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Primate population dynamics: variation in abundance over space and time

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Abstract   The rapid disappearance of tropical forests, the potential impacts of climate change, and the increasing threats of bushmeat hunting to wildlife, makes it imperative that we understand wildlife population dynamics. With long-lived animals this requires extensive, long-term data, but such data is often lacking. Here we present longitudinal data documenting changes in primate abundance over 45 years at eight sites in Kibale National

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Park, Uganda. Complex patterns of change in primate abundance were dependent on site, sampling year, and species, but all species, except blue monkeys, colonized regenerating forest, indicating that park-wide populations are increasing. At two paired sites, we found that while the primate populations in the regenerating forests had increased from nothing to a substantial size, there was little evidence of a decline in the source populations in old-growth forest, with the possible exception of mangabeys at one of the paired sites. Censuses conducted in logged forest since 1970 demonstrated that for all species, except black-and-white colobus, the encounter rate was higher in the old-growth and lightly-logged forest than in heavily-logged forest. Black-and-white colobus generally showed the opposite trend and were most common in the heavily-logged forest in all but the first year of monitoring after logging, when they were most common in the lightly-logged forest. Overall, except for blue monkey populations which are declining, primate populations in Kibale National Park are growing; in fact the endangered red colobus populations have an annual growth rate of 3%. These finding present a positive conservation message and indicate that the Uganda Wildlife Authority is being effective in managing its biodiversity; however, with constant poaching pressure and changes such as the exponential growth of elephant populations that could cause forest degradation, continued monitoring and modification of conservation plans are needed.

Introduction

Global assessments indicate that 2.3 million km^2 of forest was lost between 2000 and 2012, and in the tropics, where most primate species are found, forest loss increased by 2101 km^2 per year (Hansen et al. 2013). Threats to wildlife are further exacerbated by bushmeat hunting for local, national, and international consumption (Chapman and Peres 2001; Fa et al. 2002). Ultimately, changes in forest cover are driven by increasing human population size and consumption rates. The UN Population Division estimates that the world's population is expected to rise from 7 billion in 2011 to 9 billion by 2050. In African countries with tropical forests, human population density increased from 8 people km^{-2} in 1950 to 35 people km^{-2} in 2010 (Estrada 2013). Today, human population density exceeds 400 people km^{-2} in some areas of Africa bordering protected forests (Hartter et al. 2015). It is not surprising that this increase in human population density corresponds with an increase in the extent of cropland, which globally expanded by 48,000 km^2 per year between 1999 and 2008, largely at the expense of forest (Phalan et al. 2013). It is also not surprising that this has caused primate populations to decline and it is estimated that 61% of the world's primates are at risk of extinction and 14% of primates species are listed as critically endangered (Mittermeier et al. 2009; Estrada 2013; Estrada et al. 2017; IUCN 2017).

Wildlife conservation is a complex activity that requires detailed information. To protect and conserve populations it is necessary to monitor population changes in response to environmental stressors. However, populations often change slowly (Struhsaker 1976; Chapman et al. 2006) requiring careful long-term evaluation (Jacobson 2010; Kuhar et al. 2010). Furthermore, populations must be monitored at an appropriate scale and conservation of protected areas of substantial size requires that monitoring be done at a large scale. This is because animals move as habitat quality or predation risk change (Isbell 1990;

Cowlishaw 1997; Teelen 2008; Chapman et al. 2010a). However, many monitoring programs are restricted by logistical constraints to small and medium spatial scales (e.g., only monitor populations within walking distance from a field station)(Chapman et al. 1988; Hassel-Finnegan et al. 2008; Lwanga et al. 2011; Watts and Amsler 2013; Mugume et al. 2015).

In the present study, we document diurnal primate abundance trends at eight sites in Kibale National Park, Uganda (795 km^2). For some sites, data have been collected using the same method for 45 years, while in others monitoring spans 19 years. This analysis is timely to evaluate the success of several recent (last decade) community-based conservation programs and protection activities carried out by the Uganda Wildlife Authority. Population data also span a time of natural forest regeneration following official protection of areas within the park and restoration efforts, which allows us to evaluate population responses to regenerating forest. We examine whether any documented increases in primate abundance in regenerating forest corresponded to concomitant declines in abundance in old-growth forest. Lastly, we summarize patterns of change over several decades in population abundance in old-growth, lightly-logged and heavily-logged forests to examine long-term impacts of logging (Skorupa 1988; Struhsaker 1997; Chapman et al. 2010b).

Methods

Study sites

The study was conducted between September 1970 and July 2015 (179 months) in Kibale National Park (795 km^2), Uganda, with different areas being continuously sampled for different durations over 45 years (Table 1). The park is in western Uganda (0°13′–0°41′N and 30°19′–30°32′E) near the foothills of the Rwenzori Mountains (Fig. 1). Kibale is a mid-altitude (920 - 1590 m), moist-evergreen forest that receives a mean annual rainfall of 1689 mm (1990–2014), in two rainy seasons (measured at Kanyawara, Chapman and Lambert 2000; Stampone et al. 2011). Within Kibale, there is an elevational gradient decreasing from north to south, which corresponds an increase in temperature and decrease in rainfall. Kibale received National Park status in 1993 and is now managed by the Uganda Wildlife Authority. Prior to 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing sustained hardwood timber production (Struhsaker 1997; Chapman et al. 2005).

