

Jeremiah S. Lwanga

## Spatial distribution of primates in a mosaic of colonizing and old growth forest at Ngogo, Kibale National Park, Uganda

Received: 10 March 2005 / Accepted: 11 November 2005 / Published online: 15 February 2006  
© Japan Monkey Centre and Springer-Verlag 2006

**Abstract** Primate censuses were conducted in a mosaic of colonizing (two locations) and old-growth forests using line transect methods at the Ngogo study site, Kibale National Park, Uganda. Black and white colobus monkeys (*Colobus guereza*) were encountered more frequently in the colonizing forests than in the old growth forest, while chimpanzees (*Pan troglodytes*) were encountered more frequently in the old growth forest than in colonizing forests. Although not significant, results suggest that blue monkeys (*Cercopithecus mitis*) frequented colonizing forests more often than old growth forest. The encounter rates of mangabey (*Lophocebus albigena*), and redtail (*Cercopithecus ascanius*) groups were ambiguous with their density being higher in some colonizing forests but not others as compared to old-growth forest. No significant differences were detected for baboons (*Papio anubis*), L'hoest's (*Cercopithecus lhoesti*), and red colobus monkeys (*Piliocolobus tephroscales*). The conversion of forests to farmland is one of the major problems encountered in primate conservation. This study shows that secondary forests replacing anthropogenic grasslands have the potential of supporting some primate species such as black and white colobus, redtail monkeys, and possibly blue monkeys. Therefore, such areas should not be given up but should be conserved for the benefit of primates that can survive in secondary forests; as the forests mature further, primate species that are adapted to old growth forest will colonize the area provided there is a nearby source.

**Keywords** Censuses · Conservation · Primates · Tropical forest

### Introduction

Primates are an important part of tropical rain forest ecology. Many of them feed on fruit and serve as seed dispersing agents for a wide range of forest tree species (e.g. Chapman 1989, 1995; Dew and Wright 1998). They constitute a significant part of the diet of some forest predatory species such as the crowned eagle *Stephanoaetus coronatus* (Skorupa 1989; Struhsaker and Leakey 1990; Hart et al. 1996; Mitani et al. 2001). Furthermore, primates are among the most important tourist attractions in African tropical rain forests (Weber 1993). Therefore, the conservation of primates and their habitats is of ecological and economic importance. Of great significance to their conservation is the constant monitoring of their populations and habitat. In Kibale National Park, Uganda, primates populations have been monitored at two sites since the early 1970s (Skorupa 1988; Struhsaker 1997; Chapman et al. 2000; Mitani et al. 2000). Nonetheless, these studies either focused on primate populations in old-growth forests or the impact of logging on primate populations. No attempt has been made to compare populations in forests regenerating from anthropogenic grasslands, though this habitat type is common in the park and may favor some primate species. For example, Chapman et al. (2002) found that the abundance of colobine monkeys is influenced by the ratio of protein to fiber in the mature leaves of trees in a given locality. Forest structure and composition can vary over short distances and such variations may influence primate abundance. Furthermore, it appears that not all primate species in old-growth forests that are not subjected to hunting will attain stable populations. Studies from Kibale strongly suggest that blue monkeys (*Cercopithecus mitis*) at Ngogo and Kanyawara (Chapman et al. 2000; Mitani et al. 2000) and red colobus (*Piliocolobus tephroscales*) at Ngogo

J. S. Lwanga  
P.O. Box 409, Fort Portal, Uganda

Present address: J. S. Lwanga (✉)  
Department of Anthropology, Yale University,  
New Haven, CT 06520-8108, USA  
E-mail: jeremiah.lwanga@yale.edu  
Tel.: +1-256-077-466228

(Mitani et al. 2000) in the old-growth forests may be declining. Because the causes of these declines are natural and possibly nothing can be done to reverse the trends, it is imperative to assess alternative habitats such as colonizing forests for suitability for primate conservation.

The Ngogo study area with a mix of old-growth forest and colonizing forests offers an opportunity to investigate primate usage of these different habitats. The colonizing forests sampled were grasslands as of 1955 (Uganda Government 1965). It should be emphasized that these are forests that naturally colonized anthropogenic grasslands; Ngogo has never been affected by mechanized logging. A little pit sawing has occurred in recent times, but its impact is negligible. In this paper, I test the hypothesis that the relative density (encounter rate) of some primate species differs between old growth and colonizing forest.

