



## Primate Community Dynamics in Old Growth Forest over 23.5 Years at Ngogo, Kibale National Park, Uganda: Implications for Conservation and Census Methods

John C. Mitani,<sup>1,4</sup> Thomas T. Struhsaker,<sup>2</sup> and Jeremiah S. Lwanga<sup>3</sup>

Received December 23, 1998; accepted October 18, 1999

---

*Few data exist regarding long-term changes in primate populations in old-growth, tropical forests. In the absence of this information, it is unclear how to assess population trends efficiently and economically. We addressed these problems by conducting line-transect censuses 23.5 years apart at the Ngogo study area in Kibale National Park, Uganda. We conducted additional censuses over short time intervals to determine the degree to which the temporal distribution of censuses affected estimates of primate numbers. Results indicate that two species, blue monkeys and red colobus, may have experienced significant reductions over the past 23.5 years at Ngogo. In contrast, five other species, baboons, black-and-white colobus, chimpanzees, mangabeys, and red-tailed guenons, have not changed in relative abundance. Additional findings indicate that different observers may vary significantly in their estimates of sighting distances of animals during censuses, thus rendering the use of measures of absolute densities problematic. Moreover, censuses conducted over short periods produce biased estimates of primate numbers. These results provide guidelines for the use of line-transect censuses and underscore the importance of protecting large blocks of forests for primate conservation.*

---

**KEY WORDS:** conservation; censuses; population dynamics; primates.

<sup>1</sup>Department of Anthropology, University of Michigan, Ann Arbor, MI, 48109-1382; E-mail: mitani@umich.edu.

<sup>2</sup>Department of Biological Anthropology and Anatomy, Duke University, Box 90383, Durham, NC 27708-0383.

<sup>3</sup>Makerere University Biological Field Station, P.O. Box 409, Fort Portal, Uganda.

<sup>4</sup>To whom correspondence should be addressed.

## INTRODUCTION

Little is known about the long-term population dynamics of nonhuman primates living in tropical rain forests. Given protection against hunting and major habitat alteration such as logging, it is logical to assume that primate communities living in old-growth, mature rain forest will remain stable in species composition, proportional representation, and population density. In the absence of disturbance, such communities have been historically envisioned as living in a state of equilibrium (Connell, 1978). We compare long-term census data of primates at an old-growth, rain forest site in the Kibale National Park, Uganda, that suggest a dynamic community and one that may represent a nonequilibrium system (Hutchinson, 1961; Newberry *et al.*, 1998).

Our analyses utilize line-transect census data to evaluate the abundance of primates, and here we also examine the inherent problems of such observations with respect to four issues. First, how many replications are necessary to reach asymptotic precision? Second, can results from multiple observers be compared reliably? Third, how does the temporal distribution of censuses affect results? Fourth, what are the limitations of using the social group as a unit of measure to estimate abundance? Our findings have important implications for studies that employ line-transect censuses to assess primate numbers and provide guidelines for their execution and interpretation.

## METHODS

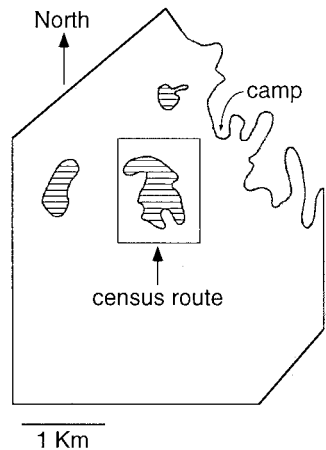
### Study Site and Subjects

We conducted censuses at Ngogo in the Kibale National Park, Uganda. The 12-km<sup>2</sup> Ngogo study area covers old-growth, moist, evergreen rain forest as well as a wide range of successional habitats and has been the site of behavioral research on primates since 1974 (Ghiglieri, 1984; Butynski, 1990; Struhsaker, 1997). We censused the seven diurnal anthropoid primates commonly encountered at Ngogo: two colobines, black-and-white colobus (*Colobus guereza*) and Pennant's red colobus (*Procolobus pennantii*); four cercopithecines, baboons (*Papio anubis*), blue monkeys (*Cercopithecus mitis*), mangabeys (*Lophocebus albigena*), and red-tailed guenons (*Cercopithecus ascanius*); and a single pongid, chimpanzees (*Pan troglodytes*). One additional cercopithecine, l'Hoest's monkey (*Cercopithecus lhoesti*) ranges within the study area, but because it is rare, it is excluded from the analyses.

## Censuses

We conducted censuses during four periods between 1975 and 1998. Twenty-four censuses were conducted by Struhsaker over 23 months between January 1975–November 1976. Lwanga completed 36 censuses during 18 months between January 1997–June 1998. Struhsaker carried out an additional 16 censuses during a 3-week period in July 1996. We refer to these latter samples by Struhsaker as rapid-assessment censuses given that they were completed within a relatively short period of time. Finally, Mitani conducted 14 censuses over 6 months from July–December 1996. Lwanga and Mitani completed two censuses every month, making one during each half of each month. Two exceptions applied to Mitani's censuses in July and August 1996; both censuses were conducted during the latter half of the month in July 1996, and he performed two additional censuses in August 1996 for a total of four during that month. Struhsaker averaged one census each month during the 1975–1976 sample period (S.D. = 1.3; median = 1).

We employed line transect methods to obtain census data (National Research Council, 1981; Whitesides *et al.*, 1988). All censuses were completed over the same, approximately square route, running about 1 km on each side and covering the middle of the Ngogo study area (Fig. 1). Each observer varied the direction of travel along the census route to equalize the numbers started and stopped in one way or the other. The 1975–1976 census route covered 4.03 km. Subsequent censuses carried out after 1976 were conducted over a slightly longer 4.4-km route by walking an additional 370 m on one end. The four corners of the 1996–1998 census route were located at the following trail intersections: F 4 - F 10 - K 10 - K 4.



