

## Understanding long-term primate community dynamics: implications of forest change

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**Abstract.** Understanding the causes of population declines often involves comprehending a complex set of interactions linking environmental and biotic changes, which in combination overwhelm a population's ability to persist. To understand these relationships, especially for long-lived large mammals, long-term data are required, but rarely available. Here we use 26–36 years of population and habitat data to determine the potential causes of group density changes for five species of primates in Kibale National Park, Uganda, in areas that were disturbed to varying intensities in the late 1960s. We calculated group density from line transect data and quantified changes in habitat structure (cumulative diameter at breast height [dbh] and food availability [cumulative dbh of food trees]) for each primate species, and for one species, we evaluated change in food nutritional quality. We found that mangabeys and black-and-white colobus group density increased, blue monkeys declined, and redtails and red colobus were stable in all areas. For blue monkeys and mangabeys, there were no significant changes in food availability over time, yet their group density changed. For redtails, neither group density measures nor food availability changed over time. For black-and-white colobus, a decrease in food availability over time in the unlogged forest surprisingly coincided with an increase in group density. Finally, while red colobus food availability and quality increased over time in the heavily logged area, their group density was stable in all areas. We suggest that these populations are in nonequilibrium states. If such states occur frequently, it suggests that large protected areas will be required to protect species so that declines in some areas can be compensated for by increases in adjacent areas with different histories.

*Key words:* forest change; group density; Kibale National Park, Uganda; nonequilibrium; population dynamics; primate community; primate diets.

### INTRODUCTION

Conservation threats are typically considered in terms of readily apparent factors such as habitat loss and degradation (Cowlishaw 1999, Chapman and Peres 2001, Kerr and Deguise 2004) and overhunting (Caughley 1994, Oates 1996, Balirwa et al. 2003). However, animal populations are declining not only in disturbed habitats, but in protected areas and pristine habitats as well (Twinomugisha and Chapman 2007). When declining populations are considered in detail, it often becomes apparent that they are associated with a complex set of interactions involving environmental changes, which in combination overwhelm a population's ability to persist (Czech et al. 2000). The complexity of these interactions arises from nonequilibrium states, nonlinear biotic interactions, demographic

anomalies, and complex evolutionary histories, among other factors (Connell and Sousa 1983, Sinclair and Byrom 2006). It is only by understanding the nature of these interactions that it will become possible to make meaningful predictions concerning population or ecosystem change beyond what is intuitively obvious (e.g., populations will decline if they are overharvested).

Understanding the complexity of these interactions is often difficult because both a community of organisms and their habitat must be monitored over a biologically meaningful time frame. This is difficult to accomplish for long-lived species because the time frame over which populations change is often longer than the career of a single researcher. Consequently, there are few long-term studies documenting changes in habitat composition and structure and even fewer documenting the associated changes in animal populations because demographic responses to habitat change may not be observed for several years following disturbance.

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Here we use data collected over 26–36 years to determine the population dynamics of five species of primates in Kibale National Park, Uganda, in relation to changes in habitat structure and food availability. Kibale has a long history of primate research and substantial information is available for a number of species. Line transect censuses were initiated in the 1970s to monitor primate biomass and have been replicated several times (Struhsaker 1970–1975, Skorupa 1980–1981, Chapman 1996–1997) using identical methods and trails. Detailed, long-term habitat quantification data are also available for both primary and disturbed areas of the park (Chapman et al. 2000). We established vegetation monitoring plots in 1989 and have repeatedly measured species composition and tree size structure in these plots since that time. Using these data, we here compile a long-term assessment of the variation in Kibale primate and tree communities through time and space. We use diet records from primate behavioral studies to identify important food resources so that we can examine the relationships between dynamics in group density and food availability and, for one species, food quality. Finally, we take advantage of Kibale's known history of disturbance, because it provides the conditions necessary to examine the complex species–habitat interactions that may influence population declines and lead us to uncover cause-and-effect relationships within the system.

## METHODS

### *Study site*

Kibale National Park (795 km<sup>2</sup>) is located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the foothills of the Ruwenzori Mountains (Struhsaker 1975, 1997). Kibale is a mid-altitude, moist-evergreen forest receiving 1698 mm of rainfall annually (1990–2008). Currently, this area receives ~300 mm more rainfall per year than it did at the start of the 20th century. Furthermore, Kibale is now experiencing less frequent droughts, an earlier onset of the rainy season, and a 4.4°C increase in average maximum monthly temperature over the last 40 years (Struhsaker 1997, Chapman et al. 2004b; C. A. Chapman and L. J. Chapman, unpublished data). These changes are much greater than global averages (but see Altmann et al. [2002] for a similar example from East Africa).

Kibale was gazetted a forest reserve in 1932 and became a national park in 1993. As a forest reserve, the area was managed to continuously produce hardwood timber through a 70-year polycyclic felling program that was focused on harvesting trees over 1.52 m in girth and that opened the canopy by ~50% (Osmaston 1959, Kingston 1967). The Kanyawara region of Kibale has been protected from forest extraction since the 1970s, and hunting of primates ceased in the early 1960s. However, the history of logging has led to varying degrees of disturbance within the park. This study was conducted in three forest compartments (K-14, K-15,

and K-30) all within the Kanyawara study site, two of which were logged to different intensities in the late 1960s and one that was not logged.

The K-15 forest compartment is a 347-ha section of forest that experienced high-intensity selective felling from September 1968 through April 1969. Total harvest averaged 21 m<sup>3</sup>/ha or ~7.4 stems/ha (Skorupa 1988, Struhsaker 1997), and incidental damage was high. It is estimated that logging and incidental damage together destroyed ~50% of all trees (Skorupa 1988, Chapman and Chapman 1997). Eighteen tree species were harvested, with nine species contributing >95% of the harvest volume. Many of the harvested species were primate food trees, increasing the likelihood that primate populations would be affected. For example, the nine species that contributed >95% of the harvest volume were all red colobus (*Procolobus rufomitratu*s) food trees (Skorupa 1988, Struhsaker 1997).