## Materials and methods

### Study sites and subjects

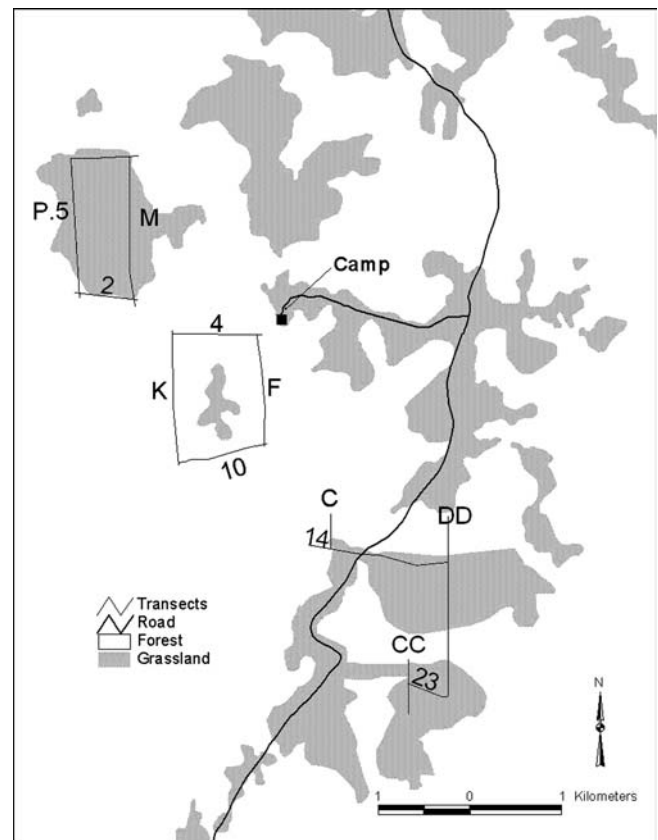
I conducted primate censuses at the Ngogo study area, Kibale National Park, Uganda. Vegetation in the study area consists of old growth, moist, evergreen tropical forests interspersed with grassland, scrub and colonizing forest. The latter three habitat types occur on hills and represent areas that were cultivated by people until the early twentieth century (Wing and Buss 1970). The study site has been described in detail by Ghiglieri (1984), Butynski (1990) and Struhsaker (1997). The study included all of the eight diurnal primate species that inhabit the Ngogo area: two colobine species, black and white colobus (*Colobus guereza*), and red colobus; five cercopithecines, baboon (*Papio anubis*), blue monkeys, mangabeys (*Lophocebus albigena*), redtail monkeys (*Cercopithecus ascanius*), L'Hoest's monkeys (*Cercopithecus lhoesti*) and one pongid (*Pan troglodytes*).

### Data collection

I conducted censuses along three transects between July 2002 and December 2003 inclusive. One transect was located in the old growth forest and the rest were established in two colonizing forests. The old growth transect has been used for primate censuses since 1975 (Mitani et al. 2000). Transects in the colonizing forests were established in 2002. Censuses began in the second half of July 2002 and I completed one census on each transect during that month. For the rest of the study period, I conducted two censuses, one during each half of the month along each transect, yielding a sample size of 35 for each transect (two censuses/month $\times$ 17.5 months). Censuses on a given transect were separated by at least 7 days and those on different transects were conducted on consecutive days unless interrupted by rain.

I used line transect methods (National Research Council 1981; Whitesides et al. 1988) to collect census data. The location of transects are presented in Fig. 1. Transects differed in length: 3.9 km in colonizing forest 1 (Southern transect), 3.75 km in colonizing forest 2 (Northern transect), and 4.4 km in the old-growth forest (Central transect). I conducted censuses between 0730 and 1330 hours. During each census, I walked slowly, at about 1 km/h, stopping regularly at intervals of 10–20 m to scan the forest and listen for movements and calls in the canopy. On sighting primates, I stopped for about 10 min to record the following data: primate species, time, location, distance to the first animal sighted, sighting angle, and number of visible individuals. Additionally, I recorded the activity of the first individual sighted, its height from the ground, tree species occupied, method of detection, and presence of individuals of other primate species. Censuses were suspended during rain, and were terminated altogether and repeated the next day, if the rain lasted more than 30 min.

Measuring sighting distance proved very difficult, especially in the colonizing forests where the ground vegetation was very thick in many places. Therefore,



**Fig. 1** Map of the Ngogo Study Area showing vegetation as of 1955 and census routes used in this study. Census routes are represented with straight lines labeled with numbers or letters; areas covered by the Northern and Southern routes have now reverted to colonizing forest

sighting distances were estimated. The accuracy of primate density estimates is dependent on the accuracy of sighting distances. However, it is difficult to rule out the possibility that differences in vegetation types and terrain biased distance estimates. Therefore, I used number of groups sighted per kilometer of transect to estimate primate abundance. This measure is referred to as relative density and is commonly used to estimate animal abundance in other vertebrate studies (Caughley 1980). In primate studies, it was used by Mitani et al. (2000) and was referred to as abundance. However, colonizing and old growth forests were adjacent to each other (Fig. 1) and it is most likely that primate groups used both habitats. Therefore, the rates of encounter in this study may actually reflect usage rather than abundance of a particular species in a given habitat type.

Estimates of chimpanzee density are often obtained through nest counts (Ghiglieri 1984; Plumptre et al. 2003). Here, I used direct counts of animals sighted; and as Mitani et al. (2000) did, I included counts of both solitary animals as well as groups of chimpanzees in the analyses. This is because chimpanzees are usually dispersed in the canopy and on the forest floor, making it difficult to ascertain if single chimpanzees are in association with other chimpanzees (Mitani et al. 2000). Because all transects were in the territory of the Ngogo chimpanzee community (D. Watts and J. Mitani, unpublished data; personal observation), counts reported here clearly represent frequency of use rather than abundance of chimpanzees in the different areas.

