

Group Size Dynamics over 15+ Years in an African Forest Primate Community

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ABSTRACT

Group size affects many aspects of the ecology and social organization of animals. We investigated group size stability for five primate species in Kibale National Park, Uganda from 1996 to 2011 at three nested spatial scales. Survey data indicated that group sizes did not change for most species, with the exception of red colobus monkeys (*Procolobus rufomitratus*), in which group size increased at all spatial scales. Mangabey (*Lophocebus albigena*) group size increased in old-growth forest, but the sample size and increase were small. To augment this survey data, we collected several years of demographic data on three habituated groups of redbellied monkeys (*Cercopithecus ascanius*), eight groups of black-and-white colobus (*Colobus guerezza*), and one red colobus group. The red colobus group increased from 59 to 104 individuals, while redbellied monkey and black-and-white colobus group sizes were stable, mirroring our survey results. To understand mechanisms behind group size changes in red colobus versus stability in other primates, we monitored forest dynamics at two spatial scales between 1990 and 2013, considered changes in predator population, and explored evidence of disease dynamics. The cumulative size of all trees and red colobus food trees increased over 24 yr, suggesting that changing food availability was driving group size changes for red colobus, while predation and disease played lesser roles. Overall, our results and evidence of changing primate densities suggest that the Kibale primate community is in a non-equilibrium state. We suggest future conservation and management efforts take this into consideration.

Abstract in Swahili is available in the online version of this article.

Key words: forest dynamics; Kibale National Park, Uganda; non-equilibrium; *Procolobus rufomitratus*; red colobus; stability.

THE SIZE OF ANIMAL GROUPS CAN ALTER STRESS LEVELS (Pride 2005), SUSCEPTIBILITY TO DISEASES (Freeland 1976, Snaith *et al.* 2008), reproductive and developmental rates (Borries *et al.* 2008), individual and group behavior (Koenig 2002, Nunn *et al.* 2009), and group survival (Heg *et al.* 2005). To effectively conserve threatened species requires understanding how threats may affect group size through time. For example, the long-term viability of populations with the same number of individuals may differ based on how these individuals are distributed in groups, with smaller groups conferring different benefits and consequences

than larger groups (*e.g.*, rates of reproduction and development vary with group size; Borries *et al.* 2008). Typically, however, the average group size of non-migratory species in a region is considered relatively stable (Wrangham *et al.* 1993, Janson & Goldsmith 1995), thus it has not generally been considered in conservation planning.

Grouping confers predictable benefits (Alexander 1974, van Schaik 1983), thus differences in size can be attributed to variation in the costs of grouping (Wrangham *et al.* 1993). One such cost is foraging efficiency, which decreases with increasing group size (Janson & Goldsmith 1995). These ideas have been formalized in the Ecological Constraints Model (Wrangham *et al.* 1993, Chapman & Chapman 2000), which predicts average group size should be stable in regions with stable environments. Yet there is

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accumulating evidence that forest environments are not stable (Turner *et al.* 1993, Turkington 2009, Chapman *et al.* 2010a, Mori 2011). While non-equilibrium dynamics are a central concept in modern ecological theory (Mori 2011), their implications for group size are infrequently considered with the exception of sudden catastrophic change (*e.g.*, disease: Gulland 1992, hurricanes: Pavelka *et al.* 2003).

Kibale National Park, in Western Uganda, represents one of the few well-studied tropical forest ecosystems for which long-term data on plant and animal communities are available. Many areas of Kibale have been well-protected since the 1930s and its forest and wildlife have been intensively studied since the 1970s. Integrating this existing long-term data suggest either ecosystem stability or instability depending on the components examined and time scale considered (Mitani *et al.* 2000, Chapman *et al.* 2005, 2010a, Struhsaker 2010, Lwanga *et al.* 2011). Chapman *et al.* (2010a) analyzed changes in tree recruitment and growth over 18 yr and concluded that the old-growth forest is in a non-equilibrium state and likely recovering from a large disturbance within the last several hundred years. Similar changes in tree species composition have been recorded in other old-growth tropical forests in other areas of Africa, including Cameroon (Hawthorne 1996), Uganda (Sheil *et al.* 2000), Gabon (Tutin & Oslisly 1995), and the Republic of Congo (Brncic *et al.* 2007); these point to the influences of large- and small-scale human disturbance, fluctuating elephant populations, and climate change (Bongers *et al.* 2009). This dynamism is evident in animal populations as well. For example, the size of blue monkey groups (*Cercopithecus mitis*) from central Kibale (Ngogo) suggested that group sizes were not in equilibrium (Mitani *et al.* 2000, Angedakin & Lwanga 2011), yet another Ngogo study suggested long-term stability in group sizes of redbell monkeys (*Cercopithecus ascanius*), black-and-white colobus (*Colobus guereza*), and mangabeys (*Lophocebus albigena*; Teelen 2007).

The objective of our research was to examine group size dynamics in five species of diurnal primates over 15 yr (1996–2011) at different spatial scales. We consider: red colobus (*Procolobus rufomitratus*), black-and-white colobus, redbell monkeys, mangabeys, and blue monkeys. We also gathered detailed demographic data from one well-habituated group of red colobus, three groups of redbell monkeys, and eight groups of black-and-white-colobus observed for 6, 4, and 4 yr respectively. We explore potential explanations for changes in group size using long-term data on forest dynamics.

