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Population Declines of Colobus in Western Uganda and Conservation Value of Forest Fragments

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Abstract The processes of habitat loss and fragmentation are probably the most important threats to biodiversity. It is critical that we understand the conservation value of fragments, because they may represent opportunities to make important conservation gains, particularly for species whose ranges are not in a protected area. However, our ability to understand the value of fragments for primates is limited by the fact that researchers have conducted many studies in protected areas, which do not represent most fragments, and studies are typically short term. Here we determine the long-term survival probability of red (*Procolobus pennantii*) and black-and-white colobus (*Colobus guereza*) inhabiting forest fragments outside of Kibale National Park, Uganda. Local communities use the fragments primarily for subsistence agriculture and fuelwood. We surveyed primate populations 3 times over

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8 yr, made a total inventory of all trees 2 times, contrasted behavior of groups inhabiting 1 fragment with groups in the continuous forest, and judged the conservation value of the fragments by quantifying patterns of forest use by local people. Of the 20 fragments surveyed, 16 supported resident populations of colobus in 1995, 2 were cleared in 2000, and an additional 2 fragments were cleared by 2003. In 1995 we counted 165 black-and-white colobus, whereas in 2000 and 2003, we counted 119 and 75 individuals, respectively. Seven fragments supported red colobus in 1995, 11 in 2000, and 9 in 2003. In 2000 we counted 159 red colobus, while in 2003, we saw 145 individuals. For both species, activity patterns in continuous forest were similar to those in a fragment, with the exception that individuals in the fragment rested more. Colobus in the fragment ate more mature leaves than colobus in the continuous forest did. Fragments supported all the fuelwood needs of an average of 32 people who lived immediately adjacent to them, and partially supported families up to 3 farms away (*ca.* 400 m), representing 576 people. Intensive harvesting for fuelwood occurred when neighboring households engaged in beer brewing (an average of 9.6% of the households), gin distilling (8.8%), or charcoal production (14.5%). Overall, between 2000 and 2003, the average density of trees declined by 14 trees/ha (range=0–60 trees/ha). If current rates of clearing continue, the probability that the fragments will continue to support colobus populations is low.

Keywords black-and-white colobus · conservation · forest fragments · population decline · red colobus

Introduction

Habitat loss is one of the most important threats to global biodiversity. Primates are particularly vulnerable because tropical forests are being deforested at an alarming rate. Cumulatively, countries with primate populations are losing *ca.* 125,000 km^2 of forest annually (Chapman and Peres 2001). The modifications to tropical forests result in both reduction in size and fragmentation. Understanding the ecological importance and conservation value of forest fragments is vital for wise management of forested landscapes. Management of small forests is an opportunity to make important conservation gains, particularly for species whose occupancy areas do not encompass a protected area. For the aforementioned reasons, the study of habitat fragmentation is an active field of inquiry in conservation biology (Laurance and Cochrane 2001). Studies include investigations quantifying changes in the physical environment (Kapos *et al.* 1997), experiments ranging from the micro to landscape scale (Debinski and Holt 2001; Laurance *et al.* 2002), metapopulation approaches (Hanski and Gilpin 1997; Lawes *et al.* 2000), and field studies in fragmented habitats (Gilbert 2003; Laurance and Bierregaard 1997). The studies have yielded valuable insights into the importance of fragment size, shape, and isolation in ecological processes and species survival probabilities.

Despite a growing body of research, we nevertheless lack information essential to understanding how primates respond to fragmentation, for 3 reasons. First, much of the previous work on primates living in fragmented habitats has involved fragments protected from human use (Gilbert 2003; Lovejoy *et al.* 1986; Tutin 1999; Tutin *et al.* 1997; *cf.* Struhsaker *et al.* 2004). In reality, most fragments are not protected and are characterized by open access by private citizens who depend on them for fuelwood, medicinals, or bushmeat. Thus, fragments change in structure and composition as landowners use the forest for grazing or to extract timber or fuelwood or allow fallow land to regenerate. Though studies in protected reserves have provided us with many insights, they may have biased our perception of the long-term value of forest fragments to primates.

Second, a number of simple logical predictions by the first researchers studying primates in forest fragments have not proven to be general. For example, researchers frequently cite home range size as influencing the ability of a species to survive in a fragment (Estrada and Coates-Estrada 1996; Lovejoy *et al.* 1986). However, Onderdonk and Chapman (2000) found no relationship between home range size and ability to live in fragments in a community of primates in Western Uganda. Similarly, some authors suggested that a highly frugivorous diet may limit the ability of a species to live in fragments (Estrada and Coates-Estrada 1996; Lovejoy *et al.* 1986). However, Tutin *et al.* (1997) found that several frugivorous species were at higher or similar densities in forest fragments than in the intact forest of Lopé Reserve, Gabon (Onderdonk and Chapman 2000; Tutin 1999). The complexity of primate survival in fragments is illustrated further by the fact that near Kibale National Park in Uganda, red-tailed guenons (*Cercopithecus ascanius*) frequently move between forest fragments via available forest corridors and crossing agricultural areas, whereas blue monkeys (*Cercopithecus mitis*), which have a similar diet and social organization, do not use the fragments or corridors (Chapman and Onderdonk 1998; Onderdonk and Chapman 2000). In contrast, blue monkeys near Budongo Forest Reserve, also in Uganda and <200 km from Kibale, often reside in fragments and travel through agricultural land (Fairgrieve 1995). Factors other than diet would appear to be responsible for this difference in patch occupancy between populations of blue monkeys.

Third, the majority of studies on habitat fragmentation and primates are short-term. Marsh (2003) offers one of the most extensive data collections in her edited volume on primates in forest fragments. Yet only 30% of the studies spanned >1 yr and only 15% reported data collected ≥3 yr. Relying on short-term studies may be ill advised given that it may take years before a population's response to disturbance can be detected. For example, Struhsaker (1976) documented that it was *ca.* 10 yr after the loss of *ca.* 90% of a major food resource that researchers detected a statistically significant decline in vervets (*Cercopithecus aethiops*) at Amboseli, Kenya.