Forestry compartment K-14, a 405-ha forest block, experienced low-intensity selective logging from May through December 1969 (averaging 14 m<sup>3</sup>/ha or ~5.1 stems/ha). Twenty-three tree species were harvested, with nine species accounting for 94% of before-harvest volume. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa 1988, Struhsaker 1997). Logging in this compartment was spatially heterogeneous, with some areas being logged heavily while other areas were largely untouched (Chapman and Chapman 2004).

Forestry compartment K-30 is a 282-ha area that has not been commercially harvested and is connected to other unlogged areas. Prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pit sawyers, but this extremely low level of extraction has had little impact on forest structure (Skorupa 1988, Struhsaker 1997). Hence, compartment K-30 serves as a control plot for some of our comparisons, and we make the assumption that all differences in forest structure between K-30 and the logged compartments are due to logging. Although there can be naturally occurring variation in forest structure, we believe that in this case it will be minor, because the compartments are arranged immediately adjacent to one another (see map in Struhsaker 1997) and because there are few clear differences between the compartments in terms of the physical characteristics known to influence forest structure (e.g., slope), with the exception that K-15 has more swamp than K-30, which may be important because black-and-white colobus (*Colobus guereza*) have been found to be more abundant near swamps (Struhsaker 1997).

### *Analytical approach*

Since the effect of logging can be variable and site specific (Johns 1987, 1988, 1992), to evaluate spatial and temporal variation in the system, we first examined variation in primate group density across forest compartments and through time. Second, we quantified the

habitat characteristics that might be associated with the documented changes, including forest tree structure and the availability of food for each primate species. Third, we used our detailed long-term data on red colobus monkeys to refine our analyses by incorporating the effects of compartment-specific diets and by determining whether the nutritional quality of the habitat varied significantly among forestry compartments and through time. Finally, we compared the primate and habitat data sets to evaluate whether changes in group density could be attributed to changes in forest structure and food availability.

#### Primate group density

Primate population dynamics were assessed by determining group density (number of groups per square kilometer) based on line transect census methods. Primate species included in the study were redbellied monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*), red colobus (*Procolobus rufomitratus*), and black-and-white colobus (*Colobus guereza*). Line transect methods are thought to be appropriate for estimating densities of large-bodied diurnal species such as these (National Research Council 1981). Primate censuses were conducted in all of the forestry compartments from February 1980 to December 1981 (J. P. Skorupa), from July 1996 to June 1997 (C. A. Chapman, S. Balcomb, and field assistants), and from July 2005 to June 2006 (C. A. Chapman and field assistants) and in the unlogged forestry compartment from August 1970 to October 1976 (T. T. Struhsaker). In total we walked 283 transects covering 1104 km. In the census we used the same methods, walking the exact same census route each year, and the last two censuses were conducted by the same observers.

A variety of methods have been proposed for estimating animal density, but considerable controversy exists regarding their accuracy (Burnham et al. 1980, Chapman et al. 1988, Skorupa 1988, Struhsaker 1997, 2002, Marshall et al. 2008). We used a modified Kelker (1945) method, and we tested for a difference in sighting distance (ANOVA) to the first animal seen among species. If the sighting distances did not differ among species, we used all sighting distances (plotted at 10-m intervals) to determine a cutoff rule to evaluate transect width. Sighting distance was calculated for each habitat, and we used a 50% cutoff rule to select the sighting distance. If  $X_i$  is the number of sightings in distance class  $i$  for a given species, the last distance considered was at the end of the first class such that  $X_{i+1}/X_i$  and  $X_{i+2}/X_i$  were both equal to 0.50 or less. We used the animal-to-observer sighting distance (A–O), rather than perpendicular distance, because empirical data indicate that perpendicular distance underestimates transect width for forest-dwelling primates (National Research Council 1981, Chapman et al. 1988, Whitesides et al. 1988, Struhsaker 1997, Teelen 2007; but see Plumptre and Cox [2006] for a different perspective). Thus, the density of

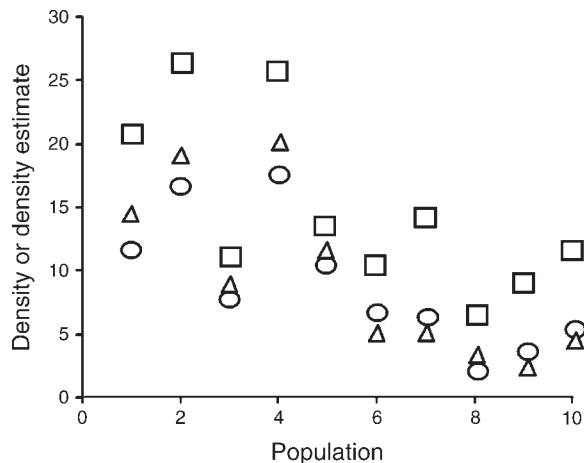


FIG. 1. Density or density estimates for 10 populations of primates for which actual density has been calculated from observation of home range size and overlap (triangles) and transects have been used to calculate density (group or individual) based on animal-to-observer distance (circles) or perpendicular distance (squares). See original publications for the detail of the methods (i.e., units for group or individual density, midpoint in range used or not; Chapman et al. 1988 [population 1, *Cebus capucinus*; population 2, *Alouatta palliata*], Struhsaker 1997 [population 7, *Procolobus rufomitratus*; population 8, *Colobus guereza*; population 9, *Cercopithecus mitis*; population 10, *C. ascanius*], Fashing and Cords 2000 [population 5, *Colobus guereza*; population 6, *Cercopithecus mitis*], Hassel-Finnegan et al. 2008 [population 3, *Hylobates lar*; population 4, *Trachypithecus phayrei*). The studies were conducted in Kibale National Park, western Uganda.