This study was conducted at eight sites selected and monitored because they differ in disturbance level (logging) and position along the elevational gradient (Fig. 1; Tables 1, 2). Sebitoli, the most northern site and recent vegetation samples showed that Sebitoli is dominated by canopy trees such as *Chrysophyllum* spp., *Diospyros abyssinica*, *Albizia* spp., *Funtumia latifolia*, *Markhamia platycalyx* and *Celtis gomphophylla* (Bortolamiol et al. 2013, 2014). The forest was commercially logged in the late 1960s, but rates of timber extraction are not known. The next three sites can be monitored from Makerere University Biological Field Station (Kanyawara) and therefore have the longest duration of monitoring; 1970 to present. In K-15 (347 ha), harvest averaged 21 m^3 ha^{-1} or approximately 7.4 stems ha^{-1} from September 1968 through April 1969 (Skorupa 1988; Struhsaker 1997). Incidental damage in K-15 was high and approximately 50% of all trees were destroyed by logging and incidental damage (Skorupa 1988; Chapman and Chapman 1997). Immediately to the south of K-15 is forestry compartment K-14. This is a 405 ha forest block that was logged at low intensity (14 m^3 ha^{-1} or 5.1 stems ha^{-1}) from May through December

Table 1 Characteristics of the primate censuses that were conducted at different locations in Kibale National Park, Uganda (ordered from North to South) at different times for this study

Area	Forest type	Logging intensity	Size (ha)	Census period	Transect length (m)	# of transects	Total distance (km)
Sebitoli	Logged	50%		1996/2014	4200	26	104
K-15	Logged	50%	347	80/96/05/14	4000	86	344
K-14	Logged	25%	405	80/96/05/14	3600	85	306
K-30	Old-growth	< 1%	282	70/80/96/05/14	4000	148	592
Nyakatojo	Regenerating	100%	60	2014	4000	12	48
Dura	Old-growth	< 1%	c	1996/2014	4450	35	156
Mainaro	Old-growth	< 1%	c	1996/2014	4000	22	88
Plantation 1	Regenerating	100%	~ 120 m^2	2014	4000	12	48

Logging intensity is an estimate of the number of stems (> 30 cm DBH) killed. Areas that are a part of continuous forest and not considered as a forestry compartment are labeled C. The exact month of initiation and completion for each period were the following September 1970 to October 1976, February 1980 to December 1981, July 1996 to June 1997, July 2005 to June 2006 and June 2014 to June 2015. Rebel activity prevented us from sampling at Mainaro in January, February and April 1997. Censuses between 1970 and 1972 were conducted by Tom Struhsaker, between 1980 and 1981 by Joe Skorupa, and in 1996–1997, 2005–2006, and 2014–2015 by CAC, Patrick Omeja, and the same Ugandan Field Assistants

1969. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa 1988; Struhsaker 1997). Immediately to the south of K-14 is forestry compartment K-30, which is a 282 ha area that has not been commercially harvested. Adjacent to K-30 is Nyakatojo (86.2 ha), which is an area of regenerating forest that was formerly a pine (*Pinus* spp.) and cypress (*Cupressus lusitanica*) plantation established on anthropogenic grasslands between 1968 and 1973 (Zanne and Chapman 2001). Since 1993, planted exotic trees in Kibale have been systematically extracted to allow forest regeneration with indigenous species and in 1998 all the pines in the Nyakatojo area were cut down and removed (clear felling) (Chapman and Chapman 1996; Chapman et al. 2002; Omeja et al. 2009).

Approximately 15 km to the south of Nyakatojo is the Dura River site that was not commercially logged. *Pterygota mildbraedii, Cola gigantea, Piptadeniastrum africanum* and *Chrysophyllum albidum* were described as the dominant canopy species (Kingston 1967). Further south by approximately 15 km is the Mainaro site. Here the forest is dominated by *Cynometra alexandri* and affiliated species (Kingston 1967). At both the Dura River and Mainaro sites, a few timber trees have been extracted by pits sawyers (approximately 0.1 trees ha^{-1}), but with little impact on the forest. Approximately 5 km to the west of Mainaro is the regenerating area known as P1, which has a long and intense history of land use. This area in southern Kibale was illegally occupied by subsistence farmers in the 1970s until their eviction in 1992 (van Orsdol 1986). At this site the Forest Absorbing Carbon Emission (FACE) Foundation started a carbon offset reforestation program in collaboration with the UWA in 1995. The regenerating area was protected from fire and planted with native seedlings(Omeja et al. 2011, 2012; Chapman et al. 2013a; Omeja et al. 2016; Wheeler et al. 2016). Some bushmeat hunting by people involved in the restoration or logging programs did occur, but since the ethnic groups in the area do not hunt monkey, this did not influence

