



Primate population dynamics in Ngogo, Kibale National Park, Uganda, over nearly five decades

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Abstract

Many anthropogenic-driven changes, such as hunting, have clear and immediate negative impacts on wild primate populations, but others, like climate change, may take generations to become evident. Thus, informed conservation plans will require decades of population monitoring. Here, we expand the duration of monitoring of the diurnal primates at Ngogo in Kibale National Park, Uganda, from 32.9 to 47 years. Over the 3531 censuses that covered 15,340 km, we encountered 2767 primate groups. Correlation analyses using blocks of 25 census walks indicate that encounters with groups of black and white colobus, blue monkeys, and baboons neither increased nor decreased significantly over time, while encounters with groups of redtail monkeys and chimpanzees marginally increased. Encounters with mangabeys and L'Hoesti monkeys increased significantly, while red colobus encounters dramatically decreased. Detailed studies of specific groups at Ngogo document changes in abundances that were not always well represented in the censuses because these groups expanded into areas away from the transect, such as nearby regenerating forest. For example, the chimpanzee population increased steadily over the last 2 + decades but this increase is not revealed by our census data because the chimpanzees expanded, mainly to the west of the transect. This highlights that extrapolating population trends to large areas based on censuses at single locations should be done with extreme caution, as forests change over time and space, and primates adapt to these changes in several ways.

Keywords Primate abundance · Population dynamics · Census · Conservation planning · Population monitoring

Introduction

Humans are devastating Earth's habitats and causing catastrophic declines in biodiversity. For example, ~600,000 km² of primary tropical forest were lost from 2002 to 2019 (Weisse and Gladman 2020). Human-created changes are having real impacts, with species extinction rates

estimated to be ~1000 times above the rate that would have occurred without anthropogenic impacts (Ceballos et al. 2015; Dirzo et al. 2014; Pimm et al. 2014). Primates are no exception: 75% of the approximately 512 primate species have declining populations; 65% are threatened with extinction (Estrada et al. 2017); and 14% are listed as 'Critically Endangered' (Estrada et al. 2020; IUCN 2018).

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Many anthropogenic activities have clear and immediate negative consequences for wild primates (Chapman and Peres 2021). For example, when forests are converted to agriculture, most species from birds to primates to elephants decline in abundance and will potentially disappear. Similarly, if there is intensive hunting in an area, there will be declines in the species that hunters target. The consequences of other anthropogenically driven changes are, however, not readily apparent and may take decades to become evident. For example, climatic changes associated with human greenhouse gas emissions relate to changes in the phenological cycles of primate foods (Potts et al. 2020), as well as decreases in nutritional quality of leaves (Rothman et al. 2015), and abundance of fruit (Bush et al. 2020) consumed by primates. While there are clear predictions about how changes in climate influence the abundance of primates, quantifying their impacts is challenging. Similarly, evidence suggests that primates in Uganda and Costa Rica are exposed to significant levels of pesticides and to halogenated and organophosphate flame retardants (Steiniche et al. 2023; Wang et al. 2019, 2020). The consequences to reproduction of such exposure are unknown. Pesticide exposure is likely to primarily affect juvenile development, suggesting that it will be years before any impacts can be detected. The effects on primates of exposure to pesticides have rarely been examined, but given their increased use in the tropics (Chapman et al. 2022), there is an urgent need for more research in this area.

Unlike hunting or habitat destruction, where primate populations can be devastated quickly, climate change, declines in food quality and abundance, and increased exposure to pesticides are predicted to have the largest impacts on birth rates and infant survival. Population declines due to these factors are thus predicted to be gradual. To derive informed conservation plans that account for these causes, population monitoring spanning decades is needed (Barelli et al. 2023; Chapman et al. 2017; Davenport et al. 2022; Lwanga and Isabirye-Basuta 2008; Strier et al. 2017).

Here we provide additional data to the previous censuses of diurnal primates at Ngogo in Kibale National Park, Uganda (Butynski 1990; Lwanga et al. 2011; Mitani et al. 2000; Teelen 2007). We expand the duration of monitoring from 32.9 to 47 years. Such long-term biological monitoring is extremely rare, particularly in tropical Africa (Davenport et al. 2022). The ultimate goal of our research is to provide data to contribute to our understanding of the changes occurring among primate populations in a relatively well-protected forest habitat and to determine appropriate management responses if populations are being impacted by factors like climate change and pesticide exposure.