#### Data analyses

For the purpose of the following analyses, each time a census was conducted, the estimate obtained was considered independent. I calculated the precision of mean number of species-specific groups for each of the three transects. Precision was computed as 95% confidence limits of the estimated means expressed as the percentage of those means (National Research Council 1981). Precision is defined as a measure of repeatability of a sample estimate when sample counts are used to estimate populations (Norton-Griffiths 1978). To ascertain if differences in habitat types did not bias sighting distance estimates, I compared the average sighting distances to examine differences among the three forests using the Kruskal-Wallis's test (Siegel and Castellan 1988). To examine differences in the shapes of distribution of sighting distances between any pair of forests, I used the two-sample Kolmogorov-Smirnov's test (Siegel and Castellan 1988). I examined differences in occurrence of each species among the three forests using the Kruskal-Wallis's test; where significant differences were detected, I used a post hoc procedure (Siegel and Castellan 1988) to ascertain which two means were different. The criterion for significance was set at  $P \leq 0.05$ .

## Results

Differences in primate encounter rates among the three areas

Sighting distance, a major factor in the determination of primate density, differed among the three areas (Kruskal-Wallis's test,  $\chi^2 = 17.3$ ,  $df = 2$ ,  $P < 0.0001$ ). Significant differences were between both colonizing forests and the old-growth forest. Sighting distance did not differ between the two colonizing forests. On average, I sighted primates further away in the old-growth forest than in the colonizing forests. Mean sighting distance was 40.8 m,  $n = 161$  in the old-growth forest, while it was 32.1 m,  $n = 171$  in colonizing forest 1, and 35.8 m,  $n = 107$  in colonizing forest 2. The distributions of sighting distances in the areas are depicted in Fig. 2. These too diverged significantly between the old growth forest and colonizing forest 1 (Kolmogorov-Smirnov's test,  $Z = 2.13$ ,  $P < 0.0001$ ). The divergences in the distribution of sighting distances between the two colonizing forests and between colonizing forest 2 and the old-growth forest were not significant.

Figure 3 shows the precision of group counts for each species as a function of the cumulative number of censuses completed in the three forests. Apart from baboons and chimpanzees in colonizing forest 1, baboons and blue monkeys in colonizing forest 2, and baboons and black and white monkeys, and blue monkeys in the old-growth forest, precision estimates for the remainder of the species were nearly asymptotic after approximately 25 censuses, suggesting that the number of censuses conducted were enough to detect differences among the three forests.

Table 1 shows differences in the number of primate species groups sighted per km along the three transects. The encounter rates of four primate species, namely, black and white colobus, chimpanzee, mangabey, and redtails, differed significantly among the three areas. Post hoc tests revealed that black and white colobus were encountered at a significantly lower rate in the old-growth forest than in either of the two colonizing forests. This species was encountered at about the same rate in the two colonizing forests. On average, chimpanzees were encountered about ten and seven times more frequently in the old-growth forest than in colonizing forest 1 and 2, respectively, and these differences were highly significant. The encounter rates of chimpanzees did not differ significantly between the two colonizing forests. The encounter rate of mangabeys in colonizing forest 2 was significantly lower than in the other two forests. This was about three times lower than in colonizing forest 1 and the old-growth forest. Redtail groups were encountered at a significantly higher rate in colonizing forest 1 than in colonizing forest 2 and the old-growth forest. The difference between colonizing forest 2 and the old-growth forest was not significant. It should however be emphasized that group size could differ and