Kibale National Park and Surroundings
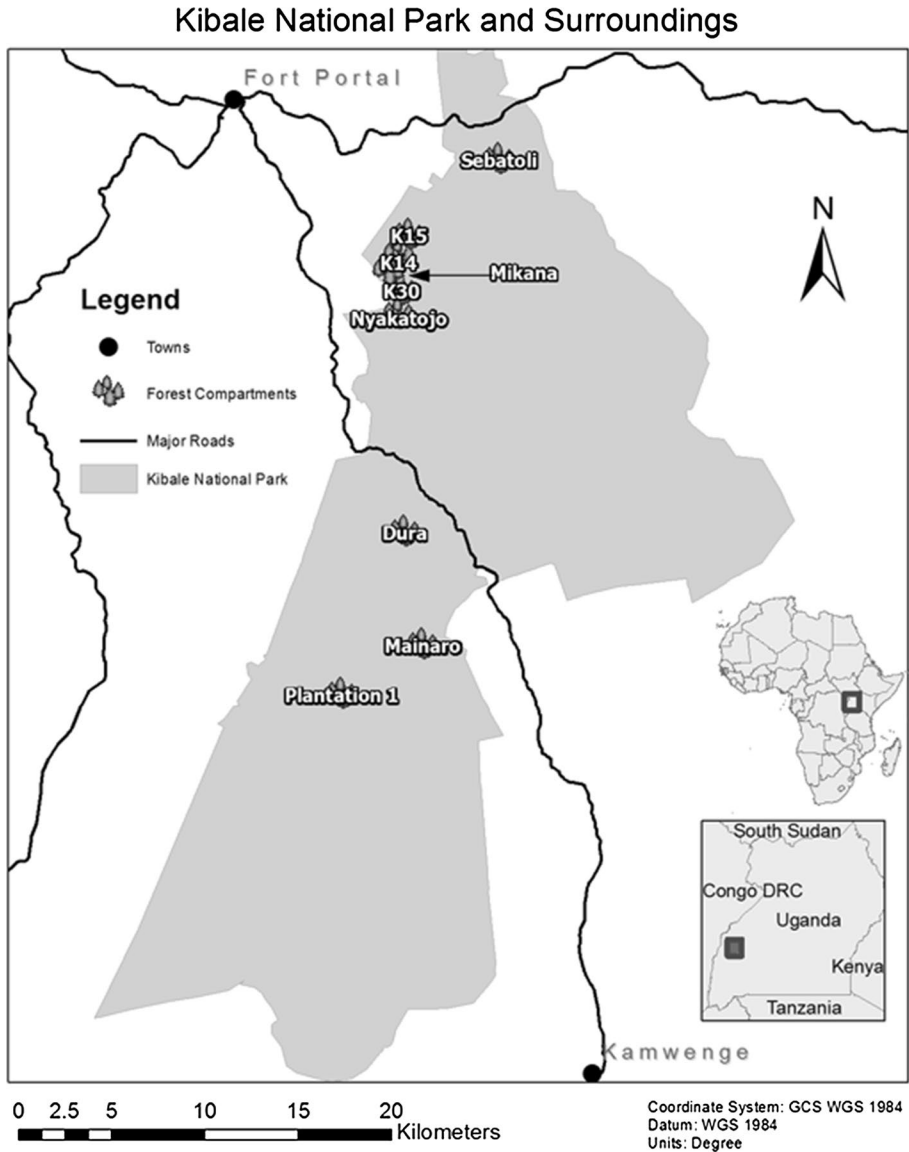
Fig. 1 Map of Kibale National Park, Uganda, showing the location of the eight study sites examined in this study

our study. Detailed enumeration of the tree communities in all areas except Nyakatojo and P1 is provided in Chapman et al. (1997).

To facilitate analysis, forest areas are divided into three types: (1) old growth forest—K30, Dura, and Mainaro (old growth is forest where there are no historical signs or record of disturbance, but forests were likely disturbed by people hundreds of years ago (e.g., when the iron age was at its height in Uganda); (2) regenerating logged forest—K15, K14,

Table 2 The abundance (number of groups encountered per kilometer walked) of the five common diurnal primates at eight sites within Kibale National Park, Uganda

Species	Sebitoli	Sebitoli	K15	K15	K15	K15	K14	K14	K14	K14	K30	K30	K30	K30	K30	Nyaka-tojo	Dura	Dura	Mainaro	Mainaro	Mainaro P1
Habitat	Log	Log	Log	Log	Log	Log	Log	Log	Log	Log	Old	Old	Old	Old	Old	Regen	Old	Old	Old	Old	Regen
Year	1996	2014	1980	1996	2005	2014	1980	1996	2005	2014	1970	1980	1996	2005	2014	2014	1996	2014	1996	2014	2014
Red Colobus	0.69	0.59	0.59	0.57	0.43	0.52	0.71	0.50	0.59	0.51	0.97	1.14	0.64	0.47	0.65	0.29	0.06	0.04	0.69	0.42	0.35
BW Colobus	0.18	0.20	0.20	1.14	0.83	0.68	0.50	0.34	0.59	0.56	0.22	0.12	0.17	0.21	0.27	0.23	0.05	0.18	0.31	0.29	0.23
Redtail	0.17	0.46	0.46	0.28	0.21	0.31	0.53	0.61	0.58	0.61	0.70	0.64	0.35	0.41	0.56	0.48	0.70	0.41	0.50	0.58	0.58
Blue	0.15	0.16	0.16	0.34	0.07	0.13	0.20	0.08	0.11	0.18	0.45	0.39	0.09	0.17	0.15	0.00	0.00	0.00	0.00	0.00	0.00
Mang-abey	0.14	0.24	0.24	0.05	0.08	0.21	0.11	0.20	0.23	0.18	0.09	0.16	0.40	0.19	0.27	0.08	0.31	0.26	0.40	0.42	0.20
Baboon	0.00	0.10	0.10	0.00	0.01	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.05	0.02	0.13	0.00	0.00	0.00	0.21	0.15

