Forest Reserves, which appear in aerial photographs from 1959 to the west of Kibale, but were almost entirely converted to agricultural land at the time of our study.

While there is too little variation in primate species richness to test a relationship between area and species richness, area is not a significant predictor of the presence or absence of any primate species. Blue monkeys and gray-cheeked mangabeys were absent even from the 130-ha patch, despite the fact that it is larger than some home range estimates for blue monkeys (36.4 ha, Butynski, 1990; 61 ha, Struhsaker and Leland, 1979). A similar pattern characterizes several bird species in the eastern United States, which use only forest remnants that are much larger than their actual home ranges (Robbins *et al.*, 1989). At Lopé, the area of patches seemed to influence whether primate species were resident or transient in patches; only patches ≥ 5 ha supported resident primate groups (Tutin *et al.*, 1997).

Black-and-White Colobus

In forest patches, black-and-white colobus demonstrate flexibility in certain behavioral and ecological parameters, but not all aspects of their behavior and ecology need change for them to live in patches. Their group size, the plant species that composed their diet, and their home range size were all very different in patches than in the continuous forest of Kibale. However, their activity budget and the plant parts that comprised their diet are virtually identical to those of a group in Kibale. Except for group size, these comparisons are mostly based on only one group of black-and-white colobus from each habitat type. Without knowing the range of the parameters across several groups in each habitat, it is difficult to know the generality of the patterns.

The smaller group size of black-and-white colobus in forest fragments relative to that in continuous forest is consistent with other studies of black-and-white colobus in degraded, patchy habitats. Oates (1977) found a smaller group size (modal size: 7, $n = 2$) at Chobe, Uganda, a site consisting of patchy riparian forest bordered by savanna, than in Kibale (modal size: 9, $n = 7$). In his study of two subpopulations of *Colobus guereza* in the Bole Valley, Ethiopia, Dunbar (1987) found that groups in gully patches were smaller than groups in riverine forest, although this

difference is not significant. In examining the relationship between habitat quality and group size across sites, Dunbar (1987) found that groups are significantly larger in more forested habitats. Furthermore, black-and-white colobus group size is smaller in lightly logged forest than in unlogged forest in Kibale (Struhsaker, 1997). Black-and-white colobus group size seems to be related to both habitat size and quality.

The apparent relationship between black-and-white colobus group size and habitat type suggests that ecological factors are influencing group size. It is generally held that group size is a trade-off between costs of reduced foraging efficiency and benefits of reduced predation risk (Chapman *et al.*, 1995; Terborgh and Janson, 1986). As group size increases, reduced foraging efficiency of individuals requires them to travel farther to meet their nutritional requirements (the ecological constraints model). For a group in a forest fragment, increasing foraging area beyond the limits of the patch may be too costly because it would involve traveling over open areas to the next food source, possibly leaving group members vulnerable to predation. Thus, the size of a group in a forest patch may be constrained by the resources within its patch.

Another possible explanation for smaller group size in forest patches than in continuous forest is that there is a decreased predation risk in patches, thus reducing the benefits of large group size. While chimpanzees, a major predator of Kibale monkeys, were present in many of the forest patches, they were probably not present in the large subgroups in which they usually hunt, since typically only 2–4 chimpanzee nests were in a given patch. We do not know whether crowned hawk-eagles (*Stephanoaetus coronatus*), the other main predator of primates in Kibale, were present in forest patches.

The difference in plant species eaten by black-and-white colobus in the patch compared to those eaten by black-and-white colobus in Kibale demonstrates a high degree of dietary flexibility. While they have a monotonous diet relative to those of other Kibale species (Struhsaker, 1978), they are clearly capable of using many different plant species, which is supported by the high variation in tree species composition of the patches (Onderdonk, 1998), but the consistent presence of black-and-white colobus. However, several genera, e.g., *Celtis*, *Ficus*, *Olea*, are consistently in the diets of black-and-white colobus at different sites (Dunbar, 1987; Oates, 1977), and species of them may be nutritionally similar.

The home range of the patch group (0.8 ha) is more than an order of magnitude smaller than that reported for the Kibale group (15.1 ha, Oates, 1977), suggesting a large degree of flexibility in terms of their ranging patterns. Since the data on home range were collected over a shorter period of time for the patch group than for the Kibale group, it is likely that the

home range estimate would have increased over time. However, the entire patch in which they resided was only 1.2 ha, and the area was shared with another group of black-and-white colobus. The Kibale group may have required a larger home range due to its larger group size, but this alone probably would not account for the large difference in home range sizes. While the entire home range reported for the Kibale group is large relative to that of the patch group, the Kibale group spent 42% of their time in a core area of only 2.75 ha, an area more comparable to the home range of the patch group. Small home ranges in forest patches relative to those in intact forest have also been reported for brown howlers (*Alouatta fusca*) in Brazil (Garcia Chiarello, 1993) and for two species of guenons (*Cercopithecus nictitans* and *C. cephus*) in Lopé, Gabon (Tutin *et al.*, 1997).

The high degree of similarity in the activity budgets of the patch group and the Kibale group demonstrates that the patch group was not spending any more time traveling or feeding in the patch, as might be expected if they were forced to search harder for food or to eat lower quality foods. They were, however, eating tree species lower on their Kibale selection list in the patch. Data comparing the nutritional content of their diet in patches to that in intact forest are needed to determine whether they are in fact maintaining a high quality diet.

Conservation Implications

Differences in the responses of primates to fragmentation at Kibale and Lopé illustrate the difficulties in making generalizations across sites. At Lopé, gray-cheeked mangabeys were at similar densities in forest patches and in continuous forest (Tutin *et al.*, 1997), while they were absent from patches around Kibale. Furthermore, all primate species from Lopé were in forest patches to some degree, while two Kibale species were absent from the surrounding patches. The high densities of nonprimate mammals in the Lopé patches stand in contrast to the virtual absence of nonprimate mammals in the Kibale patches. These sites differ from each other in several ways that may account for the discrepancies. At Kibale, the matrix surrounding the forest patches is often actively used by people, while at Lopé, humans are absent from the surrounding matrix, though there is evidence of past human occupation of Lopé (Tutin and Oslisly, 1995). Species particularly sensitive to human presence could therefore be excluded from the forest patches at Kibale. Furthermore, the process of fragmentation at Lopé has been a gradual, natural transformation due to climatic change (now maintained by fire), possibly allowing the primates and other mammals time to adapt to new conditions.

Within this study, no clear generalizations emerge as to what types of primates are most susceptible to fragmentation and what types of fragments are most likely to support primates. Home range is potentially a factor contributing to ability of primate species to persist in forest patches, and isolating distance may influence the presence of certain primate species. However, the lack of strong predictive variables, as well as the differences between other studies of fragmentation and ours, warn against making generalizations about primate responses to fragmentation and suggest that responses may be site-specific.

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