**Fig. 1.** The Ngogo study area in the Kibale National Park, Uganda. Three pockets of regenerating forest, varying in stages of succession and lying within the study area, are depicted by the hatched regions. The census route encircles the regenerating forest depicted in the center of the study area.

### Census Data

We used identical data collection methods during censuses. Observers conducted all censuses between 07:30 and 13:30 h. During each census, we walked slowly, traveling approximately 1 km per h, and pausing at regular intervals to scan the forest. Upon sighting primates, we stopped for  $\leq 10$  min and recorded the species, time, location, number of individuals, and distance to the first animal observed. During censuses conducted in the 1970s, Struhsaker calibrated his estimates of sighting distances against actual measurements; similar checks were not systematically completed by the other two observers. We recorded ancillary data including the height of subjects, their activities, the presence of heterospecific individuals, and the method of detection.

We conducted censuses at widely separated time intervals. As a result, all three observers were never in the field together, and we were not able to conduct tests of interobserver reliability in sighting distances of primates. Given our inability to standardize estimates of sighting distances between observers, we used sighting frequencies—the number of groups observed per kilometer of each census—to estimate their numbers. This measure is commonly employed in studies of vertebrates to estimate animal abundance and is typically referred to as “relative density” (Caughley, 1980; Seber, 1982). For simplicity and to maintain adherence to colloquial usage, we hereafter adopt the term *abundance* for this measure. Our measure of abundance is especially useful in detecting changes in populations over time and is simpler than computing estimates of absolute density, the number of subjects observed per area censused, also derived from line transect surveys because it makes fewer assumptions regarding the data (Seber, 1982). Comparisons involving measures of abundance made by different observers nevertheless require the use of standard methods and that individuals possess similar abilities to spot animals (Caughley, 1980).

Chimpanzees are typically widely dispersed on the forest floor and treetops, and it is often difficult to establish with certainty whether single individuals are together with other conspecifics. For this reason, we used counts of both solitary individuals and groups of chimpanzees in the following analyses.

### Analyses

For each of the four sample periods, we computed the precision of our estimates of the mean numbers of each species. Precision was calculated as 95% confidence limits of estimated means expressed as the percentage

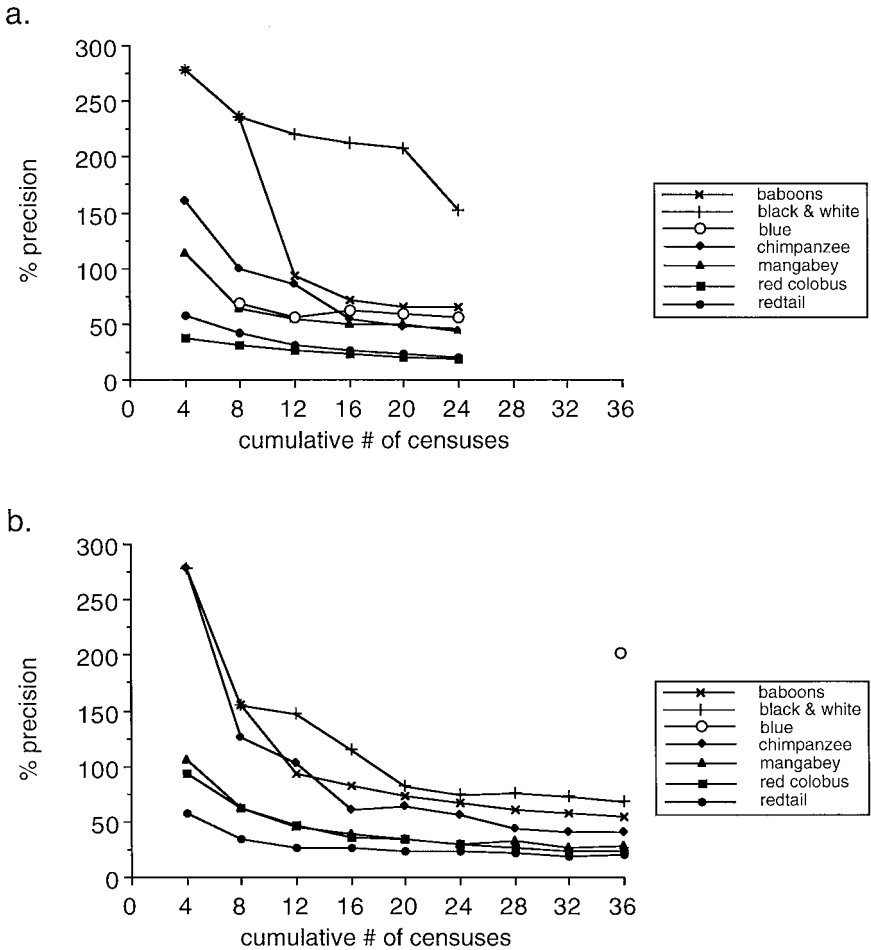
of those means (National Research Council, 1981). We compared average sighting distance estimates and the shapes of sighting distance distributions to examine differences between observers. We assessed long-term changes in the abundance of primates at Ngogo by comparing censuses conducted 23.5 years apart during 1975–1976 and 1997–1998. We conducted an additional 16 and 14 censuses over two different time frames, 3 weeks and 6 months, respectively. We compared results of these censuses to those obtained over a longer 18-mo control period ( $n = 36$  censuses) to evaluate the degree to which the temporal distribution of censuses affected estimates of the abundance of primates. All statistical tests were conducted using nonparametric techniques with the criterion of significance set at 0.05 (Siegel and Castellan, 1988).