A description of the sites is in the text and in Table 1. Three forest types are presented; Log = forests that have been logged to different intensities, see Site Description of the Intensities, Old = old growth, and Regen = regeneration forest after agriculture (P1) or pine plantation removal (Nyakatojo)

and Sebitoli were all commercially logged in the 1960s and when logging formally ceased, forest regeneration proceeded without replanting efforts; and (3) cleared and replanted forest—P1 and Nyakatojo are considered to be recently cleared. P1 was re-planted with native species as part of a carbon offset program and Nyakatojo was left to regenerate naturally following the removal of the pine.

Census methods

At each of these sites primates were censused at roughly 11 year intervals (Table 1) along a single 4 km transect from 1970 to 2014, though rebel activity prevented us from sampling at Mainaro in January, February and April 1997. Censuses were conducted between 0700 and 1400 h at a speed of approximately 1 km h^{-1}. Line-transect methods are recommended for estimating densities of large-bodied diurnal primates (National Research Council 1981). Primate species included in the study were redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*), baboons (*Papio anubis*), red colobus (*Procolobus rufomitratus*) and black-and-white colobus (*Colobus guereza*). Other species, such as l'hoesti monkeys (*Cercopithecus l'hoesti*) and chimpanzees (*Pan troglodytes*), are too rare or secretive to obtain accurate estimates, and we did not conduct nocturnal censuses.

In total, we conducted 426 transects walks and covered 1686 km. To minimize sources of error we used the same methods each year and walked the same census route once per month for 12 months in the year of sampling (Table 1). The census team has involved the same observers since 1996, but the membership did change prior to that, which could have influenced the estimates. A variety of methods have been proposed for estimating animal density or abundance from line transects and considerable controversy exists regarding their accuracy for forest dwelling mammals (reviewed by Chapman et al. 2010b), with supporting evidence from (National Research Council 1981; Defler and Pinto 1985; Chapman et al. 1988; Whitesides et al. 1988; Struhsaker 1997; Fashing and Cords 2000; Teelen 2007; Hassel-Finnegan et al. 2008; Struhsaker 2010). The DISTANCE program is often advocated as an accurate means of estimating population densities (Buckland et al. 2010). However, following Lwanga et al. (2011) we decided not to use this approach as this method has been demonstrated to overestimate densities of forest primate groups, often by more than double, when compared with the most accurate estimates of density that are based on studies of specific social groups with identifiable individuals (reviewed by Chapman et al. 2010b). Group density can also be calculated using sighting distances (estimated distance to the first animal seen), plotted at set intervals or bins (e.g., 10 m intervals) to set a cut-off rule to evaluate transect width (National Research Council 1981; Chapman et al. 2000a, b). However, with this approach sighting distance of different species (ignoring interspecific differences in sighting distance) or habitats often have to be lumped to obtain a robust sample to identify a clear cut-off distance (Teelen 2007). Also, determining strip width may be subject to error when sample sizes are small and different observers estimating distance is a potential source of error. Accordingly, we used encounter rate as a measure of relative abundance, which is the number of groups seen per kilometer of census trail walked (Mitani et al. 2000; Teelen 2007; Matsuda et al. 2011, 2016). This method does not take into account differences in detection probability among periods or differences in the ability of the observers to detect animals (although variance in observer's ability to spot groups have previously been quantified to be low (Chapman et al. 2000; Lwanga et al. 2011) and the same observers conducted the last three censuses), nor does it correct

for visibility differences due to logging or regeneration. This analysis does not account for changes in group size over time (Gogarten et al. 2015, see below).

Results and discussion

A complex pattern of change in primate abundance was documented with the magnitude of these changes dependent on site and species. With the exception of mangabeys, the relative abundance of all species in the old-growth forest (K30) was initially high in the first two surveys (1970 and 1980). This may have occurred as a result of compression—groups may have left the areas that were logged in the 1960 and entered the old-growth forest and compensatory mechanisms may not have had time to have an effect to reduce numbers to the level that the habitat could support. In contrast to what would be expected if the forest was regenerating after logging and the habitat was improving, the abundance of red colobus in either the heavily or lightly logged areas did not change a great deal over time. Black and white colobus abundance followed a somewhat similar pattern, except the estimates were more variable and their numbers were initially low in the heavily logged forestry compartment. Between the first and second survey (1980 and 1996) redtail relative abundance dropped substantially in the heavily logged area, but not in the lightly logged area. After this second survey in 1996, redtail abundance did not change substantially in either areas, which is again contrary to what would be expected if the habitat was regenerating and becoming more suitable for primates. The number of mangabey groups seen per kilometer walked in the heavily logged forest initially dropped substantially and then gradually recovered. In contrast, mangabey numbers in the lightly logged forest increased between the first and second census and then remained relatively stable. Relative to the other species considered, mangabeys in Kibale have large home ranges (1.4 km^2; Olupot et al. 1994), so some of these changes likely represent changes in habitat selection and not changes in population size.