We address some of the gaps in our knowledge by assessing the long-term survival probability of red (*Procolobus pennantii*) and black-and-white colobus (*Colobus guereza*) inhabiting a series of unprotected fragments outside of Kibale National Park, Uganda. We surveyed the populations on 3 occasions over 8 yr. To seek explanations for the population changes documented, we conducted a total inventory of all trees in all fragments at 2 times, contrasted the behavior of groups inhabiting 1 fragment with groups in the continuous forest of Kibale National Park, and judged the importance of these patches to local people by quantifying patterns of forest use.

Methods

Study Site

We censused the primates of 20 forest fragments neighboring Kibale National Park (795 km^2) in western Uganda (0 13′–0 41′ N and 30 19′–30 32′ E), near the foothills of the Rwenzori Mountains, from May through August 1995 (Onderdonk and Chapman 2000). We recensused 19 of the fragments from May through November 2000 and again from May through July 2003. Kibale is a mid-altitude, moist-evergreen forest receiving 1741 mm of rainfall annually (1990–2002) during 2 rainy seasons (Chapman and Lambert 2000; Chapman *et al.* 1997; Struhsaker 1997). Before clearing for agriculture, there was likely continuous forest throughout the region, but most land outside Kibale forest has been deforested and smallholder subsistence agriculture now dominates the landscape.

Human activities have influenced the forests and wildlife of western Uganda for centuries, but they have intensified over the past 50 yr (Howard 1991; Naughton-Treves 1999). Pollen records suggest that forest clearing began in Uganda ≥1000 yr ago with the introduction of agriculture and iron making (Hamilton 1974). Until the 20th century, the forests of western Uganda were sparsely settled by Bakonjo and Baamba gatherer-hunters (Steinhart 1971; Taylor 1962). Forest expanded at the end of the 19th century during periods when human population numbers were depressed by war and epidemics (Osmaston 1959; Paterson 1991). Shortly thereafter, Batoro herders and agriculturalists arrived in the region from the north, displaced the Bakonjo and Baamba, and began a lengthy period of deforestation (Naughton-Treves 1999). By the end of the 20th century, nearly all forest outside officially protected areas had been converted to farms, pastures, or tea plantations (Naughton-Treves 1997). Only small pockets of forest, e.g., 1–28 ha, remain in areas largely unsuitable for agriculture. Thus, the forest fragments that we studied were located in swampy valley bottoms, on steep hillsides, or on slopes of crater lake rims (Table I). Though the precise timing of isolation of the forest remnants is not known, local elders describe them as ancestral forests, and aerial photographs from 1959 confirm that most have been isolated from Kibale since at least that time.

The human population surrounding Kibale has increased 7-fold since 1920, and surpasses 272 individuals/km^2 at Kibale's western edge (vs. 92/km^2 for the District; NEMA, 1997; Naughton-Treves 1998). Population growth rate varies among parishes, but is typically between 3 and 4%; in the parishes with the majority of the fragments it averages 3.87% (NEMA 1997). The majority of residents do not eat or hunt primates, except occasionally to defend their crops. The forest fragments provide multiple resources to local people, including medicinal plants, foodstuffs, fodder, building materials, and most importantly, fuelwood. More than 98% of residents neighboring Kibale rely exclusively on fuelwood, elephant grass, crop residuals, or charcoal for energy: one of the highest levels in the world (Bradley 1991; Government of Uganda 1992). Rapid population growth, expanded commercial charcoal and brick production, industrial fuelwood demands, commercial fuelwood collection, improved regional transport, and technological change are fundamentally altering the relationship between forests and forest users. Further, the demand for forest products has intensified in a context of insecure

Table I Characteristics of forest fragments located outside Kibale National Park, Uganda

Fragment	Area (ha)	Fragment type	Distance to Kibale (km)	Distance to nearest fragment (m)	Household activity		Red-tailed guenon	Red colobus	B&W colobus	Chimpanzees
Rutoma #3 (cleared 2000)	.8	HS	2.2	100			1/0/0	0/0/0	0/0/0	1/0/0
Dry Lake (cleared 2003)	1.2	HS	6.1	153			1/0/0	0/0/0	1/0/0	0/0/0
Rutoma #1	1.2	HS	2.4	80	8	G,W	1/1/1	0/1/1	1/1/1	1/0/0
Kiko #4	1.2	VB	1.1	70	5	W	0/0/1	1/1/1	1/1/1	1/0/0
Durama (cleared 2000)	1.4	HS	1.1	60	4	B,W	1/0/0	0/0/0	0/0/0	0/0/0
Kiko #3	1.7	VB	1.1	70	3	W	1/0/0	1/1/1	1/1/1	0/0/0
Rutoma #4	2.0	HS	2.1	80	8	B,C,L,W	1/0/0	0/0/0	1/0/0	0/0/0
Lake Nyanswiga	2.2	CL	6.0	155	4	C,L,W	1/1/1	0/0/0	1/1/1	1/1/0
Kyaibombo (cleared 2003)	2.3	VB	1.1	162	7	B,G,C,L,W	1/0/0	0/0/0	1/0/0	0/0/0
Ruihamba	2.4	VB	4.1	300	8	B,G,L,W	0/1/0	0/1/0	1/1/1	0/1/0
Nkuruba-Fish Pond	2.8	VB	3.7	70	2	L,W	1/1/1	1/1/0	1/1/1	1/1/0
Lake Nyaherya	4.6	CL	6.1	300	8	C,L,W	1/1/1	0/1/1	1/1/1	0/1/0
Rutoma #2	4.9	HS	3.0	150			1/0/1	0/1/1	1/1/1	1/0/0
Rusenyi	4.9	VB	1.1	50	11	B,G,C,W	1/1/0	0/1/0	1/1/0	0/0/0
Kiko #2	5.0	VB	1.8	125	6	C,W	1/0/1	1/1/1	1/1/1	0/0/0
Kiko #1	6.2	VB	2.0	50	9	L,W	1/0/0	1/1/1	1/1/1	0/0/0
Nkuruba Lake	6.4	CL	3.6	70	2	W	1/1/1	0/1/1	1/1/1	1/1/1
CK's Durama	8.7	VB/HS	.2	150	16	B,G,L,W	1/0/1	1/1/1	1/1/1	1/0/1
Lake Mwamba	28.7	CL	7.2	100			1/?/0	0/0/0	0/0/0	0/0/0