Methods

Study site

Kibale, a 795-km² national park established in 1993, is located in western Uganda (0°13'–0°41'N and 30°19'–30°32'E) near the eastern foothills of the Rwenzori Mountains (Chapman and Lambert 2000; Chapman et al. 2005; Struhsaker 1997). The park is dominated by mid-altitude (920–1590 m above sea level), moist-evergreen forest. Prior to this, it was a forest reserve and game corridor, gazetted between 1926 and 1932, with the stated goal of providing sustained hardwood timber production and game (Chapman et al. 2005; Kingston 1967; Osmaston 1959; Struhsaker 1997). Hunting in the park is prohibited, but persists nonetheless, primarily through the setting of snares for ungulates (Sarkar et al. 2021). At Ngogo, the mean annual rainfall is 1444 mm ± 151 SD (1997–2021), and there are two rainy seasons from early March to May and from late August to early December. The study site is described in detail in Ghiglieri (1984), Butynski (1990), Struhsaker (1997), Lwanga et al. (2000), and Potts et al. (2020). We present data on the detection of all eight species of diurnal primates at Ngogo: black and white colobus (*Colobus guereza*), red colobus (*Piliocolobus tephrosceles*), blue monkeys (*Cercopithecus mitis*), redtail monkeys (*Cercopithecus ascanius*), l'Hoest's monkeys (*Cercopithecus lhoesti*), grey-cheeked mangabeys (*Lophocebus albigena*), olive baboons (*Papio anubis*), and chimpanzees (*Pan troglodytes*).

Census methods

We collected data on the relative abundance of primate groups (groups/km) using a line transect methodology (National Research Council 1981; Struhsaker 1997). To minimize sources of error, we used the same methods each year and walked the same census transect, although the length varied slightly (1975–1984 = 4.03 km; 1985–2021 = 4.40 km). The census route follows an approximate square configuration with each side being 1 km in length (see figures in Lwanga 2006; Mitani et al. 2000). Additional methodological details can be found elsewhere (Lwanga et al. 2011; Mitani et al. 2000; Teelen 2007). Censuses were conducted by Struhsaker (1975–1976, 1995–1996), Butynski (1978–1980, 1981–1984), Lwanga (1985, 1997–2014), Mitani (1996), and Angedakin (2015–2021). While their data only span some of the census period studied here, Mitani et al. (2000) found that although estimates of sighting distance could differ between observers, the same observers did not differ from one another in the number of primate groups they saw.

Several methods have been employed to estimate animal density or abundance from line transects. There remains considerable controversy, however, regarding their accuracy for forest-dwelling primates (reviewed by Chapman et al. 2010a, b). The program DISTANCE is often advocated as an accurate estimator of population densities (Buckland et al. 2010; Spaan et al. 2017). We elected not to use this approach, as in Kibale it over-estimates densities of some species of the forest primates we studied, often by more than double when compared with the most accurate estimates of density that are based on detailed, long-term studies of specific social groups with identifiable individuals and known home ranges (reviewed by Chapman et al. 2010a, b; see also Lwanga et al. 2011). Furthermore, DISTANCE assumes that the center of mass of a social group is accurately measured at the moment of sighting. This is generally impossible at Kibale, particularly when dealing with polyspecific associations (Struhsaker 2010). While the DISTANCE approach may not be suitable for the particular situation and primate species in Kibale, others have recommended its use (Buckland et al. 2010; Marshall et al. 2008; Peres 1999; Plumptre et al. 2013; Spaan et al. 2017, 2019). More research is required to investigate the effectiveness of different census approaches in different situations.