METHODS

STUDY SITE.—Kibale National Park (795 km²; 0°13′–0°41′ N and 30°19′–30°32′ E) is a moist-evergreen forest in western Uganda (Fig. S1). In 1932, Kibale was designated a Crown Forest Reserve; in 1993 it became a National Park. Anthropogenic disturbances created a mosaic of old-growth and regenerating forest habitats throughout the park (Struhsaker 1997, Chapman & Lambert 2000). In the late 1960s, much of northern Kibale was logged (Struhsaker 1997) including two study areas used in this

research: the 405-ha forestry compartment K14 was logged at 14 m³/ha (approximately 5.1 stems/ha) and the 347-ha compartment K15 was logged at 21 m³/ha (approximately 7.4 stems/ha). Although extraction rates for Sebatoli, a northern region of the park, are not available, stand structure indicates it was logged at similar levels to K15 (C. A. Chapman, unpubl. data). Compartment K30, immediately south of K14, is a 282-ha area that was not commercially harvested; although a few large stems (0.03–0.04 trees/ha) were cut by pitsawyers, this seems to have had little impact on the forest (Struhsaker 1997). Other areas included in this study are believed to have been similarly impacted in a minor way by pitsawyers, but have been less extensively studied.

STUDY SUBJECTS.—Our study was conducted on five co-occurring primate species, including two colobines (red colobus and black and white colobus). Colobines are considered to be predominantly folivorous, and overlap considerably in diet, with young leaves making up the majority of food eaten. However, red colobus groups are often substantially larger in size than black and white colobus groups (Chapman & Pavelka 2005) and exhibit substantial differences in tree species and parts consumed (Oates 1977, Chapman & Chapman 2002, Harris & Chapman 2007, Struhsaker 2010). We also examined three species of cercopithecin monkeys (blue monkeys, redbell monkeys, and mangabeys) that are predominantly frugivorous, although insects and young leaves also compose parts of their diet (Struhsaker 1978). At the broadest scale, we included data from two additional primate species: L'Hoest monkeys (*Cercopithecus lhoesti*) and olive baboons (*Papio anubis*). Both species relying primarily on fruit, but are more terrestrial than other five monkey species.

QUANTIFYING GROUP SIZE.—We counted primate group sizes in two periods (July 1996–May 1998 and July 2010–May 2011; $N = 268$ group counts across all scales) at three nested spatial scales: (1) unhabituated groups throughout the park (*broad scale*); (2) unhabituated and habituated groups in adjacent logged (K14 and K15) and old-growth (K30) forest (*intermediate scale*); and (3) unhabituated and habituated groups occurring only in old-growth forest (K30; *fine scale*; Fig. S1; Tables 1–3). The broad scale spanned the entire park, but centered around four locations each approximately 12–15 km apart along a north-south gradient (Fig. S1). The Kanyawara study area provided access to K14, K15, and K30 (Chapman & Chapman 1997, Struhsaker 1997). At the fine and intermediate scales, we used long-term (~24 yr) data on tree species composition and structure to explore relationships between food abundance, nutritional quality, and group size.

To obtain accurate primate group count, three observers selected a study area for 8 d per month. When a primate group was found in the designated area, we recorded the location and attempted to count all individuals. The time spent with each group was variable, but we monitored a group as long as was necessary to ensure that we were confident that the group count was accurate; the maximum time spent with a single group was 10 h. To ensure count accuracy, observers waited until the group

TABLE 1. Primate group sizes between two sampling periods across all of Kibale National Park, Uganda (broad scale).

Species	1996–1998 group counts			2010–2011 group counts			Delete-d jackknifed 1996–1998 group counts Welch		Welch two sample <i>t</i> -test ^a		
	N groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	N groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	Mean group-size (%) [*]	Percent of <i>t</i> -tests significant, %	<i>t</i>	df	<i>P</i>
Baboon	6	28.49	13.75–48.55	3	32.66	29.87–35.58	28.73 (34.0)	0.00	0.59	5.08	0.58
Blue monkey	11	9.31	6.08–13.23	3	10.60	1.76–26.89	9.50 (32.3)	0.00	0.39	3.53	0.72
Black and white colobus	61	8.22	7.41–9.08	27	7.84	7.18–8.53	8.23 (79.5)	1.54	0.73	82.75	0.47
L'Hoest monkey	4	19.63	8.90–34.55	–	–	–	–	–	–	–	–
Gray-cheeked mangabey	17	13.75	10.86–16.97	8	16.52	12.47–21.14	13.77 (4.1)	13.22	1.20	17.13	0.25
Red colobus	55	28.44	24.25–32.97	27	46.63	39.11–54.81	28.50 (0)	99.97	4.32	53.71	<0.001
Red-tailed monkey	34	19.29	16.14–22.73	14	19.18	12.75–26.92	19.38 (52.9)	0.00	0.03	19.61	0.98

^aComparing group sizes between the sampling periods, 1996–1998 and 2010–2011. Group size was square root transformed to improve normality.

^bValues were back-transformed following Sokal and Rohlf (1995) for square root transformed data.

^{*}To account for different sample sizes in the two surveys, we used delete-d jackknifing to down-sample the 1996–1998 data to the number of samples in the 2010–2011 survey (10,000 replicates). We present the mean of this down-sampled data along the percentage of these replicates that are greater than the mean from the 2010–2011 survey.