The presence (1) and absence (0) of each species in 1995, 2000, and 2003 are indicated (95/00/03). If a solitary individual was in a fragment, we assumed that the fragment could not support the species. For Fragment Type, HS=hillside, VB=valley bottom, and CL=Crater Lake. For Household activity, B=beer, G=gin, C=charcoal, L=livestock, and W = woodlot.

property rights that perpetuates an open access system, resulting in rapid deforestation.

Surveying Primate Fragment Occupancy and Fragment Characters

In 1995, forest fragments were selected if they had a clearly defined boundary, were isolated from other fragments or tracts of forest by >50 m, and were small enough to count all black-and-white colobus groups. We visited 20 fragments in the first survey and measured the following parameters: primate species present, black-and-white colobus group size and composition, tree species richness, area of the fragment, and distance to the nearest fragment (Onderdonk and Chapman 2000). We visited 1 large fragment in the first survey, but did not consider it further, because a complete count of all groups was not possible. The fragments ranged from .8 ha to 28.7 ha (mean size=4.7 ha).

We counted primate species in a fragment over 1–4 d. For each group of colobus encountered we determined size and composition. In 1995 we were able to count only black-and-white colobus, but in the subsequent surveys we obtained group size and composition for red and black-and-white colobus. To obtain reliable estimates of group size and composition, observers would often stay with a group for up to 12 h and wait for members to make a coordinated movement across an opening in the canopy.

From long-term research at 1 fragment (Lake Nkuruba, Chapman *et al.* 1998), we know that red-tailed guenons and chimpanzees (*Pan troglodytes*) frequently move among fragments, i.e., they use many fragments in a week. In contrast, the colobus displayed much more site fidelity and rarely moved among fragments, usually only to colonize a new fragment. As a result, we focus on the colobines.

At 17 of the 19 fragments we identified and measured diameter-at-breast height (DBH) of all trees >10 cm in 2000 and 2003. When trees were on extremely steep sides of the craters, we visually estimated their size (error in visual estimation±3.8%), which represents a nearly complete inventory of all major potential colobus food sources because colobus rarely feed in small trees (Gillespie and Chapman 2001). In the 2000 survey, we also counted all tree stumps arising from harvesting by local people. For most tree species the stump will remain for several years, thus we used this inventory of tree stumps as an index of recent change. We searched vine tangles and dense herbaceous vegetation for hidden stumps. During the surveys, it was often possible to assess the major cause of deforestation, e.g., charcoal mounds or pitsawing platforms, allowing verification of statements by local agriculturalists.

To understand better the potential impact of human activity on primate survival, we collected detailed data on forest use, as well as general socioeconomic parameters from households immediately adjacent to each fragment. For 16 of the 19 fragments, we determined the number of households that were settled on land directly adjacent to the forest. Residents of households consider forest fragments to be their property, though the government does not recognize the claims; therefore, the number of households and their level of participation in commercial forest use should represent an index of harvesting pressure on the fragment. We also noted the presence of eucalyptus (*Eucalyptus* spp.) woodlots on or near homesteads. Woodlots may take pressure off fragments by providing an alternative source of fuelwood. However, the presence of woodlots may also indicate that fuelwood resources in the fragments are sufficiently depleted that tree planting on farmland is a necessity. Finally, we interviewed the residents of each household to determine if they were using fuelwood from the fragment for commercial activities, especially to brew beer, distill gin, or produce charcoal. We also recorded the presence of goats or cattle or both for each household, because they are often allowed to graze in fragments.

Behavioral Observations

We gathered dietary data during behavioral observations from dawn to dusk on 4 d each month from July 1998 to June 1999 for 2 groups of black-and-white colobus and 2 groups of red colobus in the unlogged forest of Kibale National Park (forestry compartment K30, black-and-white colobus *ca.* 600 h of observation, red colobus 710 h) and from August 1999 to April 2000 for 1 group of each species at the Crater Lake Nkuruba forest fragment (black-and-white colobus *ca.* 330 h of observation, red colobus 320 h; see Table II for group sizes). Lake Nkuruba is a small forest fragment, but the condition of the forest has remained relatively pristine. We established a conservation/education school at the fragment in the early 1990s and the project is funded by tourists who come to the lake. As a result, the forest has not been dramatically degraded in the past 14 yr.