## RESULTS

### Long-term Changes in Primate Abundance

Figure 2 shows the precision of group counts for each species as a function of the cumulative number of censuses conducted during 1975–1976 and 1997–1998. With the exception of black-and-white colobus in 1975–1976 and blue monkeys in 1997–1998, estimates of precision for both observers reach an asymptote after approximately 20 censuses and suggest that the number of censuses completed during these two periods was sufficient to detect differences between samples. Despite the efficacy of our samples in this regard, there were significant differences between observers in their sighting distances of primates (Fig. 3). On average, Struhsaker recorded subjects significantly farther away than did Lwanga (Mann–Whitney  $U$  test,  $Z = -4.63$ ,  $N_1 = 148$ ,  $N_2 = 223$ ,  $p < 0.001$ ). In addition, the distributions of sighting distances recorded by these two observers diverged substantially (Kolmogorov–Smirnov test,  $Z = 2.58$ ,  $p < 0.001$ ; Fig. 3).

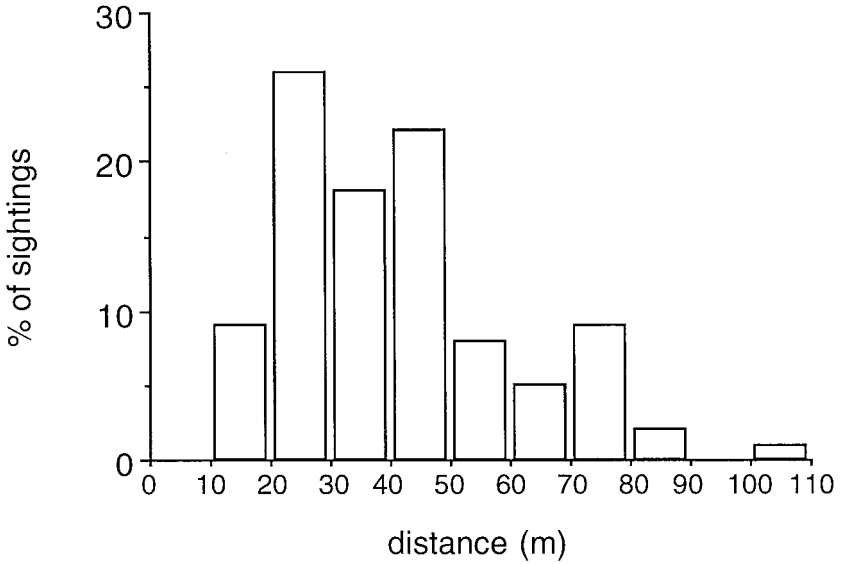
The differences in sighting distances between observers may have been due to one of three factors: 1) actual differences in distances between observers and subjects; 2) an artifact of differences in distance estimations; or 3) an artifact of differences in the ability to record the presence of animals. The third possibility appears unlikely because the average number of primates censused per day per km of travel did not differ between the two observers (Struhsaker  $\bar{x} = 1.53$ , S.D. 0.64; Lwanga  $\bar{x} = 1.40$ , S.D. = 0.67; Mann–Whitney test,  $Z = -0.71$ ,  $N_1 = 24$ ,  $N_2 = 36$ ,  $p > 0.45$ ). It is unclear whether observers differed in their abilities to detect different species. We did not collect data on interobserver reliability in distance estimations to address the second possibility directly. This lack of informa-



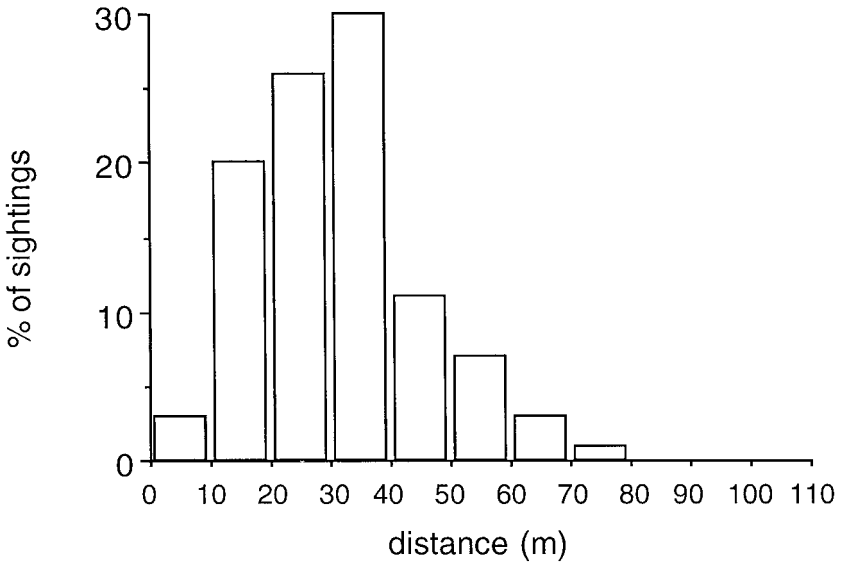
**Fig. 2.** Precision of estimated mean number of primate groups as a function of the cumulative number of completed censuses. (a) Estimates of precision based on censuses conducted during 1975–1976 by Struhsaker. (b) Estimates of precision based on censuses conducted during 1997–1998 by Lwanga.

tion raises an important methodological problem. Our inability to exclude the reported differences in distance estimates as artifactual makes it impossible for us to assess the areas surveyed by different observers during censuses and produce reliable absolute density estimates of primates. Given this methodological problem, we forego an attempt to evaluate absolute densities and instead rely on estimates of abundance expressed as the

a.



b.



**Fig. 3.** Frequency distributions of sighting distances of primates during censuses. (a) Sighting distance distributions from censuses conducted during 1975–1976 by Struhsaker ( $n = 148$ ). (b) Sighting distance distributions from censuses conducted during 1997–1998 by Lwanga ( $n = 223$ ).

number of conspecific groups observed per kilometer of census. Like estimates of absolute density, calculations of abundance are subject to error if differences between observers exist. Specifically, these computations may be biased if there are differential abilities to spot animals. This possibility does not appear to be a serious problem for our comparisons, however, because the number of subjects censused per day did not differ between the two observers. In addition, there was no obvious change in visibility along the census route over the 23.5-year period of the study (Struhsaker, personal observation). This conclusion is reinforced by two facts. No major change in vegetation occurred across the study site (Lwanga, Struhsaker, and Butynski, unpublished data), and Struhsaker's sighting distances of primates showed remarkable consistency over the time in question.