TABLE 2. Primate group sizes during two sampling periods in K30, K15, and K14 in Kibale National Park, Uganda (intermediate scale).

Species	1996–1998 group counts			2010–2011 group counts			Delete-d jackknifed 1996–1998 group counts Welch		Welch two sample <i>t</i> -test ^a		
	N groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	N groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	Mean group-size (%) [*]	Percent of <i>t</i> -tests significant, %	<i>t</i>	df	<i>P</i>
Blue monkey	9	9.74	5.69–14.88	3	10.60	1.76–26.89	9.98 (40.1)	0.00	0.24	4.27	0.82
Black and white colobus	45	8.89	7.90–9.93	13	7.89	7.26–8.55	8.90 (90.2)	10.51	1.74	54.62	0.09
Gray-cheeked mangabey	11	12.05	9.87–14.45	3	17.31	13.75–21.29	12.08 (0.0)	17.89	3.79	9.95	0.0036
Red colobus	33	35.26	30.51–40.34	16	47.47	38.56–57.31	35.31 (0.0)	61.28	2.52	27.49	0.018
Redtail monkey	20	20.54	17.14–24.24	7	13.99	6.18–24.96	20.61 (100.0)	1.06	1.45	7.66	0.19

^aComparing group sizes between the sampling periods, 1996–1998 and 2010–2011. Group size was square root transformed to improve normality.

^bValues were back-transformed following Sokal and Rohlf (1995) for square root transformed data.

^{*}To account for different sample sizes in the two surveys, we used delete-d jackknifing to down-sample the 1996–1998 data to the number of samples in the 2010–2011 survey (10,000 replicates). We present the mean of this down-sampled data along the percentage of these replicates that are greater than the mean from the 2010–2011 survey.

made a single-file movement across a canopy opening, such as a treefall gap or road, where it is possible to easily count individuals. Repeat counts were made of the same group. We found this method to be effective for all species, regardless of level of

habituation and species-specific behaviors (e.g., canopy height selection). Differences between species, such as their density, home range size, and habituation, influenced the ease with which we could accurately count groups. To ensure this did not affect

TABLE 3. Primate group sizes during two sampling periods in K30 in Kibale National Park, Uganda (fine scale).

Species	1996–1998 group counts			2010–2011 group counts			Delete-d jackknifed 1996–1998 group counts Welch		Welch two sample <i>t</i> -test ^a		
	<i>N</i> groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	<i>N</i> groups	Mean group-size ^b (\bar{x})	95% confidence limit ^b	Mean group-size (%) [*]	Percent of <i>t</i> -tests significant, %	<i>t</i>	df	<i>P</i>
Blue monkey	3	12.16	1.77–31.88	2	10.40	–	12.30 (67.10)	67.10	0.28	1.85	0.80
Black and white colobus	17	7.82	5.92–9.99	3	7.66	6.28–9.18	7.95 (48.3)	48.34	0.16	18	0.87
Mangabey	1	16	–	1	19	–	–	–	–	–	–
Red colobus	14	37.17	27.47–48.34	11	52.07	39.50–66.38	37.25 (0.0)	0.00	1.95	22.24	0.065
Redtail monkey	6	21.05	11.40–33.65	5	17.05	7.72–30.04	21.13 (100)	100.00	0.68	8.82	0.52

^aComparing group sizes between the sampling periods, 1996–1998 and 2010–2011. Group size was square root transformed to improve normality.

^bValues were back-transformed following Sokal and Rohlf (1995) for square root transformed data.

^{*}To account for different sample sizes in the two surveys, we used delete-d jackknifing to down-sample the 1996–1998 data to the number of samples in the 2010–2011 survey (10,000 replicates). We present the mean of this down-sampled data along with the percentage of these replicates that are greater than the mean from the 2010–2011 survey. This would need to be <2.5% to be significant at the $P < 0.05$ level.

our data, we took a conservative approach and only included counts for which we were totally confident in accuracy and precision. Due to logistic constraints, fewer groups were counted in the 2010–2011 census than in the 1996–1998 census period; we accounted for these differences in sample sizes statistically (see: Analysis of Group Size Data).

As a means of verifying changes in group counts at the three nested spatial scales, we examined changes in group size using detailed demographic data from habituated study groups of red colobus, black-and-white colobus, and redbtail monkeys that ranged in logged and old-growth forest around Kanyawara. These groups have each been studied for at least 4 yr, group size and composition were known, and all adults are individually recognizable. We repeatedly counted the number of individuals in one group of red colobus between July 2006 and September 2011 ($N = 28$ counts), in eight groups of black-and-white colobus between February 2008 and January 2012 ($N = 83$ counts), and in three groups of redbtail monkeys between August 2008 and January 2012 ($N = 6$ counts).

ANALYSIS OF GROUP SIZE DATA.—We tested group size for normality using the Shapiro-Wilks test and normalized it with a square root transformation (Sokal & Rohlf 1995). We tested for changes in group sizes on the broad scale for each primate species between the two time periods (1996–98 and 2010–11) using Welch's two sample *t*-tests. We present back-transformed means and 95% confidence limits following Sokal and Rohlf (1995). Statistical comparisons between sample periods were not possible for three primate species for the following reasons: (1) we did not count any L'Hoest monkey groups in 2010–11; (2) we did not count any baboon or L'Hoest monkey groups in compartments K14, K15, or K30 in either time period; and (3) we counted only one group of mangabeys in K30 in each period. We counted few blue monkey groups in each period as these

animals are widely dispersed, typically at very low density, and secretive (Butynski 1990), so these results are interpreted with caution.