groups was calculated as the number of groups sighted within the truncated animal-to-observer sighting distance divided by the area sampled (length of the census route  $\times$  width). Empirical data support the use of A–O estimates. Based on a number of studies from 10 primate species (Struhsaker 1975, 1997, National Research Council 1981, Chapman et al. 1988, Fashing and Cords 2000, Hassel-Finnegan et al. 2008) that contrasted actual density derived from long-term records of home ranges and density estimates derived from A–O estimates and perpendicular distance (see Marshall et al. [2008] for a discussion of census methods for primates), the A–O estimate overestimated density for six of the 10 species and underestimated it in four of the 10 species, while for all species the perpendicular estimates overestimated the actual density, often by  $>100\%$  (mean percentage over =  $104\%$ ; Fig. 1). Both methods were related to actual density (A–O,  $r^2 = 0.97$ ,  $P < 0.001$ ; perpendicular,  $r^2 = 0.92$ ,  $P < 0.001$ ), but the slope for perpendicular distance was 4.1 to 1, while that of A–O distance was 1.73 to 1.

We used the same census techniques in each time period. Identical census routes were typically walked once every two weeks in each compartment in all periods (Table 1). Censuses were conducted between 07:00 and 14:00 at a speed of  $\sim 1$  km/h. Data collected for all census periods (except 1970–1974) included primate

TABLE 1. Characteristics of primate census routes used at Kibale National Park, Uganda.

Logging status and year	Route length (km)	No. census walks	Census length (km)
Unlogged			
1970–1976	4.0	61	245
1980–1981	4.0	28	112
1996–1997	4.0	25	100
2005–2006	4.0	22	88
Lightly logged			
1980–1981	3.6	27	97.2
1996–1997	3.6	23	82.8
2005–2006	3.6	23	82.8
Heavily logged			
1980–1981	4.0	26	104
1996–1997	4.0	24	96
2005–2006	4.0	24	96

species observed, time of observation, straight-line distance between the animal and observer (visually estimated), and mode of detection. Solitary individuals were recorded, but excluded from the analysis. During the 1970–1974 censuses, estimating strip width was not consistent, and consequently, censuses during this time period are not used in calculations of group density (45 census walks), but data from 1975 and 1976 were used. At the beginning of the 1996–1997 and 2005–2006 studies, observers trained together to estimate observer-to-animal distance. Variation between observers in sighting estimates was assessed at the end of the study and was determined to be acceptable ( $\pm 4\%$  or less across distances up to 50 m).

We did not take group spread into account because the assumption of circular group spread is often violated (Struhsaker 1997, 2002), and the reported group spread from Kibale varies tremendously (for blue monkeys, 0–120 m; for mangabeys, 5–480 m; summarized in Struhsaker and Leland [1979]; for red colobus, 50–1000 m; C. A. Chapman and T. V. Snaith, *unpublished data*). Group spread also changes seasonally and by time of day and thus should not be incorporated in density estimations (Plumptre 2000). Not accounting for group spread overestimates density since groups with centers outside the cutoff distance are still included if the first individual seen was inside limits (peripheral animals have a greater probability than center animals to be the first individual seen [Fashing and Cords 2000]). However, such overestimates are unlikely to alter the relative change we document among time periods or forestry compartments, since the same method was used in each time period and habitat. Also, group spread is not just highly variable, but the distribution is highly skewed, such that the median and mean estimates will probably give wildly divergent answers. Thus, a researcher would need to have a large sample size of group spread estimates in each time period and in each habitat to demonstrate that group spread is equal among compartments and does not change over time.

Skorupa (1988) observed a group of red colobus that subdivided into subgroups in K-15 and speculated that this might occur more frequently in the logged areas (see also Struhsaker 1997). Group fissioning has since been documented in K-14 and K-30, but it is still not known whether the frequency of fissioning differs among logging compartments. We thus make no attempt to account for this phenomenon in our census estimates. We calculated transect width to standardize the area sampled and the sighting distances of different observers at different time periods that might be caused by changes in visibility due to logging or regeneration. However, this method does not correct for inter-observer variation in estimating distances, and we were unable to assess this bias for the earliest census periods. We reanalyzed the raw data for each sample period using identical methods, thus the group density estimates here differ from previously published estimates for which methods differ (e.g., Skorupa [1988] corrected sighting distance for average group spread).

#### *Habitat characteristics*

We established 26 permanent vegetation plots in December 1989. Each plot was  $200 \times 10$  m, providing a sampling area of 5.2 ha. Plots were placed randomly within the existing trail system. Twelve plots were placed in unlogged forest (K-30; initial number of trees/plot =  $97 \pm 6.3$  trees [mean  $\pm$  SE]), nine plots in lightly logged forest (K-14;  $73 \pm 3.7$  trees), and five plots in the heavily logged area (K-15;  $59 \pm 9.5$  trees). Each tree with diameter at breast height (dbh, measured at 1.2 m above ground level)  $\geq 10$  cm within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (dbh). This provided an initial sample of 2111 trees.

Plots were resurveyed in May 2000 and September–November 2006. All tagged trees were located and remeasured to assess growth, and trees recruiting into the size class of dbh  $\geq 10$  cm were identified and tagged. Mortality was noted and, when possible, the cause of death evaluated. We calculated the cumulative dbh of trees in each plot. Diameter at breast height has been found to vary reliably with both fruit crop size and leaf biomass, is practical and easy to measure, and has low inter-observer error (Harrington 1979, Catchpole and Wheeler 1992, Chapman et al. 1992, 1994, Brown 1997).