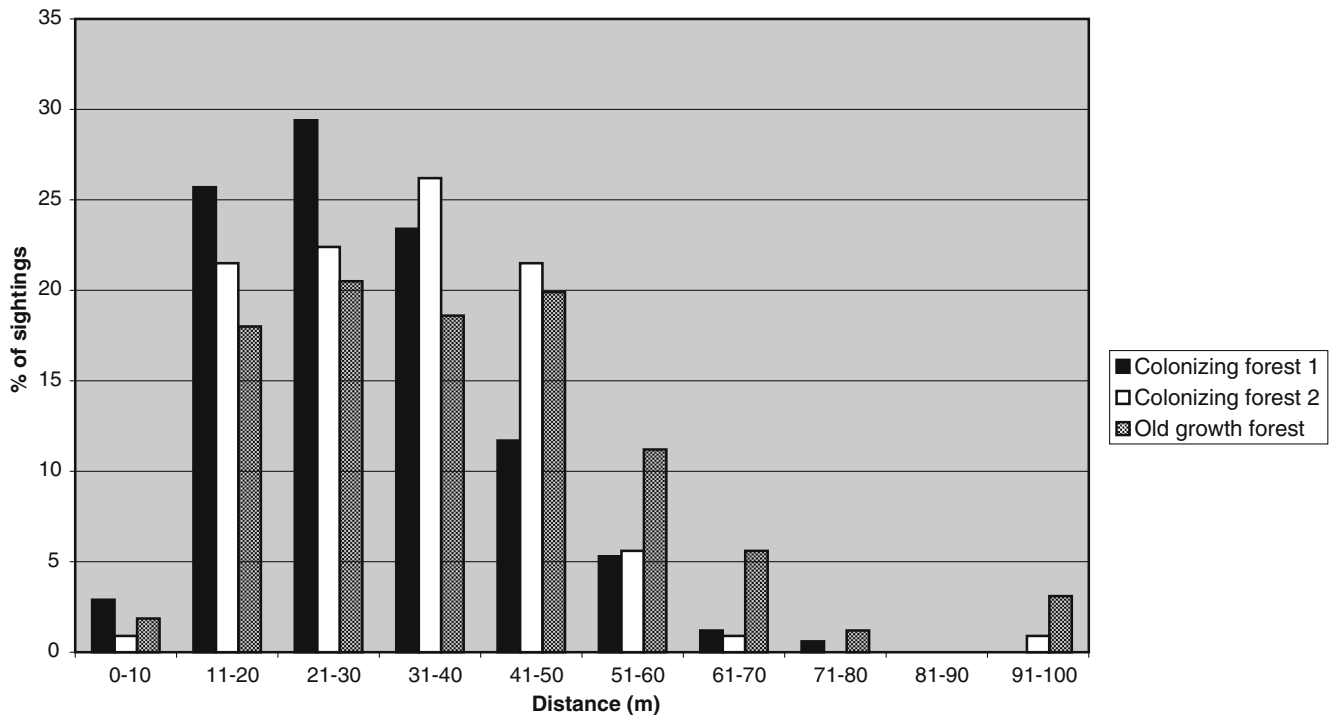


Fig. 2 Frequency distributions of sighting distances of primate groups in colonizing forests 1, 2, and old-growth forest

thus individual density might not follow the same trends as group density.

Apart from redtails, solitary individuals of the other primate species were encountered infrequently or not at all (Table 2). Statistical analysis on sightings of solitary individuals was performed on redtails only. The number of solitary individuals encountered per km of census differed significantly among the three areas (Kruskal-Wallis's test,  $\chi^2 = 8.49$ ,  $df = 2$ ,  $P < 0.05$ ). Colonizing forest 2 supported more solitary redtails than the old-growth forest and colonizing forest 1. Although results suggest that there are more solitary redtails in colonizing forest 1 than in the old-growth forest (Table 2) this difference was not significant.

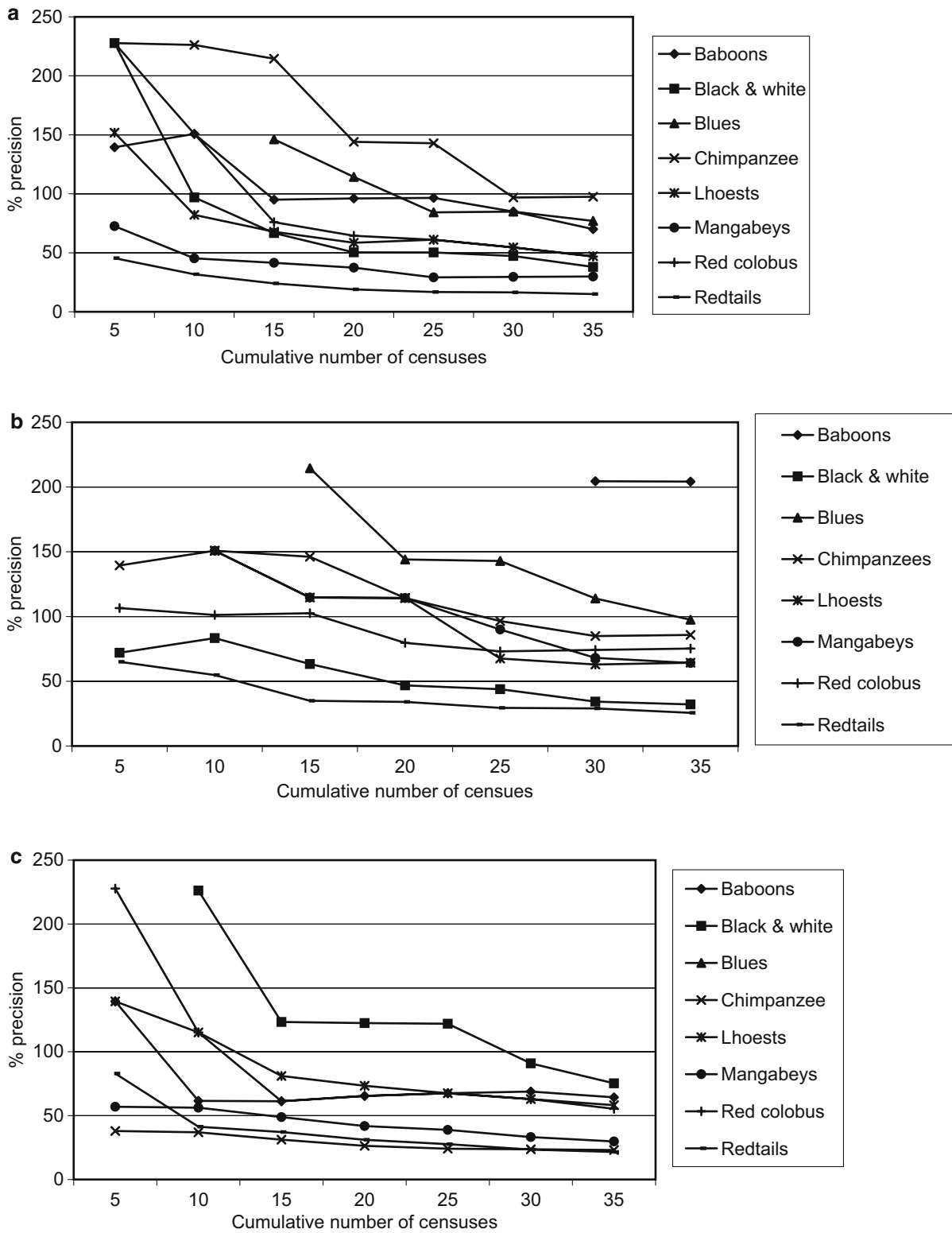
All male groups of two and three redtails were encountered in colonizing forests 1 and 2, respectively. The monkeys were within 10 m of one another and did not fight.