Comparisons of the abundance of groups of primates censused in 1975–1976 and 21 years later in 1997–1998 suggest that populations of two species, blue monkeys and red colobus, may have declined over time (Mann–Whitney  $U$  tests,  $p < 0.001$  for both comparisons; Table I). There was also a nonsignificant trend suggesting a reduction in chimpanzee numbers (Mann–Whitney  $U$  test,  $p = 0.08$ ). In contrast, the four other species included in our surveys—baboons, black-and-white colobus, mangabeys, and red-tailed guenons—showed no change in the abundance of groups (Mann–Whitney  $U$  tests,  $p > 0.20$  for all four comparisons; Table I).

### Census Timing and Estimates of Abundance

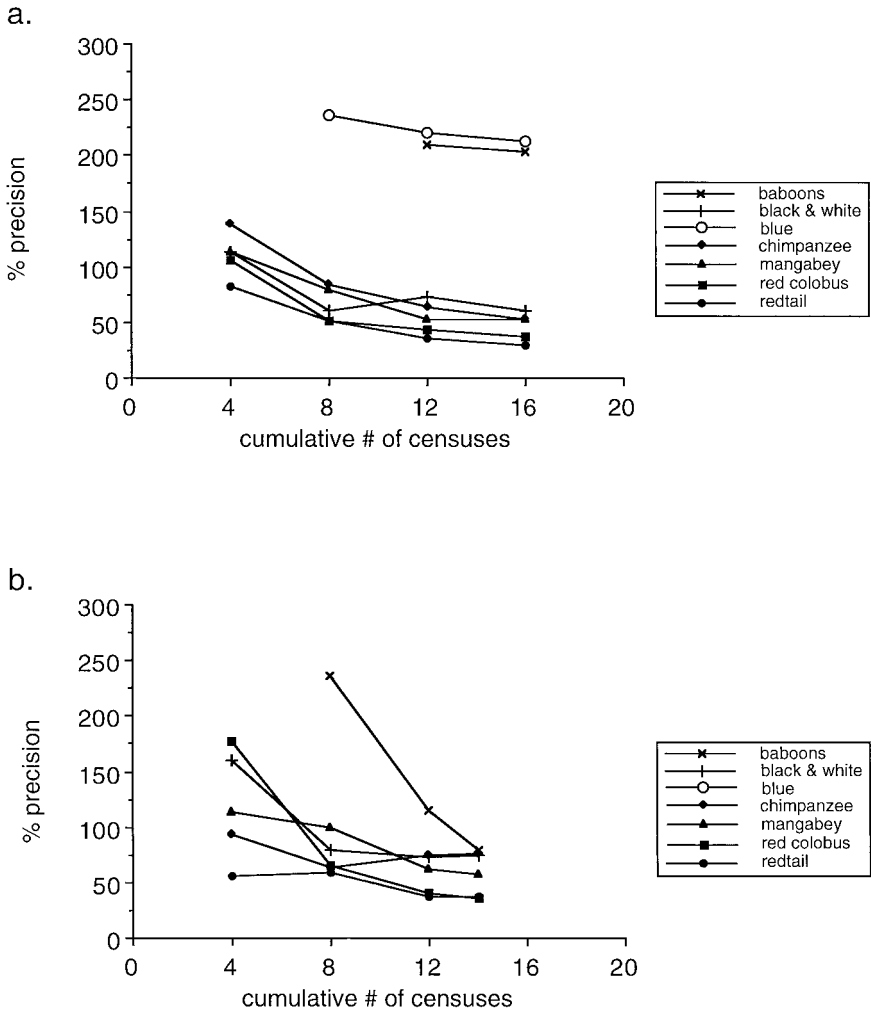
Figure 4 shows estimates of precision of the mean number of groups of each species observed during censuses conducted over 3 weeks and 6 months. Sample sizes are relatively small, and estimates of precision for

**Table I.** Long-term changes in the abundance of primates at Ngogo<sup>a</sup>

Species	1975–1976 ( $n = 24$ censuses)	1997–1998 ( $n = 36$ censuses)
Baboon	0.09(0) $\pm$ 0.03	0.08(0) $\pm$ 0.02
Black-and-white colobus	0.03(0) $\pm$ 0.02	0.06(0) $\pm$ 0.02
Blue monkey <sup>b</sup>	0.09(0) $\pm$ 0.03	0.01(0) $\pm$ 0.01
Chimpanzee	0.16(0.25) $\pm$ 0.03	0.13(0) $\pm$ 0.02
Mangabey	0.17(0.25) $\pm$ 0.04	0.23(0.23) $\pm$ 0.03
Red colobus <sup>b</sup>	0.53(0.50) $\pm$ 0.06	0.30(0.23) $\pm$ 0.04
Red-tailed guenon	0.47(0.50) $\pm$ 0.05	0.60(0.46) $\pm$ 0.06

<sup>a</sup>Cell entries indicate the number of groups observed per kilometer of census. Means, medians (in parentheses),  $\pm 1$  standard error are shown.

<sup>b</sup> $p < 0.001$  for comparisons between the two sample periods.