It is likely that primate populations are more strongly influenced by changes in the abundance of tree species that produce food items than by the overall abundance of all trees. Kibale is an unrivaled location because a large number of studies have been conducted on the foraging behavior of its primates and we could rely on published diet data or raw data available. We used these data to determine what should be considered to be food for each primate species. We included foods (i.e., a specific part from a particular species) that constituted  $\geq 4\%$  of the time spent feeding reported by Rudran (1978) and Butynski (1990) for blue monkeys, by Waser



(1975) and Olupot (1994) for mangabeys, by Harris and Chapman (2007) and Oates (1977) for black-and-white colobus, by K. D. Rode et al. (2006, *unpublished data*) and C. M. Stickler (2004, *unpublished data*) for redtails, and by C. A. Chapman and L. J. Chapman (2002, *unpublished data*) and by Struhsaker (1975) for red colobus. We chose the 4% cutoff because it included specific food items that were consistently considered important by previous researchers studying these species in this area and our team, while avoiding incorporating large numbers of rarely used species (Table 2). Using the vegetation plot data, we estimated the cumulative dbh of food trees in each area, for each primate species, at each time period.

#### *Red colobus food availability and quality*

We used our long-term red colobus data set to further explore issues between changes in group density and food resource availability and to examine three limitations of the analysis done with all species. First, to test the validity of the 4% cutoff rule for defining food items, we reran the analysis for red colobus using a 1% cutoff. This did not produce different results than using the 4% cutoff.

Second, we addressed the possibility that because some of the foraging data sets were collected from only one or a few groups and/or in restricted areas of the forest, the foods lists might not be representative of other groups in other areas. We used red colobus foraging data that were collected from groups using each of the different logging compartments, produced compartment-specific 1% cutoff food lists, calculated the cumulative dbh of these foods in the appropriate compartments, and repeated all analyses. Details of red colobus foraging data can be found in Chapman et al. (2006a).

Third, the above analyses examines the effect of the quantity of food available to primates; however, our previous research has demonstrated that it is important to consider both the quantity and the quality of available food when considering the ecological determinants of colobus population size (Chapman and Chapman 2002, Wasserman and Chapman 2003, Chapman et al. 2004a). We thus incorporated data on the nutrient composition of items used by red colobus to examine habitat quality (Chapman and Chapman 2002, Chapman et al. 2002, 2004a). We used the protein: fiber ratio as an index of food quality because it has been found to be a good predictor of folivore leaf choice (Milton 1979) and biomass (Waterman et al. 1988, Oates et al. 1990, Chapman and Chapman 2002, Chapman et al. 2002, 2004a, Ganzhorn 2002). These relationships have been demonstrated using the overall protein: fiber ratio of mature leaves in an area. However, because young leaves constitute a large portion of the red colobus diet, we ran the analysis twice, to measure the effect of the protein: fiber ratio of both mature and young leaves. For further discussion of

the application of the protein: fiber ratio see Chapman et al. (2004a). Details of sample collection, processing, and the determination of protein and fiber can be found in Chapman and Chapman (2002). To incorporate the effect of food quality, we weighted our dbh measures by the protein: fiber ratio of both young and mature leaves of species constituting  $\geq 4\%$  of total feeding time.

#### *Statistical comparisons*

We calculated group density of each primate species for each time the census route was sampled and used these as independent sample points. To test the significance of spatial and temporal variation in primate populations, we compared repeat samples of group density across compartments and years. Nonparametric Kruskal-Wallis tests were used when there were three compartments or time periods to compare. When significant differences were detected, post hoc Mann-Whitney tests were used to determine which pairs of categories differed (Day and Quinn 1989). These statistics are presented in Fig. 2.

Statistical analyses of changes in forest composition and food availability were conducted in a similar fashion: we calculated the cumulative dbh of each species for each vegetation plot and used these as independent sample points. However, because the vegetation data met the assumptions of parametric statistics, repeated-measures ANOVA tests were used to test the significance of temporal (among years) and spatial (among compartments) variation and their interactions. Following Potvin et al. (1990), Mauchly's criterion was used to test for the compound symmetry of the variance-covariance matrix. When the criterion was rejected, the Greenhouse-Geisser test, which relaxes the symmetry assumption, was used to obtain corrected significance levels (Potvin et al. 1990). Statistical evaluation of whether changes in group density were related to changes in the size and density of food trees was not possible due to sample size constraints. However, we present a qualitative discussion of how the variation in group density trends corresponds to habitat variation.

## RESULTS

### *Primate group density*

The group density of blue monkeys and mangabeys exhibited significant changes over the 26–36 years of our monitoring; blue monkey populations decreased, while mangabey numbers increased. These changes were generally consistent across compartments, regardless of the logging history (Fig. 2). In contrast, redtail and red colobus group density remained fairly stable over time in all areas. Black-and-white colobus group density increased significantly across all three forestry compartments.

The number of sightings of blue monkeys was generally low and analyses lack statistical power (Fig. 2). However, in general, blue monkey group density was

TABLE 2. Species-specific food items constituting  $\geq 4\%$  of the total reported diet of five primate species from Kibale National Park, Uganda.