Baboons, which are not entirely forest-dependent, generally increased in abundance park-wide, and now occupy northern areas of the park where they were largely absent a decade ago (CC unpublished data; R. Wrangham personal communication). Factors leading to this northern expansion are not known, however, while baboons have historically been considered pests, there is no records of extensive eradication program that could account for this and detailed records were evaluated back to the 1920s (L. Naughton and CC unpublished analysis of the Uganda Game Department records).

This is the first study in Kibale to do extensive surveys of primates in the regenerating areas where the pine plantation (Nyakatojo) had been harvested and in the areas replanted and protected from fire (P1). All species, except blue monkeys, colonized these areas of regenerating forest, which is a positive conservation message (Table 2; Fig. 2).

### Populations in regenerating forests adjacent to old-growth forest

We expected either that abundances in the old-growth forest would decline as individuals moved into the regenerating forests or that old-growth populations would remain stable and as populations in the regenerating area grew and only 'surplus' animals would move into the regenerating areas. The latter scenario was supported. We compared two areas of old growth forest for which population data were collected with adjacent cleared replanted forest: (1) K30 (old growth) and Nyakatojo (a regenerating

Fig. 2 The encounter rate of each species monitored in old-growth forest (K-30) between the 1970 and 2014 (Gogarten et al. 2015). The average red colobus group size increased over time as indicated by measurements conducted in 1996 and 2011 and indicated at those dates by the average group size in brackets
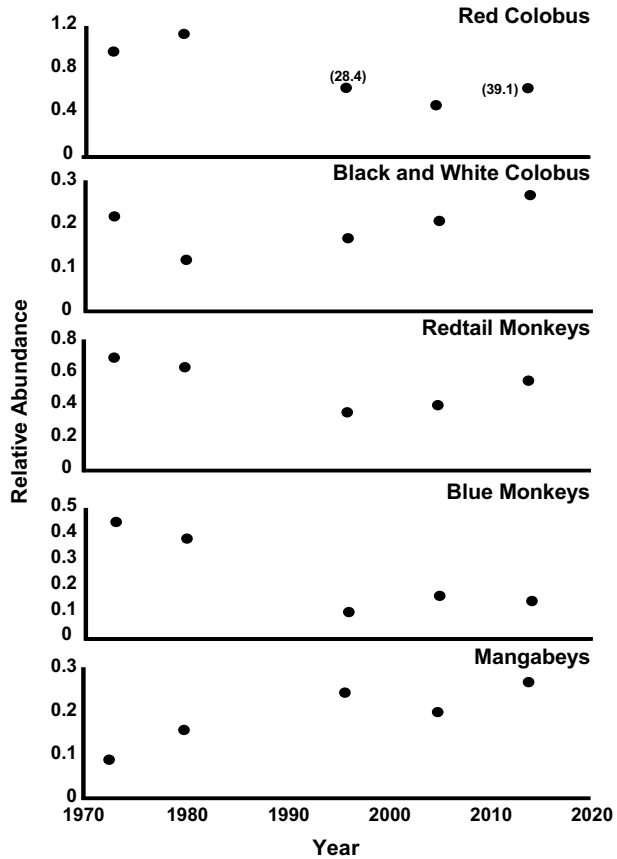
plantation), and (2) Mainaro (old growth) and P1 (cleared agricultural land that was replanted). While abundance in the regenerating forest increased from zero to substantial sizes for most species in just 16 years, there was no evidence of a decline in the source populations in adjacent old-growth (Fig. 1), with the possible exception of mangabeys at the K-30—Nyakatojo area (Figs. 3, 4) where the source populations in old-growth forest declined. It is possible that since mangabeys are large-bodied, ripe fruit specialists with a slow life-history (Olupot et al. 1994), that some animals were drawn to the fruit sources common in secondary forest and new recruitment (births) have not yet occurred in groups remaining in the old-growth forest to compensate for this; however this speculation must be substantiated. At Nyakatojo the redtail and black and white colobus populations occurred to the degree that in just 16 years their relative abundance was not statistically different between the areas ($\chi^2 = 0.308$, P = 0.579, $\chi^2 = 0.160$, P = 0.689, respectively; Table 2). However, the relative abundance of red colobus and mangabeys was less in the former pine plantation than the old-growth forest ($\chi^2 = 7.156$, P = 0.007, $\chi^2 = 5.630$, P = 0.0176, respectively; Table 2). In the area that was formerly agricultural land and was replanted as part of a carbon offset project (P1), the recovery of the populations was even greater and only mangabeys had lower relative numbers in the regenerating area as compared to the old-growth forest
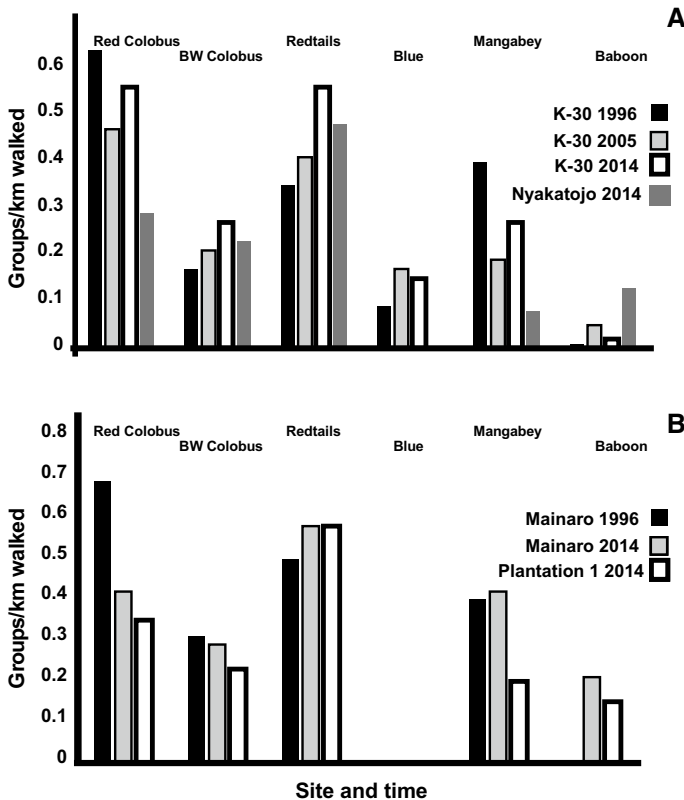
Fig. 3 a Number of groups per km walked for each primate species monitored in the old-growth forest of K-30 in 1996, 2005, 2014 and the adjoining forest block (Nyakatojo) that was a pine plantation prior to being logged starting in 1993. **b** Number of individuals per km walked for each primate species monitored in the old-growth forest of Mainaro in 1996 and 2014 and the adjoining regenerating forest (Plantation 1)