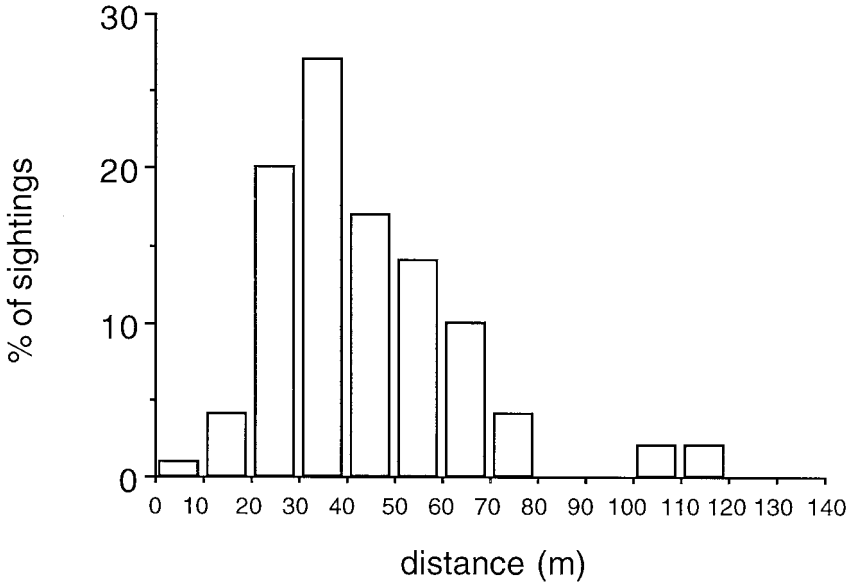


**Fig. 4.** Precision of estimated mean number of primate groups as a function of the cumulative number of completed censuses. (a) Estimates of precision based on rapid assessment censuses conducted during three weeks in July 1996 by Struhsaker. (b) Estimates of precision based on censuses conducted over six months during July–December 1996 by Mitani.

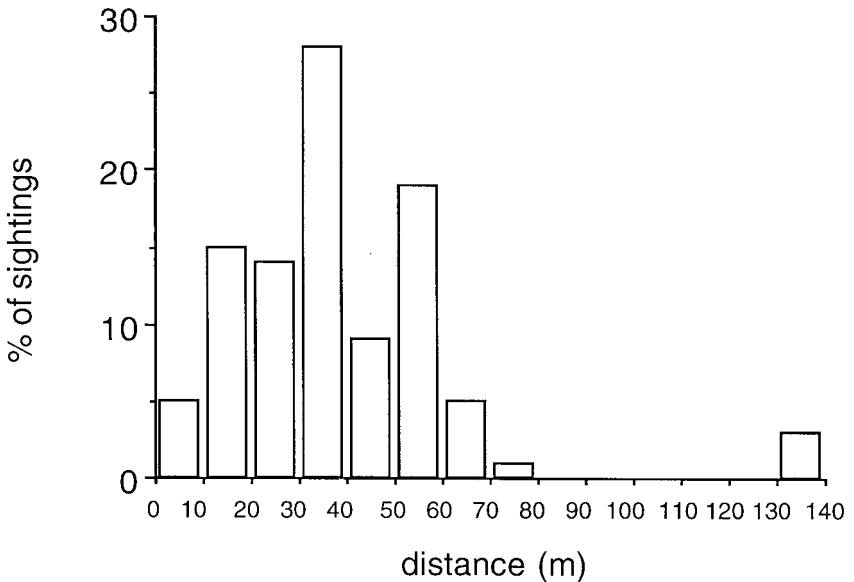
the final samples of 16 and 14 censuses, respectively, are correspondingly high (cf. Fig 2). The following comparisons should be interpreted guardedly within this context.

Figure 5 shows the sighting distances of primates made by Struhsaker during his censuses conducted over 3 weeks and Mitani during censuses

a.



b.



**Fig. 5.** Frequency distributions of sighting distances of primates during censuses. (a) Sighting distance distributions from rapid assessment censuses conducted during 3 weeks in July 1996 by Struhsaker ( $n = 101$ ). (b) Sighting distance distributions from censuses conducted over 6 months during July–December 1996 by Mitani ( $n = 74$ ).

completed over 6 months. We compare these sighting distances with those made by Lwanga over 1.5 years (Fig. 3b). There is significant heterogeneity among the three observers in their sighting distances of animals (Kruskal–Wallis one-way ANOVA,  $\chi^2 = 31.63$ , 2 *df*,  $p < 0.001$ ). Significant differences also existed in the overall shapes of sighting distance distributions obtained by Struhsaker and Lwanga and by Mitani and Lwanga (Kolmogorov–Smirnov tests,  $p < 0.04$  for both comparisons). Despite differences among observers, Struhsaker showed remarkable consistency over time in his estimation of sighting distances. His frequency distribution of sighting distances in 1975–1976 did not differ from the one he obtained 1996 (Kolmogorov–Smirnov test,  $p > 0.35$ ; cf. Figs. 3a and 5a).

Because we are unable to determine whether these differences are real or artifactual, we again rely on estimates of the abundance of subjects to assess whether the timing of observations affects estimates of primate numbers. Our estimates of abundance, assessed through the number of groups observed per kilometer of census, are not likely to be biased by differences in the ability of observers to spot animals because heterogeneity did not exist among the three individuals in the number of all primate groups observed per day per kilometer of census (Kruskal–Wallis test,  $\chi^2 = 1.19$ , 2 *df*,  $p > 0.50$ ). Lacking direct tests of interobserver reliability, we are again unable to ascertain whether differences exist between individuals in the ability to detect particular species.

A comparison between censuses conducted over a short 3-week period with those carried out over a longer 18-month time frame revealed two significant differences: more black-and-white colobus monkeys and fewer baboons were observed during the 16 censuses conducted over 3 weeks than during the 36 censuses completed over 1.5 years (Mann–Whitney *U* tests,  $p \leq 0.05$  for both tests; Table II). In addition, there were trends toward higher numbers of chimpanzees and lower numbers of mangabeys during the 16 rapid assessment censuses conducted over 3 weeks compared with the long-term data collected over 18 months (Mann–Whitney *U* tests,  $p = 0.10$  for both tests; Table II).

Results based on 14 censuses conducted over 6 months did not produce any statistically significant difference in estimates of abundance compared with those from the longer 18-month sample (Table II).