Plant species	Plant part eaten	<i>Cercopithecus mitis</i> †	<i>Lophocebus albigena</i> ‡	<i>Cercopithecus ascanius</i> §	<i>Colobus guereza</i> ¶	<i>Procolobus rufomitratus</i> #
<i>Albizia grandibracteata</i>	leaves	...	...	...	6	...
		.../...	...	...	...	...
<i>Blighia unijugata</i>	fruit	...	...	...	...	...
		.../...	...	4.8	...	...
<i>Celtis africana</i>	fruit	4.1	...	...	...	...
		6.6/6.8	...	...	...	...
<i>Celtis africana</i>	leaves	...	...	...	4.8	7.6
		.../...	...	...	...	8.1
<i>Celtis durandii</i>	fruit	...	12.4	23.1	...	...
		4.1/5.2	6.3	5.8	...	...
<i>Celtis durandii</i>	leaves	...	...	...	34	21.3
		.../...	...	...	...	7.2
<i>Croton macrostachys</i>	fruit	...	4.3	...	...	...
		.../...	...	...	...	...
<i>Diospyros abyssinica</i>	fruit	...	6.2	8	...	...
		.../...	22.6	27.4	...	...
<i>Diospyros abyssinica</i>	leaves	4.8	...	...	...	...
		.../...	...	...	...	...
<i>Dombeya mukole</i>	leaves	...	...	...	...	7.5
		.../...	...	...	...	...
<i>Ficus brachylepis</i>	fruit	...	4.2	...	...	...
		4.9/...	6.1	...	...	...
<i>Ficus exasperata</i>	fruit	...	4.6	...	...	...
		.../11.2	...	...	...	...
<i>Funtumia latifolia</i>	leaves	...	...	...	...	8.2
		.../...	...	...	...	8.9
<i>Linociera johnsonii</i>	fruit	...	...	13.1	...	...
		.../...	...	4	...	...
<i>Macaranga schweinfurthii</i>	fruit	...	...	4.2	...	...
		.../...	...	...	...	...
<i>Markhamia lutea</i>	leaves and petioles	8.8	...	...	4.4	9
		.../...	...	...	...	...
<i>Pancovia turbinata</i>	fruit	...	...	...	...	...
		6.6/...	4.1	...	...	...
<i>Parinari excelsa</i>	fruit	...	...	...	...	...
		.../...	...	6.7	...	...
<i>Parinari excelsa</i>	leaves	...	...	...	...	6.7
		.../...	...	...	...	8.1
<i>Premna angolensis</i>	flowers	...	...	...	...	...
		4.3	...	...	...	...
<i>Prunus africana</i>	leaves	...	...	...	11.8	4.1
		.../...	...	...	...	17.2
<i>Symphonia globulifera</i>	flowers	...	...	...	...	...
		.../...	...	6.7	...	...
<i>Teclea nobilis</i>	fruit	...	...	...	...	...
		5.3/...	...	...	...	...
<i>Trilepsium</i> sp.	leaves	...	...	5.7	...	7.8
		.../...	...	...	...	4.1
<i>Uvariopsis congensis</i>	fruit	...	...	...	...	...
		5.3/8.5	...	...	...	...

Note: Ellipses indicate that the particular plant species and part was not eaten for  $>4\%$  of that primate species' foraging time.

† For each specific food item for *Cercopithecus mitis*, the data in the first line are from Butynski (1990), and these values are the averages of study groups 1–4. The data in the second line are from Rudran (1978), and the values are for groups 1 and 2, respectively, separated by a solidus.

‡ For *L. albigena*, Olupot (1994) and Rudran (1978) reported percentages of vegetable diet. Their data have been recalculated as percentages of total diet. The order of sources is constant, with Butynski (1990) and Olupot (1994) above and Rudran (1978) and Waser (1975) below for all foods for *L. albigena*.

§ For *Cercopithecus ascanius*, the data are from Stickler (2004); the first line is for unlogged, and the second is for heavily logged forest.

¶ For *Colobus guereza* we present the mean of six groups from Harris and Chapman (2007).

# For *P. rufomitratus* the data are from Chapman and Chapman (2002); the first line is for a large group, and the second line is for a small group.

greatest in the unlogged forest, followed by the lightly logged forest, and they were lowest in the heavily logged area. These differences were significant in 2006 and occasionally significant prior to this. For mangabeys,

the group density in the unlogged forest and the lightly logged forest did not differ, but group density was lower in the heavily logged forest. For redbellied monkeys, group density generally suggests that their populations were