Each group had recognizable individuals, allowing verification of group identity. We made 5 point samples of different individuals during each half-hour. If the individual was feeding, we recorded the species and plant part, e.g., fruit, young leaf, or leaf petiole. We avoided repeatedly sampling conspicuous individuals by moving

Table II Foraging effort (% of foraging scans) devoted to different plant parts by the red and black-and-white colobus groups in unlogged forest (groups 1 and 2) in Kibale National Park, Uganda and a Crater Lake forest fragment outside the park

Food item	Unlogged (1)	Unlogged (2)	Fragment
Black-and-white colobus			
Ripe fruit	.00	2.4	9.5
Unripe fruit	7.4	7.2	2.8
Flower	2.3	.1	6.2
Young leaf	85.2	77.7	64.9
Mature leaf	3.7	5.8	14.1
Leaf petiole	.8	.4	.8
Leaf bud	.6	1.0	.0
Bark	.0	3.8	.7
Other	.0	1.7	1.0
Group size	9	6	6 to 7
Red colobus			
Ripe fruit	6.4	5.0	3.3
Unripe fruit	2.5	1.6	4.1
Flower	.8	3.5	1.8
Young leaf	62.8	75.3	59.2
Mature leaf	13.3	5.6	22.4
Leaf petiole	6.4 7.9	1.7	
Leaf bud	1.3	.3	.5
Bark	6.4	.3	6.3
Other	.1	.5	.7
Group size	48	24	21

throughout the group when selecting subjects and by sampling individuals that were both in clear view as well as those that were more hidden. Often the observer had to wait a number of minutes to determine what a less observable individual was doing.

We calculated interspecific dietary overlap between species or between neighboring groups of the same species via the following formula:

$$D = \sum S_i$$

wherein D=dietary overlap and S_i=percentage of diet shared between 2 species, evaluated on the basis of species-specific plant parts. Holmes and Pitelka (1968) first used the formula, which has become a standard means of expressing dietary overlap for primates (Chapman 1987; Maisels *et al.* 1994; Struhsaker 1975; Struhsaker and Oates 1975).

Results

Colobus Population Change in Forest Fragments

Of the 16 fragments that supported resident primate populations in 1995, 2 had been cleared to the extent that primates were no longer present in 2000 and an additional 2 had been cleared by 2003. Of the 4 fragments cleared by 2003, only 2 had previously supported black-and-white colobus (23 individuals). The total counts for the black-and-white colobus are 165 in 1995, 119 in 2000, and 75 in 2003 (Fig. 1). Between 1995 and 2000, the population decline averaged 9.2 individuals/yr, while between 2000 and 2003 it averaged 14.7 individuals/yr.

During the first census, there were .405 infants per adult female, while in the 2000 recensus there were only .023 infants per female and in 2003 there were .233 infants per female. The populations in 2 fragments increased significantly between 1995 and 2000 (400 and 240%). Both fragments were part of a community-based conservation project we established in 1993 at Crater Lake Nkuruba and are protected to provide an attraction to tourists who camp at the lake. The proceeds from tourist visitation go to the local community, which therefore does not allow tree cutting and helps support a guard to watch the forests. The growth of the 2 populations likely represents the immigration of individuals from a neighboring fragment that was cleared, because the increase in population size is greater than natural reproduction rates could achieve and because the population grew by 15 individuals, which is the number of individuals that were in the fragment that was cleared when last surveyed. By 2003, the population size in one of the fragments had returned to its original 1995 size, while in the second fragment the population size was still 200% larger than its 1995 level. In the 2000 survey, there was no infant or juvenile in either fragment, whereas in 2003 there were 2 infants and no juvenile with the 7 adult females. We do not know what happened to the individuals that disappeared; however, population declines were very gradual (Chapman *et al.* 2005); thus we suspect weaker individuals died. However it is possible that individuals dispersed as solitary individuals.

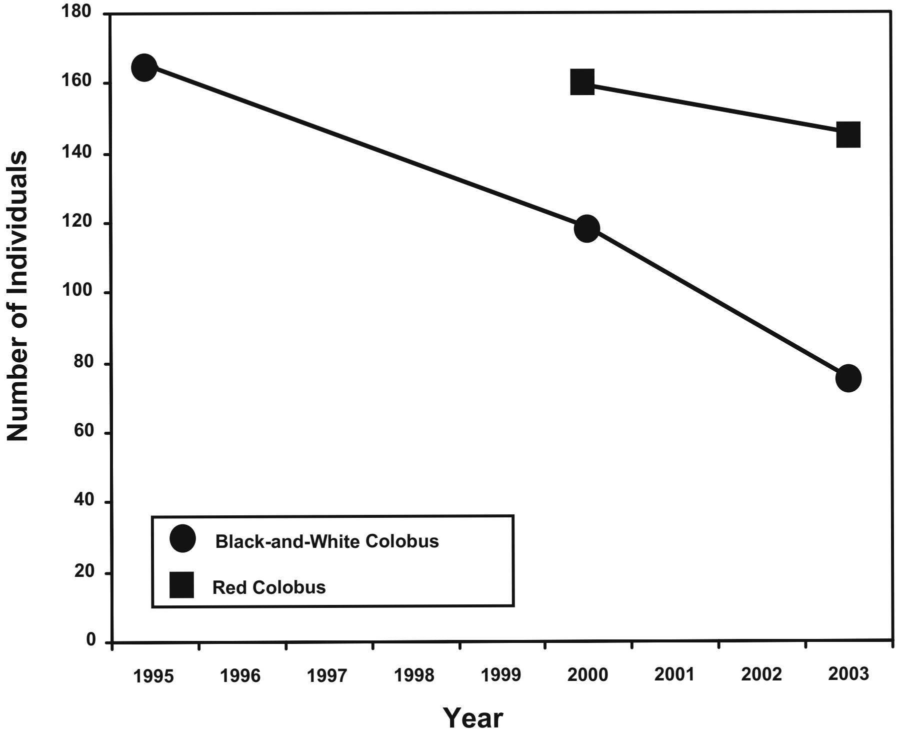

Fig. 1 Number of black-and-white colobus (*Colobus guereza*) and red colobus (*Procolobus pennantii*) counted in forest fragments neighboring Kibale National Park, Uganda during the 1995, 2000, and 2003 censuses.