(mangabeys $\chi^2 = 4.030$, P = 0.045, red colobus $\chi^2 = 0.321$, P = 0.571, black and white colobus $\chi^2 = 0.347$, P = 0.556, redtail monkey $\chi^2 = 0$, the estimates are the same; blue monkeys are not found this far south in the park).

Population dynamics old-growth versus lightly-logged and heavily-logged forests

Given the extent of logging occurring in the tropics, investigations of the effect of timber harvesting is of great interest to conservation (Johns 1987; Chapman et al. 2000; Chapman and Chapman 2004; Felton et al. 2013). In Kibale, differences in relative abundance among forestry compartments with different histories of logging were similar to what has been previously reported (Struhsaker 1975; Skorupa 1988; Struhsaker 1997; Chapman et al. 2010b). However, here we extend the temporal scale of evaluation to up to 44 years and evaluate the effect of logging history on the encounter rate of groups for each species.

Fig. 4 The encounter rate (groups seen per km walked) for each primate species monitored in K-15 (heavily-logged forest), K-14 (lightly-logged forest), and K-30 (old-growth forest) sampled at various intervals between 1970 and 2014. Note that to show encounter rates of rare species, the axes are not the same in each panel
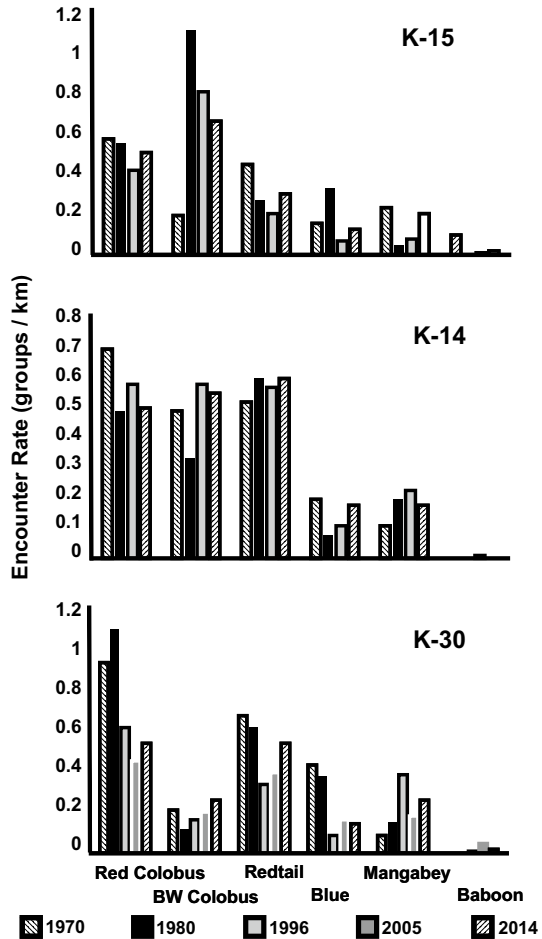
Red colobus

Red colobus abundance was relatively stable in the heavily-logged compartment between 1980 and 2014 and declined slightly in the lightly-logged and old-growth forests (1970–2014; Figs. 1, 2). However, as discussed below, group size increased over time in these areas countermanding the decline in abundance and thus population size has likely been stable in the old-growth and lightly-logged area (1996 mean group size = 28.4 (n = 55 groups), 2014 = 39.1 (n = 27 groups); (see also Gogarten et al. 2015).

Black and white colobus

The encounter rate of black and white colobus in the heavily-logged area initially increased right after logging, but then declined thereafter; however, to levels still higher than those immediately recorded in the earliest record (1980). This initial increase likely happened because black and white colobus could feed on the largely undefended young leaves of fast

growing pioneer species (e.g., *Trema orientalis*), that rapidly establish after logging, but were replaced in the 1990s by less palatable herbaceous species such as *Acanthus pubescens* (Lawes and Chapman 2006; Omeja et al. 2014). Of all the species, black and white colobus thrive in heavily-logged areas (Struhsaker 1975; Skorupa 1988; Struhsaker 1997). In contrast to the red colobus, the size of black and white colobus groups did not increase (1996 mean group size = 8.22 (n = 62 groups), 2014 = 7.84 (n = 27 groups); (see also Gogarten et al. 2015).