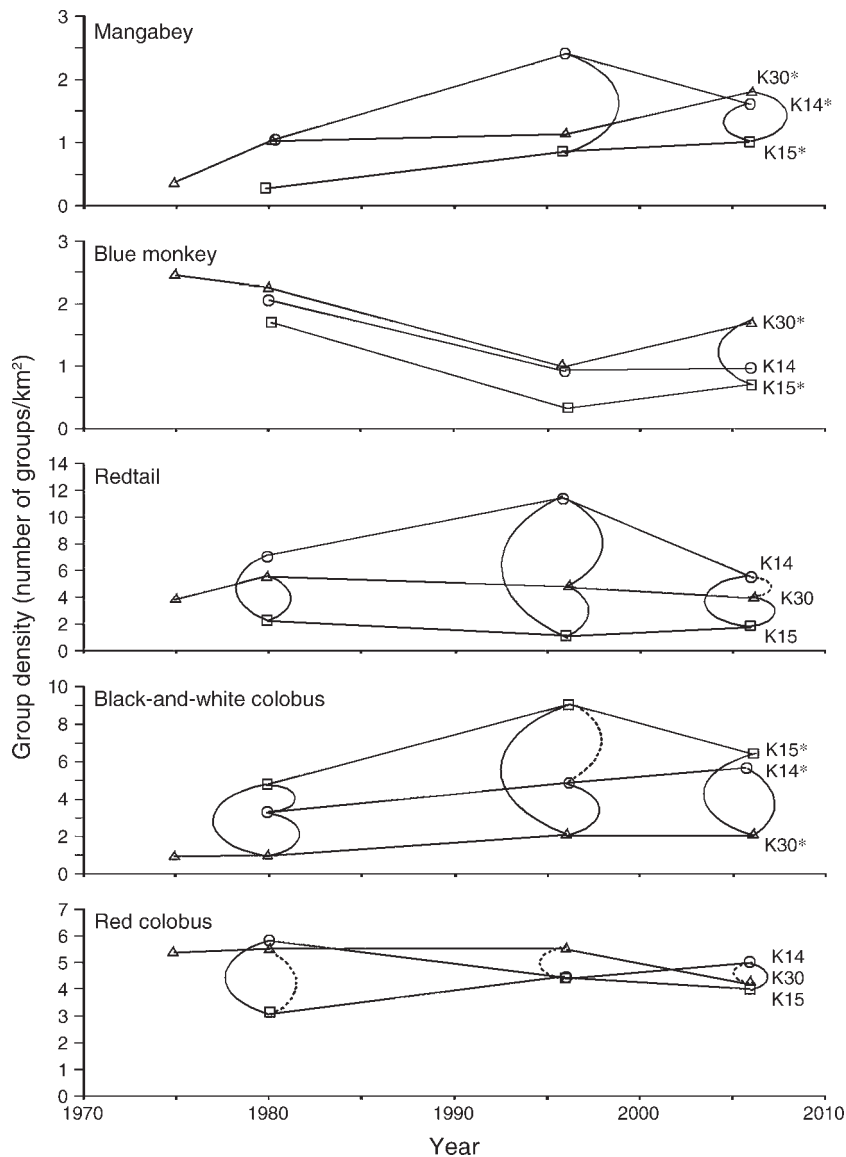


FIG. 2. Group density of the five common diurnal primates in Kibale National Park (K-30, unlogged forest; K-14, lightly logged forest; K-15, heavily logged forest) over 26–36 years. An asterisk indicates that there is a significant ( $P < 0.05$ ) change in density from the first estimate to the last estimate within a compartment; curved lines connecting forestry compartments indicate a significant ( $P < 0.05$ ) difference in group densities between areas differing in logging history (solid lines) or a marginal difference (dashed lines).

larger in the lightly logged forest than the unlogged area, and they did poorly in the heavily logged areas. These differences were significant in most time periods, although the difference between lightly logged and unlogged forest only developed after 1980. Black-and-white colobus group density was greatest in the heavily logged area, followed by the lightly logged area, and was lowest in the unlogged area (Fig. 2); these results were significant in each time period. Red colobus group density was initially greater in the unlogged and lightly logged areas than the heavily logged area, but the difference became less marked over time.

*Habitat characteristics*

To test the importance of spatial (among compartments) and temporal (across years) variation in forest structure, we compared repeat samples of the cumulative dbh of trees along the transects that had been repeatedly sampled. In a repeated-measures ANOVA the effects of forestry compartment ( $P = 0.018$ ) and time ( $P = 0.001$ ) were significant (Fig. 3). However, the interaction among these factors was not ( $P = 0.260$ ), indicating that the three sites showed the same trends in increasing dbh over time. This is a surprising result as a significant interaction would have been expected if there was major

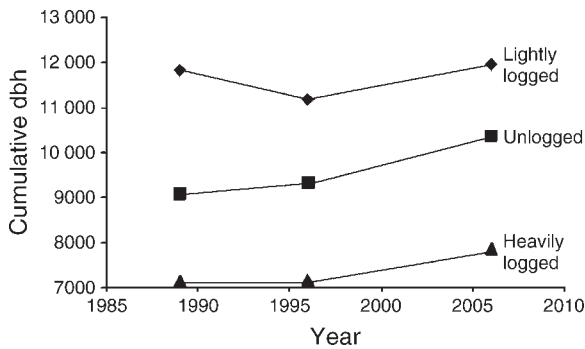


FIG. 3. Change in the cumulative diameter at breast height (dbh) of trees on vegetation plots in areas that differed in their history of logging.

forest regeneration in the logged areas and a stable situation was found in the unlogged area. Separate repeated-measures ANOVAs on each compartment were used to identify time periods in which the change in cumulative dbh was significant (Fig. 3). In the unlogged area there were fluctuations, but no significant change between the first and last sampling periods was documented in cumulative dbh. In addition, counter to what would be expected if the heavily logged area was regenerating from the disturbance caused by logging, there was no significant change in cumulative dbh between the first and last sampling period in the heavily logged area. We used similar analyses to determine whether there were habitat differences across compartments within each time period (Fig. 3). No compartment effects were found.

It seems more likely that primate populations would be more strongly influenced by changes in the abundance of tree species that produce food items, rather than all trees. Thus, we turned to the literature and to unpublished data to determine species-specific lists of food trees and the proportion of time spent eating from each species (Table 2). There was no significant effect of time, compartment, or their interaction ( $P > 0.121$  in all cases) for blue monkeys, mangabeys, redtails, or black-and-white colobus (although there was a weak trend for an interaction effect [ $P = 0.075$ ] for black-and-white colobus in which the cumulative dbh of food trees decreased over time in the unlogged forest, but not in other areas). For red colobus there was a significant effect of time ( $P = 0.002$ ), but not compartment ( $P = 0.339$ ). Separate repeated-measures ANOVAs for red colobus for each compartment indicated that food tree availability increased in the heavily logged area ( $P = 0.002$ ) and increased marginally in the lightly logged area ( $P = 0.090$ ), but remained unchanged in the unlogged forest ( $P = 0.312$ ). It should be noted that for some of these primates food tree species may have declined prior to this study, and, given the time lag between environmental change and primate population change (Struhsaker 1976), primate populations may have been responding to earlier changes in food tree

abundance. For example, Struhsaker et al. (1989) documented declines in *Newtonia buchananii*, *Lovoa swynnertonii*, and *Aningeria altissima* in the mid-1980s, and all of these species were important food species for red colobus.

#### *Red colobus food availability and quality*

When all species eaten for  $>1\%$  of the feeding time were included, we again found a significant effect of time ( $P < 0.001$ ), but not compartment ( $P = 0.734$ ) on changes in the cumulative dbh of food trees. Separate analyses for each compartment similarly indicated that the cumulative dbh of food trees increased in the heavily logged area ( $P = 0.003$ ) and in the lightly logged area ( $P = 0.008$ ), but not in the unlogged forest ( $P = 0.191$ ).

When we incorporated the protein: fiber ratio of young leaves into the measure of food availability, we found a marginal effect of time ( $P = 0.072$ ) and no compartment effect ( $P = 0.575$ ). The individual analyses by compartment indicated that there was an increase in the availability of high-quality foods in the heavily logged forest ( $P < 0.001$ ), but not in the lightly logged ( $P = 0.633$ ) or unlogged forest ( $P = 0.613$ ). The same pattern was revealed using the protein: fiber ratio of the mature leaves.