Density can also be calculated using sighting distance to the first animal seen, plotted at set intervals or 'bins' (e.g., 10-m intervals) to establish a cut-off rule to evaluate effective transect width (Chapman et al. 2000; Chapman et al. 2010a, b; National Research Council 1981; Teelen 2007). However, to obtain a robust sample to identify a clear cut-off distance, sighting distances of different species or in different habitats often have to be lumped. Also, determining strip width is subject to error when sample sizes are small and different observers estimating distance is a potential source of error (Teelen 2007). Thus, following Lwanga et al. (2011), we used encounter rate as a measure of relative abundance, which is the number of groups seen per kilometer of census transect walked (Matsuda et al. 2016, 2011; Mitani et al. 2000; Teelen 2007). This method does not take into account changes in detection probability over time due to, for example, vegetation change or habituation, differences among observers in the ability to detect animals (Chapman et al. 2000; Lwanga et al. 2011), or changes in group size (Gogarten et al. 2015). It has been shown that visibility and sighting distances did not change in any obvious way between 1975 and 1996 and, since the Ngogo census transect is in old growth forest, significant changes in forest structure are not expected (see Lwanga 2003 for details on succession in the area). We report abundances of chimpanzees including encounters with parties, as well as solitary chimpanzees, to allow comparisons with previous research (Lwanga et al. 2011; Mitani et al. 2000). We note, however, that obtaining reliable estimates of chimpanzee numbers through censuses

is difficult due to their fission–fusion social organization that is influenced by food availability that varies among years (Chapman et al. 1995).

Analysis

We standardized the data to account for differences in transect length by making the unit of analysis the number of groups encountered per kilometer of transect walked. Solitary individuals were excluded from our analysis, except for solitary chimpanzees. Typically, censuses were conducted approximately 1 month apart. This was not always possible, however, and depended on the presence and availability of the responsible researchers in the field. Some of the censuses, particularly those in 1995 and 1996, were conducted on consecutive days or within a few days of one another. When this happens, it raises the potential bias that might occur in situations where monkey groups repeatedly use the same food sources near the census route on consecutive days or simply do not travel far in a day. To address this potential bias, censuses conducted within 10 days of one another were averaged. This 10-day separation period is arbitrary, but it was considered a conservative approach to reduce this potential bias. Research is needed to determine whether this bias exists, and if it results in the under- or over-reporting of different species. If this bias occurs, then additional work is required to minimize it by determining an appropriate interval between censuses for different species.

There is often considerable variation in the number of encounters between successive censuses, but the estimates increase in accuracy and precision with replication (National Research Council 1981). When the precision of group encounters reaches an asymptote, it can be concluded that sufficient repetitions have been undertaken to provide a representative sample (Lwanga et al. 2011; National Research Council 1981). Precision was calculated following National Research Council recommendations (National Research Council 1981). In previous studies (Lwanga et al. 2011; Mitani et al. 2000), precision curves were viewed to reach an asymptote after 15–20 censuses. However, because of the longer interval between many of the censuses in our study, we elected to use 25 censuses as a 'block', which is the number of censuses used to derive a single estimate of groups sighted for that time period. Ideally, this means 25 consecutive censuses for a given time period provide a precise estimate of primate relative abundance. However, over the 47 years there were interruptions in data collection and observers changed. Thus, census blocks were adjusted to accommodate breaks in data collection and changes in observers. The mean block included 24.8 censuses (range, 15–35), yielding 19 census blocks. Census blocks: 1 = 1/1975–11/1976 ($n = 15$ censuses), 2 = 10/1978–12/1981 ($n = 35$), 3 = 1/1982–9/1984 ($n = 30$),

4 = 7/1995–7/1997 ($n = 25$), 5 = 8/1997–1/1999 ($n = 25$), 6 = 2/1999–6/2000 ($n = 25$), 7 = 7/2000–9/2001 ($n = 25$), 8 = 9/2001–10/2002 ($n = 25$), 9 = 11/2002–2/2004 ($n = 25$), 10 = 3/2004–8/2005 ($n = 25$), 11 = 9/2005–12/2006 ($n = 25$), 12 = 12/2006–3/2008 ($n = 25$), 13 = 4/2008–9/2009 ($n = 25$), 14 = 10/2009–9/2011 ($n = 25$), 15 = 11/2011–1/2014 ($n = 25$), 16 = 2/2014–6/2016 ($n = 25$), 17 = 7/2016–7/2018 ($n = 25$), 18 = 8/2018–8/2020 ($n = 25$), 19 = 9/2020–12/2021 ($n = 16$). We ran Pearson correlations (abundance versus month since the first census) to evaluate whether there was a consistent change in the frequency of encounters over time. Results of the Pearson tests were confirmed by performing Spearman's rank correlations.