Redtail monkeys

Encounter rates of redtail monkey groups did not change in old-growth and lightly-logged forests, but initially declined in heavily-logged areas. Red-tail monkeys tend to occur at lower abundance in heavily-logged forest (Struhsaker 1975, 1997; Rode et al. 2006; Chapman et al. 2010b). However, redtail monkeys actively colonized the cleared regenerating forest at Nyakatojo and P1, the southern regenerating area, where their populations are equal to those of old growth areas within a mere 16 years after the onset of regeneration. There group size remained similar over time (1996 mean group size = 19.29 (n = 34 groups), 2014 = 19.18 (n = 14 groups) (see also Gogarten et al. 2015).

Blue monkeys

Encounter rates suggest that blue monkeys have declined over time, in all forest types regardless of logging history (Fig. 2). Surprisingly, they have not colonized the regenerating forests. There group size remained similar over time (1996 mean group size = 9.31 (n = 11 groups), 2014 = 10.60 (n = 3 groups) (see also Gogarten et al. 2015).

Grey-cheeked mangabeys

Mangabey groups were more abundant in old-growth forest, than in either the heavily or lightly logged forests. There group size remained similar over time (1996 mean group size = 13.75 (n = 17 groups), 2014 = 16.52 (n = 8 groups) (see also Gogarten et al. 2015).

Baboons

Baboons were too infrequently sighted to determine whether their populations were changing over time or to identify habitat preferences with respect to logging. On a park-wide scale they appear to be increasing in abundance since they have occupied areas, such as Sebitoli, where they previously did not occur (but see Lwanga et al. 2011).

Implications for change park-wide

It is rare to have data on primate population dynamics over both many decades, in this case up to 44 years, and over a large geographic scale, in this case Kibale National Park (Chapman et al. 2017). Of course it would be ideal to have data at more locations in the park and at more time intervals. However, our data provides an opportunity to see how the park has changed in the last 40 + years and can help predict future biodiversity conservation issues. These populations have been affected by many changes including: logging that resulted in decreased food availability and compression caused by animals moving away from the

disturbed areas (Chapman et al. 2000; Osazuwa-Peters et al. 2015a, b), the disappearance of fragments outside of the park and the immigration of animals into Kibale (Chapman et al. 2013b), climate change (Rothman et al. 2015), exponentially rising elephant numbers impacting vegetation (Omeja et al. 2014), changing forest tree community structure (Chapman et al. 2010a; Omeja et al. 2012), and the impact of invasive plant species (*Lantana camera*) (Omeja et al. 2016). None of these processes are likely to have a linear affect, they will change at different rates, and the processes will likely combine in unexpected ways. Thus, finding simple clear causal relationships are is unlikely. If drivers of change and their interactions were known, predicting how these populations change in the future, could be evaluated with greater precision and management plans could be derived to aid in the recovery of endangered species. While this is not possible at the present time, we can predict future population levels based on the past trends documented here.

Population changes in Kibale can be considered to have occurred primarily in two ways. First there were changes that were occurring in pre-existing forest (either logged or old-growth) and second new regenerating forest habitat became available in areas that were disturbed. Logging only occurred in the northern quarter of the park and after the 1980s population changes in these areas were not dramatic, so the habitat that drives park-wide population change is old-growth forest. The areas near the field station provides the longest and most detailed records and with the exception of mangabeys, the relative abundance of all species was initially high, numbers fell and then populations grew (see also data on Ngogo field site Lwanga et al. 2011). The initial fall likely occurred as a result of compression.

The most detailed park-wide data is available for red colobus as this was the species that both Thomas Struhsaker (1970–1987) and Colin Chapman (1989 to present) studied. Estimates of the size of Kibale's red colobus population varies (Chapman and Lambert 2000; Struhsaker 2005). For conservation management purposes it seems advisable to select a conservative estimate (Struhsaker 2005). Thus, based on data from 1996 and before, a conservative density is between 25 and 50 red colobus/km^2 (37.5 animals/km^2 used in calculations). To determine the park wide population numbers this value is multiplied by the area of suitable habitat as determined from analysis of satellite images, which is 60% of the 795 km^2 total areas of the park. Thus, we consider that a conservative estimate for 1996 is $\geq$ 17,000 (see also Struhsaker 2005).

Since 1996 the size of red colobus groups have increased park-wide (Gogarten et al. 2015). A detailed, year long study in 1996 where 55 groups of red colobus we located and repeatedly counted (a single count of a large group can take a day or more) determined that the average red colobus group contained 28.4 members. A similar study conducted in 2011 revealed that the population's group size had increased to 46.6 members—a 61% increase. Since then groups in the Kanyawara area have continued to increase in size and sometimes fission (Chapman unpublished data) and a third park wide survey to determine group size will begin in 2018. A 61% increase in the population would mean that Kibale would conservatively contain 27,000 red colobus (rounding down to be conservative).