#### *Primate responses to habitat change*

For blue monkeys and mangabeys, there were no significant changes in food tree cumulative dbh, yet the group density of these primates was changing. For redtails, neither group density nor cumulative dbh of food trees changed over time. For black-and-white colobus monkeys, a decrease in food tree cumulative dbh over time in the unlogged forest surprisingly coincided with a possible increase in group density. Finally, while red colobus food tree cumulative dbh and food quality increased over time in the heavily logged area, their group density did not show a corresponding increase in this area. In the lightly logged forestry compartment, red colobus group density was stable and it was not related to a change in food availability.

#### DISCUSSION

We used 26–36 years of monitoring data to examine whether temporal and spatial variation in food resources contributes to predictable changes in primate population dynamics. The picture that emerges is complex. Our comparisons among areas that have been logged to different intensities largely confirm previous findings (Struhsaker 1975, 1997, Skorupa 1988, Chapman et al. 2000) that the three frugivores were found at lower group density in the heavily logged areas, while the folivorous black-and-white colobus occur at a high group density in these areas. We found no difference in the folivorous red colobus group density between the unlogged and the heavily logged areas. Most species were doing well in the lightly logged area. Data on groups seen per kilometer walked are available; this



measure can vary from group density (Chapman et al. 2000).

This study suggests that in Kibale forest low-intensity selective logging could be compatible with the conservation of primates; however, high-intensity logging, which is typical for most logging operations throughout Africa and elsewhere, is not. Following the assumption that forests should be recovering after logging, primate group density should converge over time across logging compartments, but in a number of situations they did not (e.g., blue monkey or black-and-white group density). Our finding that there was no significant interaction between time and forest compartment suggests that the logged areas were not regenerating as expected. In fact, the change in cumulative dbh between 1995 and 2005 appears to be very similar among all three forest areas (Fig. 3).

Surprisingly, we found little evidence to suggest that the changes in population size over time or differences among forestry compartments were related to differences in food availability. For redtails, blue monkeys, and mangabeys, there was no significant affect of time, compartment, or their interaction. For black-and-white colobus, a trend suggested that food tree availability decreased over time in the unlogged forest, but not in the other areas. Paradoxically, this corresponded to a possible increase in group density. Furthermore, although red colobus food tree abundance and food quality increased over time in the heavily logged area, there was no evidence of an increase in their group density in this area.

Our results suggest that primate population changes are associated with a complex set of interactions among environmental and biotic factors; however, there are several reasons to view these findings with caution. First, this analysis does not consider temporal or spatial variability in the ability of the trees to produce food items. This should be considered in future analyses because Skorupa (1988) demonstrated that in Kibale the annual fruiting intensity was 26% lower in the heavily logged forest than in unlogged forests, and studies that have incorporated information on the availability of food items on specific trees have found differences between the heavily logged and unlogged areas (Rode et al. 2006). Second, Chapman et al. (2005) presented evidence to suggest that climate change was responsible for changing patterns of fruit production in some tree species. For this reason, changes in the density and size of food trees may not directly reflect changes in food availability. Third, it is possible that group size has changed over time, and this has not been evaluated (L. A. Isbell, *personal communication*). Finally, future research should consider the scale of vegetation sampling in relation to animal movement patterns. All members of this primate community are using areas of regenerating forest where pine plantations were removed (Chapman and Chapman 1996, Duncan and Chapman 2003). These areas of regenerating forest were not

included in the original vegetation sampling because at that time they were pine plantations. The harvesting of the plantations started in 1991. Since that time, they may have become important in determining primate abundance. Olupot et al. (1994) suggested that these regenerating areas are related to increasing mangabey numbers. However, it is not clear why only mangabey populations responded positively when other species, such as red colobus monkeys, which feed on many of the species recruiting into these regenerating areas, were not increasing in group density (C. A. Chapman and P. A. Omeja, *unpublished data*).

An elegant series of studies of blue monkeys provides clear evidence that a number of factors work in conjunction to drive population change. Based on a six-year study (1978–1984) of food production and primate feeding strategies, Butynski (1990) hypothesized that the population of blue monkeys at Ngogo in Kibale was recovering from an episodic crash due to a disease event in the past and predicted that their population would soon grow. Continued monitoring of this population has found the opposite; blue monkey populations have been declining at this site (Mitani et al. 2000). Based on information on the history of the forest, Mitani et al. (2000) suggested that this decline reflects the fact that the Ngogo primate community represents a nonequilibrium system and that blue monkeys are being out-competed by old-growth specialists, such as mangabeys, as Kibale continues to recover from decades or centuries of human disturbance. Although much of Kibale is considered to be old-growth forest, there is evidence of human disturbance that may have occurred 70–100 or more years ago. Kibale National Park obtained its first legal status in 1932, but the first detailed descriptions of the area were not made until the late 1950s (Osmaston 1959), and these describe how people were moved out of the area to facilitate its management. Pollen diagrams from the Ruwenzori Mountain Lakes (Livingstone 1967) and Kigezi in southwestern Uganda (Hamilton 1974, Hamilton et al. 1986) suggest extensive forest clearance by humans ~1000 years ago. Furthermore, a number of pits for storing grain and an array of potsherds have been discovered in what has traditionally been considered undisturbed forest (Lang Brown and Harrop 1962, Mitani et al. 2000). It seems likely that human activities have altered African forest composition for a considerable period of time. Blue monkeys are considered to be generalists that do not compete well with old-growth specialists, such as mangabeys (Struhsaker 1978, Lawes 1991), and Struhsaker (1978) suggested that the density of blue monkey groups was negatively correlated with mangabey density. Interestingly, here we found that mangabey numbers increased, while blue monkey populations decreased. Given this evidence, the decline of blue monkeys suggests that this primate community is in a nonequilibrium state and that blue monkeys are at an increasing competitive disadvantage as the forest

recovers (Mitani et al. 2000). It should be noted that this explanation is called into question because of the suggestion that mangabey populations (the old-growth specialist) are suggested to be increasing because they are using the regenerating areas, while blue monkey populations (the generalists) are declining and rarely use the regenerating areas (C. A. Chapman and P. A. Omeja, *personal observations*).