Seven fragments supported red colobus in 1995, 11 in 2000, and 9 in 2003. None of the original fragments that red colobus occupied were cleared in the 8 yr between censuses. In 2000 we counted 159 red colobus, while in 2003, we saw 145 individuals (Fig. 1). In the 2000 census, we counted 40 adult female red colobus, and the ratio of infants to adult females was .25. In the 2003 census, we counted 70 adult females, and the ratio of infants to adult females was .27.

Interspecific comparison of the population trends is complicated by the fact that 22 black-and-white colobus were in fragments that were cleared, while no red colobus were in cleared fragments. We strongly suspect 15 of the 22 black-and-white colobus immigrated into 1 of the fragments we were monitoring (Crater Lake Nkuruba). In the years after the immigration, the black-and-white colobus in the fragment declined, while the resident red colobus did not. The fate of the 8 black-and-white colobus in other fragment that was cleared is not known. For comparative purposes, a conservative approach, i.e., one that would decrease the difference between species, would be to eliminate the black-and-white colobus from the cleared fragments from the initial assessment of population numbers. This would mean that between 1995 and 2000, the population decline averaged 4.6 individuals/yr (142 in 1995 and 119 in 2000), while between 2000 and 2003 it averaged 14.7 individuals/yr. In contrast, red colobus declined from 159 individuals in 2000 to 145 in 2003, a rate of 4.6 individuals/yr.

We found evidence of forest clearing in all fragments; however, the extent of clearing was extremely variable. The average size of the fragments that supported black-and-white colobus populations in 2000 was 3.7 ha (n=13). In the small fragments we counted on average 186 stumps (SD=155, range 1–405), and the density of stumps averaged 98/ha (SD=121, range=.16–338 /ha). The fragment with the fewest stumps was Crater Lake Nkuruba, the site of the community-based conservation project. The average size of the fragments with red colobus was 4.1 ha (n=11) and the density of stumps averaged 84/ha (SD=101, range=.16–337/ha). There was no difference in the stump density of fragments red colobus occupied and those black-and-white colobus occupied (t=.392, p=.699). Smaller fragments tended to have higher stump density than larger ones ($r_{sp}=-.609$, p=.004), and it was the small fragments with high stump density that did not retain colobus populations over the duration of the study.

Cercopithecus ascanius and *Pan troglodytes* move among forest fragments; thus documenting changes in their population size is much more difficult. However, there were changes in the number of fragments in which the 2 species occurred (Table I).

Diet and Behavioral Patterns in Fragment and Main Forest Groups

For both species, the activity patterns between the 2 groups in the undisturbed forest of Kibale (K30) and the forest fragment were very similar (Fig. 2). However, for both species, individuals in the forest fragment rested more than other groups.

We characterized the diets of the black-and-white colobus based on 3249 foraging records. For all groups, young leaves were the most commonly eaten plant part (Table II). However, the group in the forest fragment fed on mature leaves more often (14.1%) than the groups from within the park (3.7 and 5.8%). Based on 4579 foraging records, young leaves were also the most commonly eaten plant parts for all red colobus groups (Table II). Here again, the group in the forest fragment ate more mature leaves than the groups within Kibale.

The 2 neighboring groups of red colobus in the undisturbed forest in the park (K30; home range overlap was up to 49% and up to 70% of the time was spent in the area of overlap) had diets that overlapped by a monthly average of 37.3%. The dietary overlap between the red colobus and the black-and-white colobus group that had its home range entirely within the home range of the red colobus was 43.2%. In contrast, the dietary overlap of the 2 colobines in the forest fragment was 17.5%.

Environmental Factors and Forest Use by Local Landowners

On average, 6.7 households had access to the resources in any given fragment (range 2–16; average size of the fragments was 4.7 ha). Though there is a correlation between the size of the fragment and the number of households that they support, the strength of the relationship is not strong (r=.54, p=.04). For example, the largest fragment surveyed (8.7 ha) supported the most households (n=16), but the second largest fragment supported only 2 households. Given the fact that the average household in the area contains 4.8 people (NEMA 1997), the fragments are supporting the fuelwood needs of an average of 32 people. Our survey results show that the fragments also support the domestic fuelwood needs of most of the

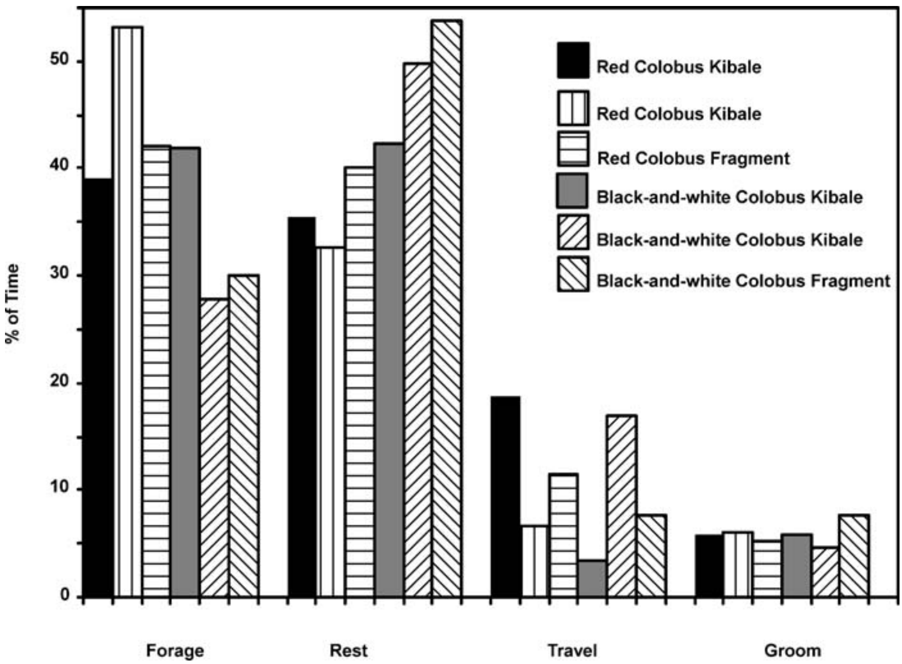

Fig. 2 Activity budgets of 2 groups of black-and-white colobus (*Colobus guereza*) and two groups of red colobus (Proc*olobus pennantii*) in the undisturbed forest of Kibale National Park, Uganda and 1 group of each species the Crater Lake Nkuruba forest fragment.

neighboring families up to 3 farms away (*ca.* 400 m; *ca.* 120 families or *ca.* 576 people, L. Naughton-Treves, *unpub. data*).