To visualize changes and explore potential non-linear increases or decreases in primate group encounters between censuses through time, we used locally estimated scatterplot smoothing (LOESS) regression and the ggplot2 R package and R v4.2.1 (R Core Team 2022; Wickman 2016). We conducted LOESS regressions, a robust non-parametric method for each primate species separately and used them to explore changes in group encounters over time (i.e., we are not testing significance with this regression). To emphasize larger-scale shifts in group encounters through time, we set LOESS span values, which help determine the degree of regression smoothing that is used by the models to 0.35.

Our research adhered to the legal requirements of Uganda and to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. It was approved by the University Committee on the Use and Care of Animals, University of Michigan (#6793A, 7472, 8436, and 9035), and by the Department of Forestry, Uganda Wildlife Authority, Uganda National Council of Science and Technology, and Makerere University.

Results

Over the 3531 censuses that covered 15,340 km, we encountered 2767 primate groups during 21 field years. The number of encounters varied dramatically among species and blocks ($N_{\text{red colobus}} = 292$, range among blocks = 1–54; $N_{\text{black and colobus}} = 136$, range among blocks = 0–19; $N_{\text{redtail monkeys}} = 1177$, range among blocks = 23–85; $N_{\text{blue monkeys}} = 80$, range among blocks = 0–9; $N_{\text{mangabeys}} = 512$, range among blocks = 7–40; $N_{\text{L'Hoesti's monkey}} = 113$, range among blocks = 0–12; $N_{\text{baboons}} = 112$, range among blocks = 2–11; $N_{\text{chimpanzees}} = 351$, range among blocks = 5–28).

Correlation analyses indicate that encounters with black and white colobus $r = -0.050$, $p = 0.839$; blue monkeys $r = 0.147$, $p = 0.548$; and baboons $r = 0.249$, $p = 0.303$ neither increased nor decreased significantly over time. For redtail monkeys ($r = 0.413$, $p = 0.079$) and chimpanzees ($r = 0.401$, $p = 0.089$), our data suggest a marginal increase over time

with p values < 0.10 , while mangabeys ($r = 0.662$, $p = 0.002$) and L'Hoesti monkey encounters ($r = 0.678$, $p = 0.001$) increased significantly over time. In contrast, red colobus encounters dramatically decreased ($r = -0.903$, $p < 0.001$; Fig. 1). Correlation analyses test for consistent change over time; however, some species seem to have variable patterns of population change over the years (Fig. 1). For example, encounters with blue monkeys appeared to decrease between 1984 and 1996, after which encounters increased.