## DISCUSSION

### Census Methods

The line-transect method of censusing primates has been considered a relatively efficient method to obtain estimates of primate densities over

**Table II.** The effect of the timing of censuses on estimates of the abundance of Ngogo primates<sup>a</sup>

Species	3 weeks	6 months	18 months
	1996 ( <i>n</i> = 16 censuses)	1996 ( <i>n</i> = 14 censuses)	1997–1998 ( <i>n</i> = 36 censuses)
Baboon <sup>b</sup>	0.01(0) ± 0.01	0.08(0) ± 0.03	0.08(0) ± 0.02
Black-and-white colobus <sup>b</sup>	0.13(0.11) ± 0.04	0.11(0) ± 0.04	0.06(0) ± 0.02
Blue monkey	0.01(0) ± 0.01	0.00(0) ± 0.00	0.01(0) ± 0.01
Chimpanzee <sup>c</sup>	0.23(0.23) ± 0.05	0.13(0) ± 0.05	0.13(0) ± 0.02
Mangabey <sup>c</sup>	0.14(0.23) ± 0.04	0.15(0.23) ± 0.04	0.23(0.23) ± 0.03
Red colobus	0.30(0.23) ± 0.05	0.31(0.23) ± 0.05	0.30(0.23) ± 0.04
Red-tailed guenon	0.63(0.57) ± 0.09	0.42(0.45) ± 0.07	0.60(0.46) ± 0.06

<sup>a</sup>Cell entries indicate the number of groups observed per kilometer of census. Means, medians (in parentheses), ±1 standard error are shown.

<sup>b</sup>*p* < 0.05 for comparisons between censuses conducted over 3 weeks in 1996 and 1997–1998 censuses.

<sup>c</sup>*p* = 0.10 for comparisons between censuses conducted over 3 weeks in 1996 and 1997–1998 censuses.

large areas within a short period of time (*e.g.* Struhsaker, 1975; National Research Council, 1981). Some of the inherent problems of this approach have been reviewed earlier (National Research Council, 1981; Skorupa, 1988; Struhsaker, 1997). This study emphasizes the difficulty of comparing data collected by different observers along the same transect during different time periods. It is important to identify these problems and to understand how they affect results if one is to understand long-term trends in primate populations because the same observer will rarely be able to conduct censuses over several decades.

Determining the distance at which primate groups are seen during censuses is critical to making accurate assessments of the area surveyed and, correspondingly, estimating absolute primate densities. Estimates of sighting distances may vary significantly between observers. Observers may also differ in their abilities to detect primates, and this too may vary with the different primate species being censused. The importance of these problems, particularly the one pertaining to estimating distance, depends on the questions being asked. If one is interested in gaining a first approximation of numerical changes in a primate community over time, then the measure of abundance employed here, the number of groups seen per kilometer censused, is satisfactory, and interobserver differences in estimating sighting distances are not a problem. This is true when visibility within the area censused has remained constant as is the case in the old-growth forest along the Ngogo census route. However sighting distance, as affected by visibility, becomes extremely important when dealing with habitats where visibility changes significantly over time. For example, in moderately

to heavily logged forests, visibility increases immediately after logging, but as the dense undergrowth and semiwoody tangle develops and grows taller, visibility can decrease to a point that is less than that in undisturbed forest. Sighting distance is also important when comparing censuses from forests with different structural properties that affect visibility.

We additionally recognize that an assessment of the stability of primate populations over time utilizing counts of the numbers of groups may be compromised if there are temporal changes in group sizes. For example, a decrement in the number of groups could be compensated by larger group sizes resulting in no change in population size. At Ngogo, limited data do not support this suggestion for two of the commonest species because long-term data reveal no change in mean group size over time. Groups of both red-tailed guenons and mangabeys have remained relatively constant in size from 1974–1998 (red-tailed guenons: 1975, range = 35–50,  $n = 1$ ; 1998, range = 20–46,  $n = 4$ ; mangabeys: 1974,  $\bar{x} = 18$ , S.D. = 5,  $n = 3$ ; 1998,  $\bar{x} = 18$ , S.D. = 3,  $n = 3$ ; Freeland, 1979; Struhsaker and Leland, 1988; Windfelder and Lwanga, unpublished data).

In terms of accurately estimating absolute population and biomass densities, there is no substitute for detailed, long-term studies of several focal groups that include group counts and home range estimates. Line-transect censuses have often been used to estimate absolute densities, but rarely have these estimates been checked against the more reliable results derived from focal-group studies (Struhsaker, 1975, 1997; National Research Council, 1981; Defler and Pintor, 1985; Chapman *et al.*, 1988). When, due to financial and logistic constraints, one must utilize the line-transect method for estimating population densities, estimates of sighting distance should be checked against actual measurements and interobserver reliability should be verified. A difference of only 10 m in estimated sighting distance between observers can translate into a difference of 20% in estimated population density. At Kibale, density estimates based on animal-to-observer distances most closely approximate estimates derived from focal-group observations (Struhsaker, 1997). An alternative method, using the perpendicular distance between the census route and animals to estimate strip width, tends to overestimate primate population densities at least in mature old-growth forest (Struhsaker, 1997). Correction factors can be applied to census data that utilize perpendicular distances to obtain more accurate estimates of absolute densities (Whitesides *et al.*, 1988), but in view of this and the other problems outlined above, we suggest the use of animal abundance, measured by the number of subjects spotted per distance censused, as an alternative assay.

The temporal distribution of the censuses along a given route, e.g. whether concentrated into a few weeks or spread over an entire year,

will also affect results. In this study, the timing of censuses seemed to be particularly important for some of the species with large home ranges and low population densities, such as baboons and mangabeys. In contrast, species with relatively small home ranges and high population densities, such as red-tailed guenons and red colobus, were seen as often during the rapid assessment censuses as during the censuses spread over 6 and 18 months. It remains unclear why so many more black-and-white colobus were recorded during the rapid assessments than in the more extensive censuses; black-and-white colobus typically have smaller home ranges than either red-tailed guenons or red colobus (Struhsaker and Leland, 1979).