## Discussion

Primate density estimates require that sighting distances are measured accurately. However, this requirement is difficult to achieve in rainforest environments. In areas with thick undergrowth, this would require cutting access trails which is not only time consuming but also environmentally inappropriate. Furthermore, going off the transect line introduces other biases, such as seeing undetected groups from the transect (Brugiere and Fleury 2000). As a result,

several studies that have attempted to estimate primate densities in tropical rainforest (e.g., Skorupa 1986; Struhsaker 1997; Brugiere and Fleury 2000; Chapman et al. 2000) have relied on estimated distances. Inter-observer differences in ability to estimate distances can seriously affect density estimates (Mitani et al. 2000). Even with a single trained observer, as was the case in this study, uneven topography (Brugiere and Fleury 2000) and differences in vegetation can introduce biases in distance estimates. Distribution of sighting distances differed among transects (Fig. 2), suggesting that sighting distances were probably biased by topographic and vegetation attributes. For this reason, I did not attempt to estimate densities, but relied on encounter rates as a proxy. Furthermore, juxtaposition of colonizing and old growth forests makes it possible that primate groups used both habitats in which case these encounter rates represent usage rather than density.

Figure 3 suggests that some primate species were sampled adequately (% precision was asymptotic) while others were not. These differences are apparently due to variation in group density among species. Species with high group density and relatively small home ranges, such as redtails, should have lower variance in sightings, hence an asymptote is reached with relatively few censuses. Therefore, adequate sampling is determined by species group density, home range size and possibly mobility, and hence, in a short-term study like this one, some species will be sampled adequately while others are not.



**Fig. 3 a-c** Precision of estimated mean number of primate groups as a function of the cumulative number of completed censuses in colonizing forests 1, 2, and old-growth forest, respectively

Results in Table 1 suggest that primate abundance can vary even in forests that are not disturbed by mechanized logging. Most likely, this is related to

differences in habitat preferences by the different primate species, a suggestion that has strong implications for primate conservation. Black and white colobus were

**Table 1** Differences in mean number of primate groups per kilometer of census among the three sample areas

Species	Colonizing forest 1	Colonizing forest 2	Old-growth forest	K-W statistic	<i>P</i>
Baboon	0.05 <sup>a</sup> ± 0.10 (7)	0.02 <sup>a</sup> ± 0.09 (2)	0.05 <sup>a</sup> ± 0.10 (8)	5.730	= 0.057
Black and white colobus	0.22 <sup>b</sup> ± 0.24 (30)	0.23 <sup>b</sup> ± 0.27 (38)	0.06 <sup>a</sup> ± 0.13 (9)	21.178	< 0.001
Blue monkey	0.04 <sup>a</sup> ± 0.10 (6)	0.03 <sup>a</sup> ± 0.09 (4)	0.00 <sup>a</sup> ± 0.00 (0)	5.850	= 0.054
Chimpanzee	0.03 <sup>a</sup> ± 0.08 (4)	0.04 <sup>a</sup> ± 0.09 (5)	0.29 <sup>b</sup> ± 0.20 (45)	45.604	< 0.001
L'hoest's monkey	0.13 <sup>a</sup> ± 0.18 (18)	0.06 <sup>a</sup> ± 0.11 (8)	0.07 <sup>a</sup> ± 0.12 (11)	3.150	= 0.207
Mangabey	0.26 <sup>b</sup> ± 0.23 (36)	0.09 <sup>a</sup> ± 0.17 (13)	0.28 <sup>b</sup> ± 0.24 (43)	12.6	= 0.002
Red colobus	0.12 <sup>a</sup> ± 0.17 (17)	0.07 <sup>a</sup> ± 0.15 (9)	0.06 <sup>a</sup> ± 0.10 (10)	3.730	= 0.155
Redtail monkey	0.86 <sup>b</sup> ± 0.37 (117)	0.41 <sup>a</sup> ± 0.31 (54)	0.60 <sup>a</sup> ± 0.37 (84)	20.126	< 0.001

Means, standard error, K-W statistics, and *P*-values are shown. Figures in *square brackets* indicate total number of groups encountered along each transect. Overall significance is based on Kruskal-Wallis one-way ANOVA, degrees of freedom = 2 and *n* = 35 for each transect. Different *superscripts* indicate mean values (*a* < *b* < *c*) that were shown by the multiple comparison tests to be different (*P* < 0.05) for a given species among the three areas