To assess the impact of sample size differences between sampling periods, we used delete-d jackknifing without replacement to down-sample the 1996–1998 data to the sample size of the 2010–2011 survey ($N = 10,000$ replicates). We present the mean of this down-sampled data along with the percentage of these replicates for which the mean is greater than the mean from the 2010–2011 survey (Table 1). For each replicate we conducted a Welch's two sample *t*-test and present the percentage of these *t*-tests that were significant at the $P < 0.05$ level. These results are statistically conservative (*i.e.*, high probability of not finding a statistical effect when there is one) as they repeatedly discard a large proportion of the 1996–1998 data, but are presented to allow the reader to access the importance of sample size differences between study periods.

For the habituated group of red colobus, we used a linear regression to determine whether group size increased through time. To test for changes in group sizes for the habituated groups of black-and-white colobus and redbtail monkeys, we divided the study (2008–2012) in two equal periods, calculated the mean group size for each period, and compared them using a paired *t*-test.

QUANTIFYING FOREST CHANGE.—To identify relationships between primate food abundance, nutrition, and group size at the fine and intermediate spatial scale, we analyzed data from permanent tree plots in the Kanyawara area (200 m × 10 m; total area = 5.2 ha). These plots were established and surveyed in December 1989–January 1990 and located at random places along the existing trail system. They were re-surveyed in May 1999, September–November 2006, and January–May 2013. In each plot, trees diameter at breast height (dbh) ≥10 cm were identified

to species-level, individually marked with a uniquely numbered aluminum tag, and measured for dbh. Voucher specimens for all trees were given to Makerere University Biological Field. During each re-survey, we relocated and measured all tagged trees, recorded tree deaths, and included new trees recruiting into the ≥ 10 cm dbh size class. We measured the tree's dbh 1.2 m above the ground using parameters established previously in the study area (Chapman *et al.* 2010a).

ANALYSIS OF FOREST DATA.—The dbh of a tree varies reliably with both fruit and leaf biomass, is practical and easy to measure, and has low inter-observer error (Catchpole & Wheeler 1992, Chapman *et al.* 1994, FAO 1997, Enquist & Niklas 2001, 2002). We calculated the $\log_{10}(\text{DBH})$ of all trees in each plot and summed it (*i.e.*, the cumulative $\log_{10}[\text{DBH}]$) to assess whether forest structure changed over time. We summed $\log_{10}(\text{DBH})$ because of the allometric relationship between DBH and plant productivity; we used cumulative $\log_{10}(\text{DBH})$ as an index of food availability (Snath & Chapman 2008).

Primate populations are likely more influenced by changes in the abundance of food trees than the abundance of all trees in an area. We followed Chapman *et al.* (2010a) and used dietary data to determine food trees for each primate species and conducted a separate analysis on cumulative $\log_{10}(\text{DBH})$ of major food tree species for each primate species, in each plot, in each time period. We defined major food tree species as those that accounted for ≥ 4 percent of feeding time, as reported by Rudran (1978) and Butynski (1990) for blue monkeys, Waser (1975) and Olupot (1994) for mangabeys, Harris and Chapman (2007) and Oates (1977) for black-and-white colobus, Rode *et al.* (2006, unpubl. data) and Stickler (2004, unpubl. data) for redbtail monkeys, and Chapman and Chapman (2002, unpubl. data) and Struhsaker (1975, 2010) for red colobus.

The preceding analyses test for changes in *quantity* of food available to primates; however, analyses of the ecological determinants of red colobus abundance clearly indicate that the *quality* of available foods is also important (Chapman & Chapman 2002, Wasserman & Chapman 2003, Chapman *et al.* 2004). As a measure of food quality for red colobus, we used the protein-to-fiber ratio, which is a good predictor of folivore leaf choice (Milton 1979) that has been shown to predict colobine biomass at local and regional scales (Waterman *et al.* 1988, Oates *et al.* 1990, Chapman & Chapman 2002, Ganzhorn 2002, Chapman *et al.* 2004, but see: Gogarten *et al.* 2012). The relationship between the protein-to-fiber ratio and colobus biomass has been demonstrated with the overall protein-to-fiber ratio of mature leaves in an area. Since young leaves constitute a larger portion of the red colobus diet than mature leaves (Struhsaker 1975, Ryan *et al.* 2013), we ran the analysis to measure the effect of the protein-to-fiber ratio of mature versus young leaves. For further discussion of the application of the protein-to-fiber ratio see (Oates *et al.* 1990, Chapman *et al.* 2004), and for details of sample collection, processing, and the determination of protein and fiber see Chapman and Chapman (2002), Rothman *et al.* (2012) and Gogarten *et al.* (2012).

To test for temporal variation in food abundance parameters, we compared repeat samples of the 11 permanent tree plots (K30—fine scale) and 26 plots (K30, K14, K15—intermediate scale) between the four surveys using a linear mixed effect model, with sampling periods included as fixed effects and vegetation plot included as a random effect. These models were implemented in the R package ‘nlme’ (Pinheiro *et al.* 2012, R Development Core Team 2012). Additionally, for each of the five primate species with detailed dietary data, we calculated the percent change in cumulative $\log_{10}(\text{DBH})$ of food species in each plot during each of the four surveys. To incorporate the protein-to-fiber ratio of mature and young leaves of species eaten by red colobus into the measure of food availability, we re-ran the analysis with cumulative $\log_{10}(\text{DBH})$ weighted by the protein-to-fiber ratio of each major food tree species.