The effect of population density and home range size on the importance of the temporal spread of the sample might conceivably be overcome in species that on a daily basis cover very long distances because this might increase the likelihood of encountering them during any given census of a relatively small area within a large home range. Chimpanzees appear exceptional in that more were seen during the rapid assessment censuses than in the censuses that were spread over 6 or 18 months (Table II). This may have resulted, in part, from chance. We conducted the rapid assessment censuses during a time when the chimpanzees were widely scattered and regularly feeding in the area of the census route. Chimpanzees also differ from the other primates in this sample because they live in a fission-fusion society (Nishida, 1968). Individuals routinely split up into small units, thereby increasing the probability of encounter during a given census. This will pose a problem in censusing any species that lives in social groups that typically disperse widely or form temporary subgroups, e.g. some subpopulations of red colobus (Skorupa, 1988; Struhsaker, 1997; Siex and Struhsaker, 1999). In fact, the line-transect census method may not be particularly appropriate for estimating the abundance of species with low population densities, large home ranges, and diffuse social systems, like chimpanzees. For chimpanzees, the very time consuming approach of monitoring specific communities may represent the only means to estimate their abundance reliably. Alternatively, studies employing nest counts may provide a relatively quick and inexpensive means to assess chimpanzee numbers (National Research Council, 1981; Ghiglieri, 1984; Plumtre and Reynolds, 1997).

Given the prevailing observation conditions and primate community composition at Ngogo, it appears that censuses conducted over 6 months yield results comparable to those spread over 18 months. This finding is extremely important in terms of planning and implementing long-term monitoring programs. It implies that the same results can be obtained with one-third the effort, at least for the more abundant species. It is important to note, however, that estimates of precision differ considerably between the short 6-month study and the longer 18-month observation period (Figs. 2 and 4).

Estimates of precision indicate that for the three most common species at Ngogo—red-tailed guenons, red colobus, and mangabeys—censuses must be repeated along any given transect about 20-30 times before sample variance reaches an asymptote (Fig. 2). This is consistent with earlier studies at the Kanyawara study site in Kibale (National Research Council, 1981). Variance and measures of precision for a given species depend on the likelihood of encounter during a given census. This likelihood is, in turn, affected by the density of social groups, the dispersion of members in the group, daily travel rates, and pattern of travel. Although 20-30 censuses may be adequate for common species, several more censuses, perhaps as many as 40-60, may be required for uncommon species to reach asymptotic precision (Figs. 2 and 4). This latter point is underscored by comparing how the abundance of animals affects estimates of precision. Figure 2 indicates that as the abundance of red-tailed guenons and red colobus has changed over time, the forms and slopes of precision curves have been modified. At each time interval, the more abundant species shows uniformly lower estimates of variance and reaches asymptotic precision more quickly than the less common species.

### **Apparent Changes in Primate Community Composition**

Our results indicate that two species, blue monkeys and red colobus, declined significantly in abundance at Ngogo between 1975–1976 and 1997–1998. One possibility is that these decrements merely reflect variations in the ability of different observers to spot them. For example, one might argue that the large numbers of red colobus recorded in the early 1975–1976 sample were due to the differential ability of Struhsaker, a trained and keen observer of these monkeys, to detect them. The relative paucity of red colobus observed by Struhsaker during his 1996 sample (Table II), however, is not consistent with this proposal, and suggests that a real decline in red colobus numbers has occurred at Ngogo over time. Similarly, the uniformly low rates of encounters with blue monkeys by all three observers since 1996 indicate that their abundance has experienced a significant drop as well (Table II).

The observed decrease in blue monkeys is consistent with events in the mid-1980s and do not support Butynski's (1990) hypothesis that the Ngogo population was recovering from an episodic crash due to an historical event such as disease. In 1984, the only group of blue monkeys at Ngogo divided into two groups, one of which disappeared entirely from the study area (Lwanga, 1987; Butynski, 1990). Blue monkeys occur infrequently in the southern part of the Kibale Park (Chapman, unpublished data). This

represents a north-to-south decrease in abundance of blue monkeys and, as suggested by Lwanga (1987), their decline at Ngogo may be the consequence of interspecific competition. Blue monkeys include several different subspecies and are found in a diverse array of habitats and cover an enormous geographic range throughout eastern, central, and southern Africa (Rowe, 1996). As such, they are considered to be a generalist that does not compete well with old-growth forest specialists (Struhsaker, 1978). Their decline may reflect the fact that the Ngogo primate community represents a nonequilibrium system, and they are being excluded competitively. Additional information is consistent with this hypothesis. Although much of Ngogo consists of old-growth forest, there is evidence of significant human disturbance as recently as 60-70 years ago when Kibale was gazetted as a Crown Forest in 1932 and human occupants were moved out of the area to facilitate its management. For example, the Ngogo area, like other areas of Kibale, is a mosaic of forests of varying successional stages and grasslands that are maintained by fire (Struhsaker, 1997). These grasslands revert to forest when protected against fire. In addition, three very large stone mortars, which are used to grind cereals and indicate human habitation, have been found in the forest within about 30-100 m of the forest-grassland-colonizing bush interface. Finally, although there is an abundance of extremely large trees of *Ficus mucuso* in the Ngogo study area, no seedlings, saplings or poles of this species have been found there. Typically, this is a species that appears to require very open conditions for establishment. In other words, we speculate that the Ngogo forest is still maturing and, in the process, becoming better habitat for old-growth specialists and less well suited for generalists like the blue monkeys. Perhaps it is no coincidence that the blue monkey populations in both the old-growth and selectively logged forests at Kanyawara, 10 km north of Ngogo and connected by continuous forest, have also declined over the past 28 years (Chapman *et al.*, in prep.). Additional study regarding dietary overlap among primates and long-term floristic changes will be required to evaluate the roles of interspecific competition and forest dynamics in determining the distributional pattern of blue monkeys throughout the Kibale Park.