The estimate of domestic fuel use by a typical family living around Kibale is 8.4 kg of fuelwood each day for cooking (Wallmo and Jacobson 1998). Thus, in 1 yr a local family uses 3066 kg (the value is slightly lower than average for rural East Africa, Kammen 1995). However, most of the fuelwood gathered for cooking comprises fast-growing pioneer species such as *Acanthus pubescens* and *Vernonia* spp. that are relatively abundant on fallow land (Naughton-Treves and Chapman 2002).

Commercial use of the forest involves extraction of larger volumes of wood than are needed for subsistence use, and greater long-term impacts given the selection of slow-growing hardwood species. Extensive clearing of fragments often occurred when neighboring households were engaged in beer brewing (an average of 9.6% of the households were engaged in beer production: 8.5 kg of wood per episode, on average 19 times a year), gin (8.8%:875 kg per episode, on average 16 times a year), or charcoal production (14.5%: 5936 kg per episode, on average 18 times a year). Charcoal manufacturers had a disproportionately larger impact in that they used high volumes of wood and extracted it from neighbors' lands, many of whom were happy to have their land cleared to expand their fields. On average, 16.2% of the households had cattle or goats.

Half of the households (52.8%) adjacent to the fragments also had woodlots. Fragments where most households did not have woodlots were not necessarily more degraded than fragments with adjacent woodlots, reflecting the complex decisions affecting wood use by harvesters and local investment in woodlots amid growing scarcity.

Changes in Forest Composition

Changes in forest composition between 2000 and 2003 reflected the intensity of extraction: fragments where only small scale domestic extraction occurred changed little, while fragments with large-scale commercial use changed dramatically. Overall, the density of trees declined by 14 trees/ha, but the decline ranged from 0 to 60 trees/ha. Given the variability, there was only a marginally significant decline in stem density in a fragment between 2000 and 2003 (paired t-test t=2.192, p=.056; paired by fragment). Tree species richness in the fragments did not change over the 3 yr (2000 survey 33.3, 2003 survey 29.7, t=1.243, p=.245). However, the proportion of the tree community comprising exotic species increased over time (2000 survey 6 trees/ha, 2003 survey 11.9 trees/ha, t=2.407, p=.039). There was no change in the average size of trees between the 2 surveys (31.9 cm DBH in 2000, 32.6 cm DBH in 2003, t=.271, p=.793).

Discussion

Over the 8 yr of the study, 4 of the original 16 fragments were deforested to the extent that colobus were no longer present. The black-and-white colobus experienced a 55% decline in numbers over 8 yr, or a 47% decline only considering the individuals from fragments that were not cleared, while the red colobus declined by 9% in 3 yr. The annual rate of decline in black-and-white colobus populations has increased over time. While subsistence use of the fragments for fuelwood is an important component of the declines in colobus population size, it is the commercial use of hardwoods for brewing beer, fuelwood, distilling gin, or producing charcoal that has led to the most serious damage to the fragments and was directly responsible for the clearing of the 4 fragments.

The findings suggest the conservation value of small unprotected forest fragments that are communal resources is low. Fragments people use may differ in a number of fundamental ways from protected fragments. For example, the many methods of extraction and the multiple resources harvested from unprotected fragments may obscure any relationship between specific presence or absence and distance to a colonizing source or fragment area. If extraction targets specific types of tree species, or promotes the regeneration of other types of trees, e.g., pioneers with particular nutritional traits (Coley 1983; Ganzhorn 1995) the diet and behavioral patterns of primates in unprotected and protected fragments will differ. It will be difficult to evaluate appropriately the actual conservation value of unprotected fragments, because the rate and nature of the clearing will depend on the social and economic setting in which they exist. Fragments in areas with high human population densities and rapid economic growth, such as western Uganda, are likely most threatened (Harcourt and Parks 2003). As a result, preventing the deforestation of fragments in privately owned land, such as that outside of Kibale, will require steadfast support from governmental agencies and support for more sustainable land management beyond park boundaries. Where funding is limited and the conservation of National Parks and privately owned fragments compete for funds from the same sources, it is prudent not to invest scarce conservation funds in such fragmented areas.

The 2 colobine species responded differently to the environmental changes in the fragments. Black-and-white colobus exhibit considerable dietary flexibility and prosper in many degraded habitats, whereas red colobus do not (Oates 1977, 1996; Onderdonk and Chapman 2000). Yet, black-and-white colobus population size in the fragments has declined by *ca.* 37% over the last 3 yr, when the red colobus declined by only 9%. This is a particularly intriguing difference in light of the fact that the dietary overlap between red colobus and black-and-white colobus groups overlapping in home range is extensive (43.2%; Chapman *et al.* 2002), that the biomass of both species can be predicted by the protein-to-fiber ratio of potential foods (Chapman and Chapman 2002), and that black-and-white colobus benefit from crop raiding, while red colobus do not (Naughton-Treves 1998). Local farmers may sometimes kill black-and-white colobus to stop crop losses, but we do not think this accounts for the general trends because they have declined in 2 fragments where they are protected because they appeal to tourists (Chapman *et al.* 2005). The species also appear to respond differently to selective logging, but the nature of their responses is reversed. The long-term effects (over 28 yr) of both low- and high-intensity selective logging on the density of colobines in Kibale were as follows (Chapman *et al.* 2000): though red colobus populations were recovering in heavily logged areas, their rate of increase was slow (.005 groups/km^2 per yr) and population density in the logged areas was much lower than in the unlogged areas. In contrast, black-and-white colobus appeared to do well in logged habitats, and occurred at higher group densities in the logged areas than in the unlogged area. Struhsaker (1997) suggested that one of the key factors accounting for the higher densities of black-and-white colobus in the logged areas was that their populations do well in swampy habitats, and the habitats were more abundant in the logged areas of Kibale compared to the unlogged areas. The suggestion warrants further consideration; however, black-and-white colobus density was not higher in the fragments in valley bottoms compared to those on hillsides or crater lakes (t=1.335, p=.209). The different responses to logging vs. fragmentation highlight the danger of extrapolating results obtained from protected areas —large or small— to similar circumstances, i.e., tree removal in both cases, outside reserves.