RESULTS

At the broad scale we found a significant increase in red colobus group size between 1996–98 and 2010–11; we did not find significant increase for any other species (Table 1). When we examined groups at the intermediate scale (K30, K14, K15), we found that average group size for red colobus increased from 35.3 to 47.5 individuals (Table 2) and for mangabeys from 12.0 to 17.3. However, mangabey results should be interpreted with caution due to the small number of groups sampled in 2010–2011 ($N = 3$; Table 2). We found similar trends for these two species at the fine scale in the old-growth forest (K30), but the smaller sample size resulted in marginal significance for the red colobus and did not allow us to statistically test the change in mangabey group size (2010–2011 $N = 1$; Table 3). Chapman *et al.* (2010b) found that density of red colobus groups in K30 decreased between 1996 and 2006 (1996 = 5.5 groups/km²; 2006 = 4.2 groups/km²); however, since we document an increase in average group size, these results suggest that individual density remained relatively constant (1996 = 204 individuals/km²; 2006 = 219 individuals/km²).

For the long-term study groups with detailed demographic data, we did not detect a significant change in group size of black-and-white colobus (2008–9 mean = 7.1, 2010–12 mean = 8.7, $t = 1.766$, $df = 7$, $P = 0.121$; Fig. 1A) or redbtail monkeys (2008–9 mean = 24.4, 2010–12 mean = 28.5, $t = 1.452$, $df = 2$, $P = 0.284$; Fig. 1B). In contrast, the long-term red colobus study group increased from 59 to 104 individuals from 2006 to 11 ($R^2 = 0.863$, $F_{1,26} = 171.7$, $P < 0.001$), with an estimated increase of 7.6 individuals/yr (SE = 0.580, $t = 13.104$, $P < 0.001$; Fig. 1C); this corroborates our survey data.

A linear mixed effects model detected a significant increase in cumulative $\log_{10}(\text{DBH})$ of all trees during the 2013 tree survey at the fine scale (Table 4) and intermediate scale as well as an increase in 2006 at the intermediate scale (Table 5). No significant changes in the availability of mangabey or blue monkey foods were detected across tree surveys at either scale. Compared to previous surveys, there was less black-and-white colobus food available in 2006 and 2013 at