The apparent decrease in red colobus at Ngogo cannot be readily explained. Four nonmutually exclusive possibilities exist. First, red colobus may be living in fewer, but larger groups, which could mean there has been no change in actual numbers. Second, mortality may have increased due to disease and predation by chimpanzees and crowned hawk-eagles. Limited information from the 1970s and 1980s suggested that a herpes-like disease was killing adult males at a high rate, but not adult female or immature red colobus. Five of 10 adult males in one social group disappeared over 2.5 years (Struhsaker, in press). Between 1995 and 1998, chimpanzees killed

$\geq 3\%$  of the red colobus per year at Ngogo (Mitani and Watts, 1999); red colobus are also the most frequent prey item of crowned hawk-eagles at the nearby Kanyawara study site (Struhsaker and Leakey, 1990). We cannot assess whether rates of predation have increased over the past two decades, which would be necessary if they are to account for the red colobus decline. Finally, the decrease in numbers may be due to increased interspecific competition. This is unlikely, however, because red colobus generally have little dietary overlap with the other primates in Kibale (Struhsaker, 1978). An understanding of the red colobus population trends at Ngogo will require more thorough studies of demography, disease, and predator-prey relations in specific social groups. In any event, the Ngogo red colobus population does not appear to be stable.

One striking aspect about the changes in the Ngogo primate community is that they are not entirely consistent with our existing ideas about ecological guilds (Skorupa, 1986, 1988; Struhsaker, 1997). At least one mature-forest core species—red colobus—has declined, and so has a generalist—blue monkeys—that is considered to be highly adaptable. These trends support the idea that the Ngogo primate community is changing. Should this prove to be a more widespread phenomenon, then very large areas of forest must be protected for conservation purposes in order to buffer the effects of nonequilibrium dynamics. Large protected areas will help to ensure that population declines in one part of the forest will be compensated by immigration from stable or increasing populations in adjacent areas. It remains to be seen if the Kibale National Park (760 km<sup>2</sup>) is large enough to conserve viable populations of its full complement of primate species.

### ACKNOWLEDGMENTS

Our field work in Uganda was sponsored by the Makerere University and Ugandan National Parks. We are grateful to G. I. Basuta, J. Kasenene, and the staff of the Makerere University Biological Field Station for logistic support. David Watts provided additional assistance in the field. We thank C. Chapman and J. Oates for helpful discussion and comments on the manuscript. This research was supported by a NSF Presidential Faculty Fellowship Award SBR-9253590 to JCM and in 1975 - 1976 by grants from the New York Zoological Society to TTS.

### REFERENCES

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

- Caughley, G. (1980). *Analysis of Vertebrate Populations*. Wiley, New York.
- Chapman, C., Fedigan, L. M., and Fedigan, L. (1988). A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia* 30: 67–80.
- Connell, J. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Deffer, T., and Pintor, D. (1985). Censusing primates by transect in a forest of known primate density. *Int. J. Primatol.* 6: 243–259.
- Freeland, W. (1979). Primate social groups as biological islands. *Ecology* 60: 719–728.
- Ghiglieri, M. (1984). *The Chimpanzees of the Kibale Forest*, Columbia University Press, New York.
- Hutchinson, G. E. (1961). The paradox of plankton. *Am. Nat.* 95: 137–145.
- Lwanga, J. (1987). *Group Fission in Blue Monkeys (Cercopithecus mitis stuhlmanni): Effects on the Socioecology in Kibale Forest, Uganda*. M.Sc. thesis. Makerere University, Kampala, Uganda.
- Mitani, J., and Watts, D. (1999). Demographic influences on the hunting behavior of chimpanzees. *Am. J. Phys. Anthropol.* 109: 439–454.
- National Research Council (1981). *Techniques for the Study of Primate Population Ecology*. National Academy Press, Washington, D.C.
- Newbery, D., Prins, H., and Brown, N. (1998). *Dynamics of Tropical Communities*, Blackwell Science, Oxford.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9: 167–224.
- Rowe, N. (1996). *The Pictorial Guide to the Living Primates*. Pogonias Press, East Hampton, New York.
- Seber, G. (1982). *The Estimation of Animal Abundance, and Related Parameters*. Macmillan, New York.
- Siegel, S., and Castellan, N. J. (1988). *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Siex, K., and Struhsaker, T. (1999) Ecology of the Zanzibar red colobus monkey: Demographic variability and habitat stability. *Int. J. Primatol.* 20: 163–192.
- Skorupa, J. (1986). Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. In Benirschke, K. (ed.), *Primates: The Road to Self-Sustaining Populations*. Springer-Verlag, New York, pp. 57–70.
- Skorupa, J. (1988). *The Effects of Selective Timber Harvesting on Rain-Forest Primates in Kibale Forest, Uganda*. Ph.D. thesis, University of California, Davis, California.
- Struhsaker, T. (1975). *The Red Colobus Monkey*. University of Chicago Press, Chicago.
- Struhsaker, T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In Chivers, D., and Herbert, J. (eds.), *Recent Advances in Primatology*. Academic Press, London, pp. 225–248.
- Struhsaker, T. (1997). *Ecology of an African Rain Forest*. University Press of Florida, Gainesville.
- Struhsaker, T. (in press). Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In Kappeler, P. (ed.), *Primate Males*. Cambridge University Press, Cambridge.
- Struhsaker, T., and Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav. Ecol. Sociobiol.* 26: 435–443.
- Struhsaker, T., and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv. Study Behav.* 9: 159–228.
- Struhsaker, T., and Leland, L. (1988). Group fission in redtail monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. In Gautier-Hion, A., Bourliere, F., Gautier, J. P., and Kingdon, J. (eds.), *A Primate Radiation: Evolutionary Biology of the Guenons*. Cambridge University Press, Cambridge, pp. 364–388.
- Whitesides, G., Oates, J., Green, S., and Kluberanz, R. (1988). Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *J. Anim. Ecol.* 57: 345–367.