Primate populations that include a large amount of low-quality foods in their diet may spend more time resting, probably to facilitate fermentation (Lawes and Piper 1992). The hypothesis is supported by our study of colobines in fragments and by others (Struhsaker and Oates 1975). Groups of both species in the forest fragments ate more mature leaves and spent consistently more time resting than the groups in the continuous forest did. Because red colobus relied on mature leaves (22.4% of the diet) more than black-and-white colobus (14.1%), one would have expected the difference in resting between the fragment group and the continuous forest groups to have been greater for red colobus. That this was not the case might be attributable to differences in group size between the 2 colobus and that when food resource availability is similar between 2 groups, larger colobine groups travel further than smaller groups (Gillespie and Chapman 2001; *contra* Struhsaker and Leland 1987).

The red colobus group had 18–21 members, whereas the black-and-white colobus groups had 6 or 7 members. They shared the same home range and thus food availability was likely similar.

Our study documented a dramatic decline in the black-and-white colobus population in a system of small forest fragments in 8 yr, and a moderate decline in red colobus over 3 yr. On average, over 8 yr, local residents seeking to expand cultivated areas and sell forest products to urban markets cleared 25% of the fragments. If the rapid level of clearing continues, all remaining fragments will be cleared in 32 yr; however, it appears that the rate of clearing has increased in the last few years, so it is likely that all fragments will be cleared sooner. Reversal of the present trends requires a major conservation effort, on a scale and of a nature that has not been done in the region for any species or habitat to date. To stop fragments from being cleared requires the cooperation of the local people, and hence alternative sources of income are needed, e.g., ecotourism; fuelwood supplies from elsewhere have to be made available, e.g., a large-scale woodlot project; and, a great deal of effort has to be placed on education and outreach. In reality, it is unlikely that a project of such a magnitude will be initiated. Small and unprotected forest fragments face a bleak future. This is the reality of biodiversity conservation outside of protected areas in many areas of Africa. However, possible funding sources exist, so hope remains.

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References

Bradley, P. N. (1991). *Women, woodfuel and woodlots*. London: Macmillan.

Chapman, C. A. (1987). Flexibility in diets of three species of Costa Rican Primates. *Folia Primatologica, 49*, 90–105.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J., & Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: A 28 year comparison from Kibale National Park, Uganda. *Conservation Biology, 14*, 207–217.

Chapman, C. A., & Chapman, L. J. (2002). Foraging challenges of red colobus monkeys: Influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology, 133*, 861–875.

Chapman, L. J., Chapman, C. A., Crisman, T. L., & Nordlie, F. G. (1998). Dissolved oxygen and thermal regimes of a Ugandan crater lake. *Hydrobiology, 385*, 201–221.

Chapman, C. A., Chapman, L. J., & Gillespie, T. R. (2002). Scale issues in the study of primate foraging: Red colobus of Kibale National Park. *American Journal of Physical Anthropology, 117*, 349–363.

Chapman, C. A., Chapman, L. J., Wrangham, R., Isabirye-Basuta, G., & Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology, 35*, 287–302.

Chapman, C. A., Gillespie, T. R., & Speirs, M. L. (2005). Dynamics of gastrointestinal parasites in two colobus monkeys following a dramatic increase in host density: Contrasting density-depended effects. *American Journal of Primatology*, *67*, 259–266.

Chapman, C. A., & Lambert, J. E. (2000). Habitat alterations and the conservation of African primates: A case study of Kibale National Park, Uganda. *American Journal of Primatology, 50*, 169–186.

Chapman, C. A., & Onderdonk, D. A. (1998). Forests without primates: Primate/plant codependency. *American Journal of Primatology, 45*, 127–141.

Chapman, C. A., & Peres, C. (2001). Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology, 10*, 16–33.

Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs, 53*, 209–233.
Debinski, D. M., & Holt, R. D. (2001). A survey and overview of habitat fragmentation experiments. *Conservation Biology, 14*, 342–355.
Estrada, A., & Coates-Estrada, R. (1996). Tropical rainforest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology, 17*, 759–783.
Fairgrieve, C. (1995). *The Comparative Ecology of Blue Monkeys* (Cercopithecus mitis stuhlmanni) *in logged and unlogged forest, Budongo Forest Reserve, Uganda: The effects of logging on habitat and population density*. Ph.D. dissertation, University of Edinburgh, Scotland.
Ganzhorn, J. U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology, 76*, 2048–2096.
Gilbert, K. A. (2003). Primates and fragmentation of the Amazon forest. In L. K. Marsh (ed.), *Primates in fragments: Ecology and conservation* (pp. 145–157). New York: Kluwer Academic/Plenum.
Gillespie, T. R., & Chapman, C. A. (2001). Determinants of group size in the red colobus monkey (*Procolobus badius*): An evaluation of the generality of the ecological constraints model. *Behavioral Ecology and Sociobiology, 50*, 329–338.
Government of Uganda (1992). *1991 National housing and rural settlement census*. Kampala, Uganda.
Hamilton, A. C. (1974). Distribution patterns of forest trees in Uganda and their historical significance. *Vegetatio, 29*, 218–228.
Hanski, I., & Gilpin, M. E. (1997). *Metapopulation Biology: Ecology, Genetics, and Evolution*. San Diego: Academic Press.
Harcourt, A. H., & Parks, S. A. (2003). Threatened primates experience high human densities: Adding an index of threat to the IUCN Red List criteria. *Biological Conservation, 109*, 137–149.
Holmes, R. T., & Pitelka, F. A. (1968). Food overlap among coexisting sandpipers on northern Alaskan tundra. *Systematic Zoology, 17*, 305–318.
Howard, P. C. (1991). *Nature conservation in uganda's tropical forest reserves*. Gland, Switzerland: IUCN.
Kammen, D. (1995). Cookstoves for the developing world. *Scientific American, 273*, 64–67.
Kapos, V., Wandelli, E., Camargo, J., & Ganade, G. (1997). Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In W. F. Laurance & R. O. Bierregaard (eds.), *Tropical forest remnants: Ecology, management and conservation of fragmented communities* (pp. 33–44). Chicago: University of Chicago Press.
Laurance, W. F., & Bierregaard, R. O. (1997). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities.* Chicago: University of Chicago Press.
Laurance, W. F., & Cochrane, M. A. (2001). Synergistic effects in fragmented landscapes. *Conservation Biology, 15*, 1488–1489.
Laurance, W. F., Lovejoy, T. E., Casconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., *et al.* (2002). Ecosystem decay of Amazonian forest fragments: A 22 year investigation. *Conservation Biology, 16*, 605–618.
Lawes, M. J., Mealin, P. E., & Piper, S. E. (2000). Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. *Conservation Biology, 14*, 1088–1098.
Lawes, M. J., & Piper, S. E. (1992). Activity patterns in free-ranging samango monkeys (*Cercopithecus mitis erythrarchus* Peters, 1852) at the southern range limit. *Folia Primatologica, 59*, 186–202.
Lovejoy, T. E., Bierregaard, R. O., Jr., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. J., *et al.* (1986). Edge and other effects of isolation on Amazon forest fragments. In M.E. Soule (ed.), *Conservation biology: The science of scarcity and diversity* (pp. 257–285). Sunderland, MA: Sinauer Associates.
Maisels, F., Gautier-Hion, A., & Gautier, J.-P. (1994). Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. *International Journal of Primatology, 15*, 681–701.
Marsh, L. K. (2003). *Primates in fragments: Ecology in conservation*. New York: Kluwer Academic/ Plenum Press.
Naughton-Treves, L. (1997). Farming the forest edge: Vulnerable places and people around Kibale National Park, Uganda. *Geographical Review, 87*, 27–46.
Naughton-Treves, L. (1998). Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology, 12*, 156–168.
Naughton-Treves, L. (1999). Whose animals? A history of property rights to wildlife in Toro, western Uganda. *Land Degradation and Development, 10*, 311–328.
Naughton-Treves, L., & Chapman, C. A. (2002). Fuelwood resources and forest regeneration on fallow land in Uganda. *Journal of Sustainable Forestry, 14*, 19–32.

NEMA National Environment Management Authority (1997). *Kabarole District Environment Profile*. Kampala, Uganda: NEMA.

Oates, J. F. (1977). The guereza and its food. In T. H. Clutton-Brock (ed.), *Primate Ecology* (pp. 275–321). New York: Academic Press.

Oates, J. F. (1996). Habitat alteration, hunting, and the conservation of folivorous primates in African forests. *Australian Journal of Ecology, 21*, 1–9.

Onderdonk, D. A., & Chapman, C. A. (2000). Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology, 21*, 587–611.

Osmaston, H. A. (1959). *Working Plan for the Kibale and Itwara Forests* (pp. 60). Entebbe: Uganda Forest Department.

Paterson, J. D. (1991). The ecology and history of Uganda's Budongo Forest. *Forest and Conservation History, 35*, 179–187.

Steinhart, E. I. (1971). *Transition in western Uganda: 1891–1901.* Ph.D. Dissertation. History. Northwestern University, Chicago.

Struhsaker, T. T. (1975). *The red Colobus monkey* (pp. 311). Chicago: University of Chicago Press.

Struhsaker, T. T. (1976). A further decline in numbers of Amboseli vervet monkeys. *Biotropica, 8*, 211–214.

Struhsaker, T. T. (1997). *Ecology of an African rain forest: Logging in kibale and the conflict between conservation and exploitation* (pp. 434). Gainesville: University of Florida Press.

Struhsaker, T. T., & Leland, L. (1987). Colobines: infanticide by adult males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (eds.), *Primate societies* (pp. 83–97). Chicago: University of Chicago Press.

Struhsaker, T. T., Marshal, A. R., Ketwiler, K., Siex, K., Ehardt, C., Lisbjerg, D. D., *et al.* (2004). Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology, 25*, 615–658.

Struhsaker, T. T., & Oates, J. F. (1975). Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In R. H. Tuttle (ed.), *Socioecology and psychology of primates* (pp. 103–124). The Hague: Mouton.

Taylor, B. K. (1962). *The Western Lacustrine Bantu*. London: Sidney Press.

Tutin, C. E. G. (1999). Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates, 40*, 249–265.

Tutin, C. E. G., White, L. J. T., & Mackanga-Missandzou, A. (1997). The use of rainforest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology, 11*, 1190–1203.

Wallmo, K., & Jacobson, S. K. (1998). A social and environmental evaluation of fuel-efficient cook-stoves and conservation in Uganda. *Environmental Conservation, 25*, 99–108.