**Table 2** Mean ± SE number of solitary individuals encountered per kilometer of census in the three sample areas

Species	Colonizing forest 1	Colonizing forest 2	Old-growth forest
Baboon	0	0	0
Black and white colobus	0.022 ± 0.073	0.008 ± 0.045	0.006 ± 0.038
Blue monkey	0.007 ± 0.043	0.046 ± 0.102	0.023 ± 0.092
L'hoest's monkey	0	0.023 ± 0.075	0.006 ± 0.038
Mangabey	0.044 ± 0.098	0.008 ± 0.045	0.013 ± 0.053
Red colobus	0.007 ± 0.043	0.008 ± 0.045	0
Redtail monkey	0.140 ± 0.236	0.266 ± 0.282	0.084 ± 0.136

encountered more often in colonizing forests than in the old growth forest. This is consistent with findings from Kanyawara, where Skorupa (1986) and Chapman et al. (2000) reported higher densities of black and white colobus monkey groups in the heavily logged forest than in the unlogged forest. This was believed to be a positive response of black and white colobus to logging (Skorupa 1986). However, without information on their group density before the logging, it is difficult to conclude with certainty that logging actually benefits these monkeys. Evaluating the effects of logging on primate populations by comparing populations in logged versus unlogged forests is complicated by a number of factors, one of which is distinguishing natural pre-logging differences from those induced by logging (Struhsaker 1997). For example, (Struhsaker 1997) suggests that the high abundance of black and white colobus groups in the heavily logged forest at Kanyawara was probably influenced by prevalence of swamps in that area, which had nothing to do with logging intensity. Another factor that can influence the abundance a primate species is the density food tree species. The importance values of some trees exploited by black and white colobus for food were very high in the heavily logged forest (K15) at Kanyawara (Kasenene 1987). At Ngogo, the densities of trees such as *Celtis durandii*, *C. africana*, *Olea capensis welwitschii*, *Balanites wilsoniana*, and *Premna angolensis* that are important food sources for the black and white colobus (Oates 1974) are higher in the colonizing forests than the old growth forest (J.S. Lwanga, unpublished data). Black and white colobus at Ngogo seem to be

attracted to colonizing forests by the high abundance of food tree species.

The rate of encounter of blue monkeys did not differ significantly among transects. However, the fact that no groups were sighted in the old-growth forest while some were encountered in both colonizing forests suggests that the latter may be more suitable habitat for them. Blue monkeys generally occur at low density at Ngogo (Butynski 1990; Mitani et al. 2000), hence more censuses may be necessary to detect significant differences among sites. Long-term (28 years) data from Kanyawara (Chapman et al. 2000) detected a significant decline in the density of blue monkey groups in the unlogged forest. Similarly, long-term data (23.5 years) from the old-growth forest of Ngogo (Mitani et al. 2000) also reported a decline in the density of blue monkey groups. It should be emphasized that these changes are natural because primates in Kibale are not hunted. These findings do suggest that blue monkeys may not be well adapted to surviving in old-growth forests and may drop out of the system as the forest matures further.

Based on a single group of blue monkeys that grew rapidly and split in the early 1980s, Butynski (1990) hypothesized that the species was recovering from a historical event such as a disease epidemic that crashed their population at the Ngogo site. However, current observations do not support this hypothesis. Blue monkeys range widely, from southern Sudan to the Eastern Cape Province of South Africa, and appear to be well adapted to cope well with forest fragmentation (Lawes 2002), although factors that determine occupancy of fragments are complex and not fully understood (Chapman and Peres 2001). As suggested by Struhsaker (1978), blue monkeys are a generalist species that do not compete well with old-growth specialists. Their decline in old-growth forests suggests that they are being excluded competitively (J.S. Lwanga, unpublished data; Mitani et al. 2000).

Chimpanzees were encountered more frequently in the old-growth forest than in the colonizing forests, though all transects were within the home range of the Ngogo community (D. Watts and J. Mitani, unpublished data). This observation strongly suggests that chimpanzees prefer the old-growth forest to colonizing

ones. Apart from *C durandii*, *Teclea nobilis* and *Warburgia ugandensis* (J.S. Lwanga, unpublished data), the rest of the top 20 food tree species in the diet of the Ngogo chimpanzees (Mitani et al. 2002) were either absent or at lower densities in the colonizing forests than in the old-growth forest. Home range use by the chimpanzees is apparently governed by the availability of food resources. Therefore, meaningful conservation of wild chimpanzees should emphasize the maintenance of sizable expanses of old-growth forest.

Redtail monkeys were by far the commonest primate species in all study sites (Table 1). The differences in encounter rates of this species among the study sites are difficult to explain. One would expect the encounter rates of these monkeys in the colonizing forests to be similar, but this was not the case. Redtails were encountered at a significantly higher rate in colonizing forest 1 than in the other two sites. The difference between colonizing forest 2 and the old-growth forest was not significant. Although the two colonizing forests surveyed in this study were considered similar, some minor habitat differences may influence their usage by redtails. Results presented here suggest that some colonizing forests may be more suitable for redtails than the old-growth forest. Further indirect evidence in support of the view that colonizing forests may be more suitable habitats for redtails comes from a redtail group that split twice after becoming too large (> 50 monkeys) between 1980 and 1998 at Ngogo (Struhsaker and Leland 1988; T.L. Windfelder and J.S. Lwanga, unpublished data). Part of the home range of this group was colonizing forest in which the monkeys spent a considerable amount of their feeding time (T.L. Windfelder and J.S. Lwanga, unpublished data). Naturally, colonizing forests contain large numbers of trees and shrubs that start fruiting at an early age, and fruit massively for the most part of the year (Whitmore 1998). Although these small fruits may not be the best food types for redtail monkeys, they provide a constant food supply even at times when fruit availability in the old-growth forest is low. As such, populations of small-bodied frugivorous monkeys, such as redtails can comfortably be sustained in colonizing forests. Second, arthropods constitute about 22% of redtail diet (Struhsaker 1978). At Kanyawara, Nummelin (1989) found a positive correlation between ground vegetation cover and arthropod abundance. Colonizing forests are characterized by thick ground vegetation cover, which suggests that there were more arthropods in the colonizing forests than in the old-growth forest. The steady supply of fruit by colonizing trees and shrubs, and the high abundance of arthropods in colonizing forests, may render such habitats more attractive to redtail monkeys.