The second means by which populations are increasing for all monkeys except blue monkeys is by colonizing regenerating forests that were either former pine plantations or areas in southern Kibale that were replanted after disturbance. In many cases the populations in these newly forested areas were of comparable size to old-growth forest. Regeneration has also occurred in the grasslands in the interior of the park (Lwanga 2006), but the regeneration is dependent on the protection of the area from fire and this has not been quantified on a large scale. The area that was in pine plantation was 8 km^2 (Chapman and Lambert 2000) and the aim is to replant 100 km^2 of forest, but to date

35 km^2 has regenerated to the level at which primate populations are supported (Omeja et al. 2016; Wheeler et al. 2016). The density of red colobus in these areas was approximately 40% lower than the neighboring old growth forests (Table 2, Fig. 3), but similar to park-wide estimates (all values reported here, plus Ngogo). Thus, these regenerating areas are conservatively estimated to support 2000 animals, bringing the park-wide estimate to 29,000; a 63% increase since the mid-1990s and a 3.5% annual increase.

At the Ngogo field site in Kibale an unusually large chimpanzee community preys heavily on red colobus (Watts and Mitani 2002; Watts and Amsler 2013) and has caused their numbers to progressively decline at this one study site (Teelen 2005, 2008; Lwanga et al. 2011). This may represents a source-sink dynamic (Pulliam 1988; Holt 1997; Struhsaker 2010), where red colobus immigrate into the Ngogo area where predation by chimpanzees is severe. However, it is unlikely that the events occurring at Ngogo significantly affects the park-wide trends in red colobus abundance as their numbers are increasing. Also, there is no reason to expect that the situation found at Ngogo occurs elsewhere in the park and the area of this chimpanzee community is small relative to the park`s size.

Blue monkeys are an exception to the general pattern of population growth and their low abundance in the forests of western Uganda cannot easily be explained. Blue monkeys are abundant in north Kibale (Sebitoli), but gradually decline in abundance to the south, and are largely absent from the old growth forest in the middle of the park and are absent from the regenerating forest further south. Butynski (1990) studied blue monkeys foraging strategies and the abundance of food resources near the Makerere University Biological Field Station and approximately 12 km to the south at Ngogo. At Ngogo, blue monkey abundance was much lower than it was at Kanyawara, and Butynski hypothesized this was a result of a recent disturbance, such as disease, temporarily lowering their numbers, and predicted that their abundance would increase. However, encounter rates of blue monkey groups at Ngogo have not increased in over a decade (Lwanga et al. 2011). Blue monkeys are habitat generalists occupying diverse habitats, and they have a very large geographical range and altitudinal distribution, and occupy a diversity of habitats (Struhsaker 1978; Lawes 1990; Struhsaker 2010). Despite this, their distribution in Kibale is limited, they did not colonize the regenerating forests, they are not found in neighboring forest fragments, and their numbers are declining. At Kanyawara, blue monkeys have the greatest dietary overlap with the other monkey species (Houle et al. 2006, 2007). Based on this overlap and observations from Budongo forest (Fairgrieve 1995), a plausible explanation for lower than expected blue monkey population densities is that they are more adversely affected by diffuse competition for food than other primate species (Struhsaker 1978; Houle et al. 2006). Lwanga (1987) suggested that blue monkeys at Ngogo were relatively rare because they experienced greater food competition with grey-cheeked mangabeys, red-tailed monkeys, and chimpanzees, that are old-growth specialists. However, blue monkeys at Kibale appear to be old-growth specialist and not always habitat generalists; they are not found in forest fragments near Kibale (Onderdonk and Chapman 2000), nor did they occupy regenerating forest in the present study, and they rarely visit the forest edge where forest meets agricultural land (Worman and Chapman 2006). Providing quantitative evidence of competition or competitive exclusion has proven to be difficult (Connell 1980), but this issue has recently been evaluated for some primate species in Kibale (Houle et al. 2006) and Kalinzu Forest, just to the south (Go 2010) and its importance in behavioural interactions and feeding success have been demonstrated, but this research does not shed light on the blue monkey populations trends. An explanation for their distribution patterns or the decline in blue monkey abundance at Kibale is still wanting.

Overall, monkey populations in Kibale are growing, with the exception of blue monkeys. In fact, the endangered red colobus population is doing very well and is growing at an annual rate of over 3%. These finding present a positive conservation message and suggest that Kibale National Park is an effective conservation setting and that the Uganda Wildlife Authority (UWA) is successful in producing their desired conservation goals. However threats to the park are mounting and changing. The human population just outside the park continue to grow. Uganda has a population growth rate of 3.24%, thus population doubling would occur in just over 20 years (Ryan et al. 2017). This puts great pressure on the parks as the people living next to the park boundary are poor and resources are difficult to find (Naughton et al. 2011; MacKenzie et al. 2017). Recently the elephant population in Kibale have increased substantially (Omeja et al. 2014; Mondol et al. 2015; Omeja et al. 2016), partially as a result of immigration from the Democratic Republic of Congo (Keigwin et al. 2016), and since these animals are predominantly found within the forest and elephants can damage forest ecosystems, the success with elephant conservation may become a problem for primate conservation in the near future. To manage changes in threats like these and new ones that will arrive (e.g., climate change, introduced species like *Lantana camera*), continued monitoring and modification of conservation plans are needed.

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