Long-term monitoring and hypothesis-driven studies that target specific factors hypothesized to influence primate population dynamics are required to understand the complex relationships that drive intraspecific variation in species abundance. A range of environmental factors, in addition to the availability of food, have been shown to affect primate health, fecundity, and population trends. For example, the prevalence and richness of gastrointestinal helminth infections and the magnitude of multiple infections were greater for redbtail monkeys in logged areas than undisturbed forest (Gillespie et al. 2005), and such infections have been linked to increased stress levels and declines in primate populations in forest fragments (Chapman et al. 2006b). Male mangabeys in logged forests had lower body mass than males in unlogged forests (Olupot 2000), which may influence survivorship. A study of locomotion of red colobus in logged and unlogged habitats demonstrated that removing trees reduced canopy pathways and increased energetic demands, risks of falling, and perhaps predation risk (Gebo and Chapman 1995). Finally, intake of crude protein, lipids, and minerals were higher in diets consumed by redbtail groups in unlogged areas than in heavily logged areas (Rode et al. 2006), and there is evidence that redbtails and red colobus in heavily logged areas were limited by sodium availability (Rode et al. 2003, 2006).

It is difficult to evaluate the generality of our findings because there are very few long-term records of demographic trends in large mammals (Mduma et al. 1999, Sinclair et al. 2007). Like our study in Kibale, long-term study of the Serengeti ecosystem reveals that the signature of past disturbance may remain for decades to influence population dynamics. Sinclair et al. (2007) emphasize that slow changes may only be apparent after several decades and can become a irreversible shift into a new state, in which the system remains for a long period, which has consequences for both direct and indirect interactions. For example, an increase in dense cover for ambush facilitated lion-hunting success in the Serengeti, which affects the population dynamics of prey species (Hopcraft et al. 2005). Long-term monitoring of buffalo and wildebeest populations indicated that with the Rinderpest pandemic, which occurred ~120 years ago, there remain current indirect effects on vegetation, herbivores, and predators (Sinclair et al. 2007). These authors suggest conservation managers must consider that ecosystems can be in multiple states and prepare for the case in which, after disturbance, ecosystems may not return to their original

form. Often when data are sufficient, long-term researchers have similarly found large population changes or evidence of nonequilibrium systems (e.g., Serengeti megafauna, Sinclair et al. 2007; snowshoe hares, Krebs et al. 1995; Soay sheep, Coulson et al. 2001; moose, Saether et al. 1996).

It is possible to obtain data that suggest that the results we obtained from Kibale are general by examining forest history. Since the mid-1980s there has been an accumulation of evidence that forests that were traditionally considered "old growth" or "pristine" forests had been disturbed relatively recently in terms of forest regeneration (i.e., between 1000 and 4000 years ago [Clark 1996, Lejju 2009]). For example, the first paleoecological studies from the Darien of Panama, an area once perceived as the last untouched Neotropical forests, reveals a 4000-year history of human disturbance (Bush and Colinvaux 1994). *Brosimum alicastrum* is a common canopy-level tree and is believed to have been extensively planted and harvested by the Mayans centuries ago as dry-season forage. Thus, what appeared to be undisturbed forest to Neotropical ecologists was regenerating forest that was as young as 350 years old. Similar evidence, particularly from the Neotropics and the Amazon, has slowly accumulated that many forests have been disturbed in the distant past (Haberle and Ledru 2001, Anchukaitis and Horn 2005, Bush et al. 2007, Kennedy and Horn 2008).

Forest composition can also change when the animal populations that mediate seed dispersal and seedling survival are affected. Evidence indicates that large cats limit mid-size terrestrial mammals and the decline of large cat populations alters forest regeneration (Wright et al. 1994, Naughton-Treves 1999). There is evidence that the harvest in cat skins was substantial. For example, the trade of cat skins in the early 1960s from Brazil was thought to involve the annual kill of 15 000 jaguars (*Panthera onca*) and 80 000 ocelots (*Felis pardalis*). Huge areas of tropical forest are also being affected by the hunting of the large-bodied seed dispersers. This will have significant impacts on primate populations. Ironically while evidence has been available for a long time (Martin 1983), the magnitude of the impact of hunting has only been realized recently (Fa et al. 2002). For example, Chapman and Peres (2001) estimate that 3.8 million primates are consumed annually in the Brazilian Amazon. The potential significance of hunting on forest composition has been illustrated by Nuñez-Iturri and Howe (2007), who studied the composition of the juvenile tree community in hunted and nonhunted areas in Peru. In this region hunting exterminates the large primates and reduces populations of the intermediate body size by 80%. Recently there have been a number of studies demonstrating both the magnitude of change that can occur in forest composition of hunted forest and the complex nature of the change (Dirzo and Miranda 1991,

Chapman and Onderdonk 1998, Pacheco and Simonetti 2000, Dirzo and Mendoza 2007, Wright et al. 2007).

Such perturbations create the conditions necessary for the development of nonequilibrium communities in national parks and reserves. Evidence of pollen cores, the history of human alteration to forest by planting desired trees, and the widespread nature of hunting all suggest that perturbation that would create nonequilibrium states is widespread. This in turn suggests that very large protected areas will be required to protect species from nonequilibrium dynamics so that declines in some areas can be compensated for by increases in adjacent areas with different disturbance histories. The scale over which these dynamics operate will vary among species; however, for large mammals it is likely that reserves in the hundreds of square kilometers will be required to allow areas of declines to be compensated for by areas with different dynamics.

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