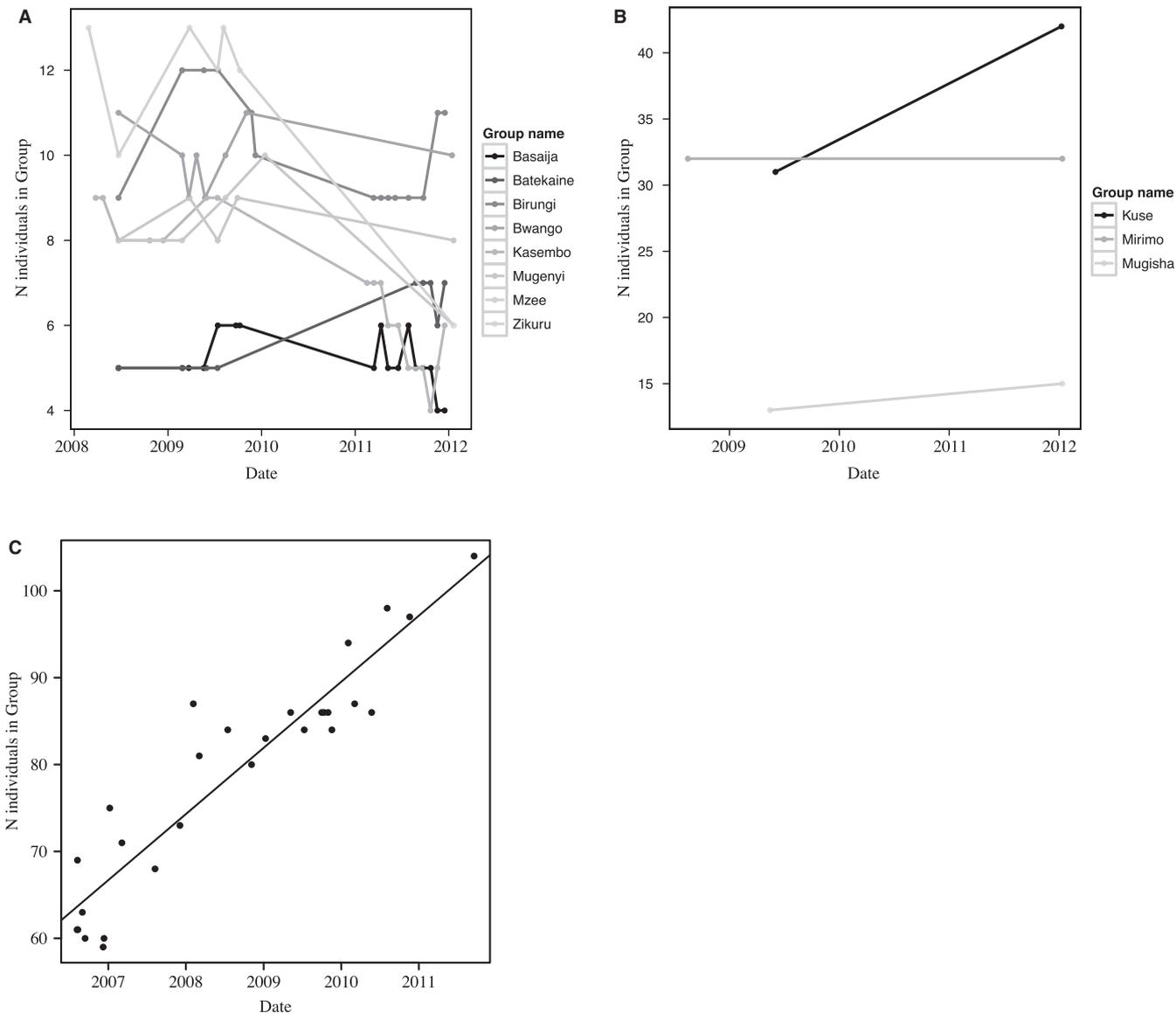


FIGURE 1. (A) Group size of eight habituated groups of black and white colobus through time. (B) Group sizes of three habituated groups of redbtail monkeys through time. (C) Group size of one habituated group of red colobus through time; a solid line represents the linear regression of group size on time.

the fine scale in the old-growth forest, but no change in food availability at the intermediate scale, which included two areas that had been logged (K14 & K15; Tables 4 and 5). We documented more redbtail monkey and red colobus foods available in 2013 than in previous times at both the mall and intermediate scales. We documented an increase in red colobus and red tail food available for both species in 2006 at the intermediate scale. When red colobus food availability was weighted by the protein-to-fiber ratio of mature leaves, there was an increase in availability of quality foods in 2013 at both scales. In contrast, food availability weighted by the protein-to-fiber ratio of young leaves remained similar across the four surveys in the old-growth forest (Table 4), but increased at the intermediate scale that included regenerating areas (Table 5).

DISCUSSION

Variation in primate group sizes have been documented across species (Janson & Goldsmith 1995), space (Stanford 1995), and time (Angeles & Lwanga 2011, Strier & Mendes 2012). To our knowledge, however, our study represents the first systematic analysis of stability in primate group sizes on large temporal and spatial scales. For most primate species we examined average group sizes remained stable across time at the park-wide scale. The only species for which we detected a change in group sizes at this broad spatial scale was red colobus. This increase was also observed at the intermediate scale in the logged and old-growth forest compartments and at the

TABLE 4. Results of the linear mixed effects models to test for changes in food availability (cumulative $\log_{10}[\text{DBH}]$) in 11 plots between the four survey periods. Means, 95% confidence intervals (CI_{95} , 1.96 times SE) and t -values of fixed effects (sampling periods) are given. Significant values are in bold. Vegetation plots included as random effect.

Food abundance measure (cumulative $\log_{10}(\text{DBH})$)	Intercept		1999		2006		2013	
	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t
All trees	125.1 + -16.6	14.74***	-4.3 + -7.8	-1.09	3.1 + -7.8	0.79	9.3 + -7.8	2.35*
BWC food trees	26.8 + -5.9	8.92***	-2.5 + -2.7	-1.84	-3.1 + -2.7	-2.28*	-3.3 + -2.7	-2.45*
MG food species	28.8 + -7.4	7.66***	-0.2 + -3.0	-0.11	-0.3 + -3.0	-0.19	-1.2 + -3.0	-0.82
RT food species	38.7 + -10.9	6.99***	0.6 + -5.6	0.21	3.1 + -5.6	0.28	5.95 + -5.6	2.06*
BM food species	61.8 + -19.4	6.23***	-3.3 + -3.6	-1.79	-2.4 + -3.6	-1.32	-2.8 + -3.6	1.55
RC food species	49.7 + -12.0	8.14***	-0.5 + -5.8	-0.18	3.8 + -5.8	1.29	9.5 + -5.8	3.21**
RC food species weighted by protein:fiber of ML	31.9 + -6.4	9.74***	0.4 + -3.0	0.24	3.1 + -3.0	1.99	6.7 + -3.0	4.35***
RC food species weighted by protein:fiber of YL	48.6 + -7.6	12.48***	-2.0 + -4.6	-0.87	-0.5 + -4.6	-0.20	1.4 + -4.6	0.58

BWC, black-and-white colobus, MG, mangabey, RT, redtail monkey, BM, blue monkey, RC, red colobus; YL, young leaves, ML, mature leaves.

***($P < 0.001$), **($P < 0.01$) and *($P < 0.05$).

TABLE 5. Results of the linear mixed effects models to test for changes in food availability (cumulative $\log_{10}[\text{DBH}]$) in 22 plots between the four survey periods in K30, K15, and K14. Means, 95% confidence intervals (CI_{95} , 1.96 times SE) and t -values of fixed effects (sampling periods) are given. Significant values are in bold. Vegetation plots included as random effect.