The high rates of encounter of solitary redtail males in colonizing forests is not easy to explain either, but the fact that there were more solitary males in colonizing forests than in the old-growth forest suggests that colonizing forests may be serving as sinks for dispersing males. This study is the first to report all male groups in

redtails; these were encountered only in colonizing forests. Although uncommon, all male groups have been reported for other guenons e.g. (*Cercopithecus mona*) (Glenn et al. 2002) and *C. campbelli lowei* and *C. mitis* (Bourliere et al. 1970 and Tsingalia and Rowell 1984, respectively, cited in Glenn et al. 2002).

Mangabeys were encountered at about the same rate in the old growth forest and colonizing forest 1. Both encounter rates were significantly higher than in colonizing forest 2. Apparently, the encounter rate of mangabeys in colonizing forest 1 was influenced by a grove of *Phoenix reclinata* palms that the transect traversed. Mangabeys frequently ranged in this grove and this could have elevated their rate of encounter in this forest. Otherwise one would expect their encounter rate to be the same in both colonizing forests.

Encounter rates of baboons, L'Hoest's monkeys and red colobus did not differ among forest types. Baboons range very widely and also use grasslands, and hence were sighted very infrequently. L'Hoest's monkeys are generally associated with secondary forests (Haltenorth and Diller 1994). As such, one would expect them to be more abundant in the colonizing forest than in old growth forests. L'Hoest's monkeys are, however, very elusive and it is possible that sometimes they went undetected especially in the thick understory of the colonizing forests.

Lack of significant differences in the encounter rate of red colobus among the three forests was surprising. Chimpanzee studies at Ngogo (D. Watts and J. Mitani, unpublished data) suggest that more red colobus monkeys are killed in the colonizing forests than in the old growth forest. However, these differences may be influenced by the degree of vulnerability to predation in the different habitats. It is possible that red colobus are more vulnerable in the colonizing forests where the trees are shorter than in the old growth forest. However, long-term data from Ngogo, 1975 to 1998, suggest that the red colobus population has declined (Mitani et al. 2000). Unfortunately, this long-term study was conducted only in the old growth forest, but it is possible that the red colobus population has declined in the whole of the Ngogo area regardless of habitat type. The decline in the red colobus population is most likely due to predation by chimpanzees. The Ngogo chimpanzee community is unusually large (over 140 individuals) and hunt red colobus with great success; during a 16-month study, the Ngogo, chimpanzees killed 213 red colobus monkeys in 51 successful hunts (Mitani and Watts 2001). In support of the view that chimpanzees are responsible for the decline in red colobus population, a recent study on the impact of chimpanzee predation on red colobus demography (Teelen 2005) suggests that this high level predation is a recent development and is not sustainable.

In summary, this study suggests that different primate species prefer different habitats. Whereas chimpanzees were encountered more frequently in the old growth forest, black and white colobus were encountered more frequently in colonizing forests. Although the difference

in the encounter rates of blue monkeys between colonizing and old growth forests was not significant, the fact some groups were encountered in the colonizing forests and none were encountered in the old growth forest suggests that colonizing forests may be beneficial to blue monkeys. Additionally, long-term data indicate that the population of blue monkeys has declined in the old growth forest. Since Kibale National Park still contain large expanses of grasslands that resulted from cultivation up to the early 1900s, it is likely that primate species that do not do well in the old growth forest will be retained in forests that colonize grasslands in the mid-to long-term, pointing to the importance of not writing off these areas entirely in the development of conservation plans. However, the fact that recovering grasslands can support populations of some primate species should not be used as justification for further disturbance of the old growth forests because, old growth forests are endangered habitats and are inhabited by many critically endangered species.

**Acknowledgments** This study was conducted under the auspices of the Ngogo Chimpanzee Project supported by grants from the University of Michigan, NSF, National Geographic Society and L.S.B. Leakey Foundation to J.C. Mitani and by L.S.B. Leakey Foundation grant to D.P. Watts and J. Lwanga. Makerere University Biological Field Station provided logistic support. James Tibisiimwa is thanked for his assistance in the field. John Mitani, Tom Struhsaker, Simone Teelen and Monica Wakefield are thanked for their useful comments on the manuscript. I thank Sylvia Amsler for her help in the drawing of the study area map. Colin Chapman and two anonymous reviewers are thanked for additional constructive comments on the manuscript.