Food abundance measure (cumulative $\log_{10}(\text{DBH})$)	Intercept		1999		2006		2013	
	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t	(mean + $-CI_{95}$)	t
All trees	111.7 + -13.7	16.6***	-1.9 + -5.1	-0.72	7.3 + -5.1	2.83**	12.4 + -5.1	4.78***
BWC food trees	28.0 + -4.8	11.4***	-0.9 + -1.9	-0.93	-0.9 + -1.9	-0.99	-1.2 + -1.9	-1.28
MG food species	28.2 + -4.6	12.10***	-0.5 + -1.8	-0.51	-0.1 + -1.8	-0.09	-0.9 + -1.8	-0.91
RT food species	35.6 + -6.9	10.07***	0.0 + -3.0	0.02	3.2 + -3.0	2.05*	4.7 + -3.0	3.03**
BM food species	57.4 + -11.3	9.99***	-2.0 + -2.8	-1.40	-0.8 + -2.8	-0.55	-0.8 + -2.8	-0.53
RC food species	46.6 + -9.7	9.44***	1.1 + -3.3	0.65	5.4 + -3.3	3.20**	8.6 + -3.3	5.09***
RC food species weighted by protein:fiber of ML	30.8 + -5.9	10.27***	1.6 + -1.9	1.70	4.5 + -1.9	4.68***	6.9 + -1.9	7.12***
RC food species weighted by protein:fiber of YL	46.4 + -7.6	12.03***	0.0 + -2.8	0.01	2.0 + -2.8	1.39	3.2 + -2.8	2.21*

BWC, black-and-white colobus, MG, gray-cheeked mangabey, RT, red-tailed monkey, BM, blue monkey, RC, red colobus; YL, young leaves, ML, mature leaves.

***($P < 0.001$), **($P < 0.01$) and *($P < 0.05$).

fine scale in the old-growth forest. Detailed demographic data from the long-term red colobus group support this trend, with average group size increasing by 7.6 individuals/yr. In contrast, other detailed data from redtail monkey and black-and-white colobus groups suggest stability in group sizes (Mitani *et al.* 2000, Teelen 2007, Chapman *et al.* 2010b). Despite small sample size in 2010–2011, we also detected an increase in mangabey group sizes between the two sampling periods at the intermediate spatial scale.

Socioecological theory suggests that grouping strategies change when food resources change. Specifically, group size is

expected to increase with increasing food availability (Milton 1984, Chapman & Chapman 2000). With respect to predation, from an evolutionary perspective an increase in predation pressure is expected to increase group size to increase group protection through vigilance or dilution effects; however, predators can decrease group size through overexploitation (Alexander 1974, van Schaik 1983, Delm 1990, Teelen 2008). Average group sizes might be expected to change if populations are recovering from a large disturbance, such as disease or natural disaster (Gulland 1992, Pavelka *et al.* 2003). Isolating particular factors responsible for the observed changes in

group sizes through time is difficult because of a paucity of long-term data on all potential factors.

POTENTIAL DRIVERS OF OBSERVED CHANGES: CHANGING FOOD AVAILABILITY AND QUALITY.—Both stability and dynamism were evident in food availability and food quality depending on the spatial scale and primate species being considered (Tables 4 and 5). Overall primate food availability in K30 appears to have increased between 1996 and 2013. Socio-ecological theory suggests that resource distributions can have major impacts on primate sociality (Clutton-Brock & Harvey 1977, Wrangham 1980). Whether folivores like red colobus defend resources and exhibit competition over resources remains a point of considerable debate (Fashing *et al.* 2007, Snaith & Chapman 2008, Isbell 2012), but observed changes in red colobus food availability and quality (high protein-to-fiber ratio) may have changed within- and between-group competition for resources. An increase in food abundance and quality might favor larger groups if resources are defensible, there is increased competition over resources, and large groups have a competitive advantage over smaller groups that outweighs increases in within-group competition that can occur with increasing group size. Fashing (2001) found evidence that male black and white colobus defended resources as part of a mate defense strategy, demonstrating the importance of resource distribution on grouping behavior; the finding that black and white colobus food availability remained stable across all periods at the larger spatial scale may explain the observed stability in group sizes. Given that food for both redbelt monkeys and red colobus appears to have increased at both spatial scales, it is puzzling that redbelt monkey group size did not increase, while red colobus group sizes did. Other factors that influence food quality such as minerals, toxins, and phytoestrogens (Wasserman & Chapman 2003, Rode *et al.* 2006, Rothman *et al.* 2012, Wasserman *et al.* 2012) might explain the stability in red tail group sizes. Overall, however, it appears that increases in the availability and quality of red colobus food resources is a likely mechanism driving the observed increases in red colobus group size across all three spatial scales.

The changes in food availability we documented highlight the dynamism of forest composition, even in a relatively well-protected old-growth forest, which may reflect forest succession (Eggeling 1947, Chapman *et al.* 2010a). Changes in forest composition or structure have been recorded in other forests including Budongo National Park, Uganda (Sheil *et al.* 2000), La Selva, Costa Rica (Lieberman & Lieberman 1987, Norden *et al.* 2009), and Lambir Hills National Park (Russon *et al.* 2005) and Sungei Menyala Forest Reserve (Manokaran & Kochummen 1987), Malaysia. Other long-term studies highlight the importance of considering unpredictable factors in forest succession, including tree species-specific reproduction events and dispersal limitation on Barro Colorado Island, Panama (Dent *et al.* 2013) and ancient, as well as recent, natural and anthropogenic disturbances (van Gemerden *et al.* 2003, Mori 2011). What roles equilibrium and non-equilibrium factors play in forest succession in Kibale is not yet clear; further study is needed to determine the rates of

change and drivers of forest composition, and their interaction with animal populations, including the roles of land use history (Synnott 1971) and an expanding elephant population (Laws 1970, Omeja *et al.* In press).

POTENTIAL DRIVERS: PREDATION AND DISEASE.—Predation is hypothesized to be an important driver of ecological and evolutionary processes, particularly with regard to sociality (van Schaik 1989, Isbell 1994), since even low rates of predation can have major impacts on primates with slow life histories (Cheney & Wrangham 1987, Isbell 1994). Although data are scarce, it is possible that group size could vary as a function of changing predation pressure (van Schaik & van Hooff 1983, Isbell 1994). In Kibale, known primate predators include leopards (*Panthera pardus*), golden cats (*Profelis aurata*), crowned hawk-eagles (*Stephanoaetus coronatus* (Struhsaker & Leakey 1990, Mitani *et al.* 2001), and chimpanzees (*Pan troglodytes* (Mitani & Watts 2001, Teelen 2008)). Bushmeat hunting of primates by humans is rare or absent altogether in the region (Struhsaker 1975). While research on felids, crowned hawk eagles, and chimpanzees does show that primates are primary prey resources, the overall predation pressure in the Kanyawara region is very low with respect to all predators. It does not appear that predation pressure has changed significantly over our study period (Skorupa 1989, Struhsaker & Leakey 1990, Mitani & Watts 1999, Teelen 2008, Lwanga *et al.* 2011, Nakazawa *et al.* 2013, C. A. Chapman, unpubl. data).

Similarly, disease can cause rapid reductions in population size and group sizes (Collias & Southwick 1952, Milton 1996). The red colobus in Kanyawara have been observed extensively since 1970 (Struhsaker 1975, 2010, Chapman *et al.* 2010b) and are known to harbor a number of parasites and viruses (Gillespie *et al.* 2005, Goldberg *et al.* 2008, 2009, Lauck *et al.* 2011, Bailey *et al.* 2014). These pathogens may impact fitness, but there has not been an observed disease outbreak in the last 40 yr that would directly implicate recovery from an epidemic in red colobus group size increases. These observations suggest that neither predation nor disease adequately explain the stability in group sizes of most primate species, or the increases in red colobus group sizes.

CONSEQUENCES OF CHANGING GROUP SIZES FOR PRIMATE ECOLOGY AND CONSERVATION.—The observed increase in red colobus group sizes will affect various aspects of their ecology and conservation (Gogarten *et al.* 2014b). When Borries *et al.* (2008) studied how development and reproductive rates varied with group size in the folivorous Phayre's leaf monkey (*Trachypithecus phayrei*), they found that infants in large groups weaned later and females had longer inter-birth intervals than in smaller groups. This suggests that large groups of arboreal folivorous monkeys have slower reproduction and ultimately lower female fitness than smaller groups, assuming survival rates are similar. This in turn suggests that a general increase in group size, may result in a slower increase in population size for a folivorous primate, although there is conflicting evidence from this population of red colobus (Snaith & Chapman 2008, Gogarten *et al.* 2014b). The observed changes

in food availability and group sizes are likely changing primate ranging patterns (Chapman & Chapman 2000), stress levels (Pride 2005), diets (Snaith & Chapman 2008, Gogarten *et al.* 2014b), activity budgets (Gogarten *et al.* 2014b), population genetic structure (Miyamoto *et al.* 2013), and disease dynamics within- and between-species (Freeland 1976, Kuehl *et al.* 2008, Snaith *et al.* 2008, Caillaud *et al.* 2013, Gogarten *et al.* 2014a). These changes, in turn may have major cascading impacts on the entire ecosystem as both folivorous and frugivorous primates have been argued to play major roles as ecosystem engineers (Chapman *et al.* 2013).

The documented changes in red colobus group size compared to the relative stability of group size in other primate species—despite apparent increases in food—suggest that Kibale primate populations and some forest habitats may be in a non-equilibrium state. If indeed primate populations in Kibale are not at equilibrium, conserving their populations and habitats requires integrating unpredictability and instability into management plans to maximize ecosystem resilience and withstand unforeseen change (Hamilton *et al.* 1986, Mori 2011). Currently, habitat management in Kibale largely focuses on returning ‘natural forest’ to areas degraded by logging, fire, or human encroachment with the goal of increasing populations of forest-dependent species of conservation concern (Uganda Wildlife Authority 2003). However, it is unclear what ‘natural forest’ means, as forest in Kibale has almost certainly been changing from anthropogenic forces for the last several thousand years (Hamilton *et al.* 1986), as have other African tropical rainforests (van Gemerden *et al.* 2003, Brncic *et al.* 2007). Managing to reduce habitat heterogeneity ignores the dynamic nature of disturbance in animal and plant population dynamics; more homogenous landscapes may be less resilient to large-scale disturbances. Instead, it may be better to manage ecosystems by incorporating small- and large-scale disturbances (Mori 2011), as well as using non-equilibrium theory in conservation planning.

CONCLUSION

Our data suggest that red colobus group sizes are increasing in Kibale across all measured scales. In measuring both food abundance and quality, we find that an increase in overall food resources may be driving this increase, with larger groups conferring benefits that are not being offset by increased competition over food. Group size has remained stable in all other primates studied, regardless of changing food resources for some species. Despite stability in group sizes, changes in group density has been recorded for some species (Chapman *et al.* 2010b). Our data suggest that the Kibale primate community is in a non-equilibrium state.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. The study area locations Sebatoli, Kanyawara, Dura, and Mainaro, and forestry compartments K30, K14 and K15.

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