## References

- Brugiere D, Fleury M-C (2000) Estimating primate densities using home range and line transect methods: a comparative test with the black colobus monkey *Colobus satanas*. *Primates* 4:373–382
- Butynski TM (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol Monogr* 60:1–26
- Chapman CA (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 2:148–154
- Chapman CA (1995) Primate seed dispersal: coevolution and conservation implications. *Evol Anthropol* 4:74–82
- Chapman A, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT (2000) Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conser Biol* 14:207–217
- Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA (2002) Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *Int J Primatol* 23:283–310
- Chapman CA, Peres CA (2001) Primate conservation in the new millennium: the role of scientists. *Evol Anthropol* 10:16–33
- Dew JL, Wright P (1998) Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30:425–437
- Glenn ME, Matsuda R, Besen KJ (2002) Unique behavior of the mona monkey (*Cercopithecus mona*): all-male groups and copulation calls. In: Glenn M, Cords M (eds) *The guenons: diversity and adaptation in African monkeys*. Kluwer/Plenum, New York, pp 133–145
- Caughley G (1980) *Analysis of vertebrate populations*. Wiley, NY
- Ghiglieri M (1984) *The Chimpanzees of Kibale Forest*. Columbia University Press, New York
- Haltenorth T, Diller H (1994) *Collins field guide: mammals of Africa including Madagascar*. Harper Collins, London
- Hart JA, Katembo M, Punga K (1996) Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *Afr J Ecol* 34:364–379
- Kasenene JM (1987) The influence of mechanized selective logging, felling intensity, and gap-size on the regeneration of a tropical moist forest in the Kibale Forest Reserve, Uganda. PhD. Dissertation, Michigan State University, East Lansing
- Lawes MJ (2002) Conservation of fragmented populations of *Cercopithecus mitis* in South Africa: the role of reintroduction, corridors and metapopulation ecology. In: Glenn M, Cords M (eds) *The Guenons: Diversity and adaptation in African monkeys*. Kluwer/Plenum, New York, pp 375–392
- Mitani JC, Sanders WJ, Lwanga JS, Windfelder TL (2001) Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav Ecol Sociobiol* 49:187–195
- Mitani JC, Struhsaker TT, Lwanga JS (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *Int J Primatol* 21:269–286
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924
- Mitani JC, Watts DP, Lwanga JS (2002) Ecological and social correlates of chimpanzee party size and composition. In: Boesch C, Hohmann G, Marchant LF (eds) *Behavioural diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp 102–111
- National Research Council (1981) *Techniques for the study of primate population Ecology*. National Academy Press, Washington DC
- Norton-Griffiths M (1978) *Counting animals*. African Wildlife Foundation, Nairobi
- Nummelin M (1989) Seasonality and effects of forestry practices on forest floor arthropods in the Kibale Forest, Uganda. *Fauna Norv Ser B* 36:17–25
- Oates JF (1974) The ecology and behaviour of the black- and -white Colobus monkey (*Colobus guereza* Ruppell) in East Africa. PhD thesis, University of London
- Plumptre AJ, Cox D, Mugume S (2003) *The status of chimpanzees in Uganda*. Albertine Rift technical report. Series No 2. Wildlife Conservation Society
- Siegel S, Castellan NJ (1988) *Nonparametric statistics for behavioral sciences*. McGraw-Hill, New York
- Skorupa JP (1986) Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. In: Benirschke K (eds) *Primates: the road to self-sustaining populations*. Springer, New York Berlin Heidelberg, pp 57–70
- Skorupa JI (1988) The effects of selective timber harvesting on rainforest primates in Kibale Forest, Uganda. PhD. Dissertation, University of California, Davis
- Skorupa J (1989) Crowned eagles *Stephanoaetus coronatus* in rainforest: observations of breeding chronology and diet at a nest in Uganda. *Ibis* 131:294–298
- Struhsaker TT (1978) Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers DJ, Herbert J (eds) *Recent advances in primatology, vol 1*. Behaviour. Academic, London, pp 225–247
- Struhsaker TT (1997) *Ecology of an African rain forest*. University Press of Florida, Gainesville
- Struhsaker TT, Leakey M (1990) Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav Ecol Sociobiol* 26:435–444
- Struhsaker TT, Leland L (1988) Group fission in redbelt monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. In: Gautier-Hion A, Bourliere F, Gautier J-P, Kingdon J (eds) *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press, Cambridge, pp 364–388
- Teelen S (2005) The Impact of Hunting by Chimpanzees (*Pan troglodytes*) on demography and behavior of red Colobus monkeys (*Procolobus rufomitratus*) at Ngogo, Kibale National

- Park, Uganda. PhD. Dissertation, Yale University, New Haven, Conn.
- Uganda Government (1965) Maps of Fort Portal and Kahunge, Series Y 732, 3rd edn. U.S.D. Department of lands and survey, Entebbe, Uganda
- Weber W (1993) Primate conservation and ecotourism in Africa. In: Potter CS, Cohen JI, Janezowski D (eds) Perspective on biodiversity: case studies of genetic resource conservation and development. AAAS Press, Washington DC, pp 129–150
- Whitesides GH, Oates JF, Green SM, Kluberanz RP (1988) Estimating primate densities from transects in a West African rain forest: a comparison of techniques. *J Anim Ecol* 57:345–367
- Whitmore TC (1998) An introduction to tropical rain forests. Oxford University Press, Oxford
- Wing LD, Buss IO (1970) Elephants and forests. *Wildl Monogr* 19