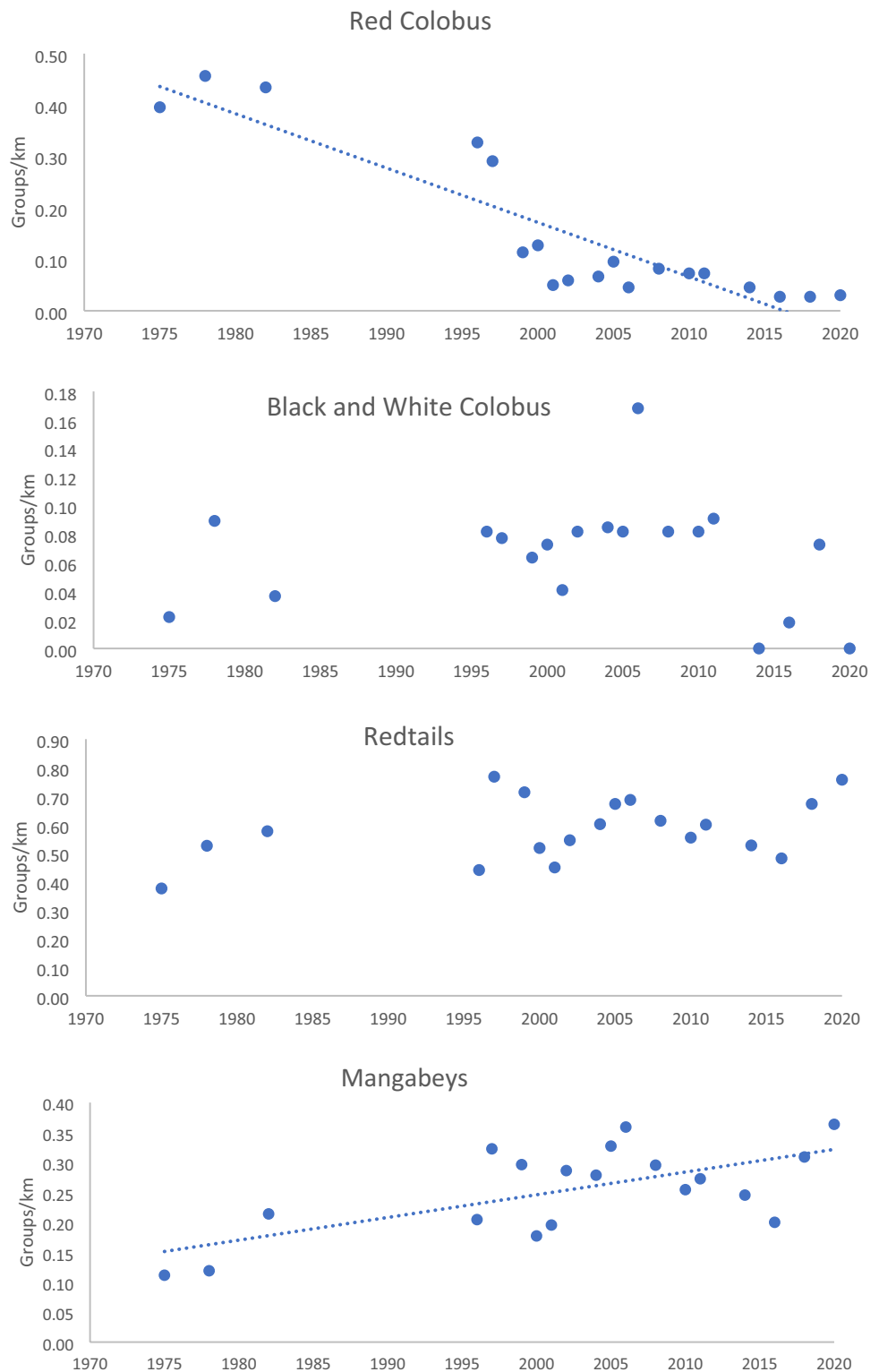
The LOESS regressions not only help visualize these large-scale trends in the encounters of the primate species described above, but they also highlight that four primate species (black and white colobus, blue monkeys, l'Hoest monkeys, and baboons) are rarely observed along this transect (Fig. 2). By contrast, redtail monkeys and red colobus were much more frequently encountered, at least during some census periods. The most dramatic change in the local populations was the near-complete collapse of the red colobus population that occurred between the mid-1990s and mid-2000s.

Discussion

Long-term data on wildlife population dynamics are crucial to inform effective conservation action. It is important to understand how undisturbed populations fluctuate in abundance over time and how quickly they recover after a decline. Unfortunately, there are very few primate studies that provide such information. Our research presents one of the rare data sets that allows such an evaluation.

Our results point to considerable demographic variability between census periods and over longer periods. This is consistent with previous empirical findings that also found considerable demographic variation over time (Barelli et al. 2023; Campos et al. 2020; Chapman et al. 2021; Davenport et al. 2022; Isabirye-Basuta and Lwanga 2008; Struhsaker 2008). Our results mostly reinforce the trends documented in the analysis of Ngogo censuses conducted between 1995 and 2007. Red colobus encounters declined over the 47 years, and this population has not recovered since the population crash between 1984 and 1996. Encounters of mangabeys and l'Hoest monkeys, on the other hand increased, while redtail monkeys and chimpanzees showed marginal increases. In contrast, blue monkey encounters declined and then increased, though these changes are not significant in our analysis by time blocks. While not significant, black and white colobus encounters increased between 1975 and 2007 (Lwanga et al. 2011), then appear to stabilize after that time. There is also an indication that encounters with this species declined from around 2014 to 2021, possibly due to increased predation by chimpanzees. This warrants further study. The increase in encounters of l'Hoest monkeys

Fig. 1 Relative abundance (groups/km) of eight species of diurnal primates at Ngogo, Kibale National Park, Uganda, between 1975 and 2021. The *dotted line* indicates if there is a significant linear change over time ($P < 0.05$; see text for exact p values). Each *point* represents a block of censuses, with the year being indicated by the start of the block (e.g., the second to last block is August 2018 to August 2020)

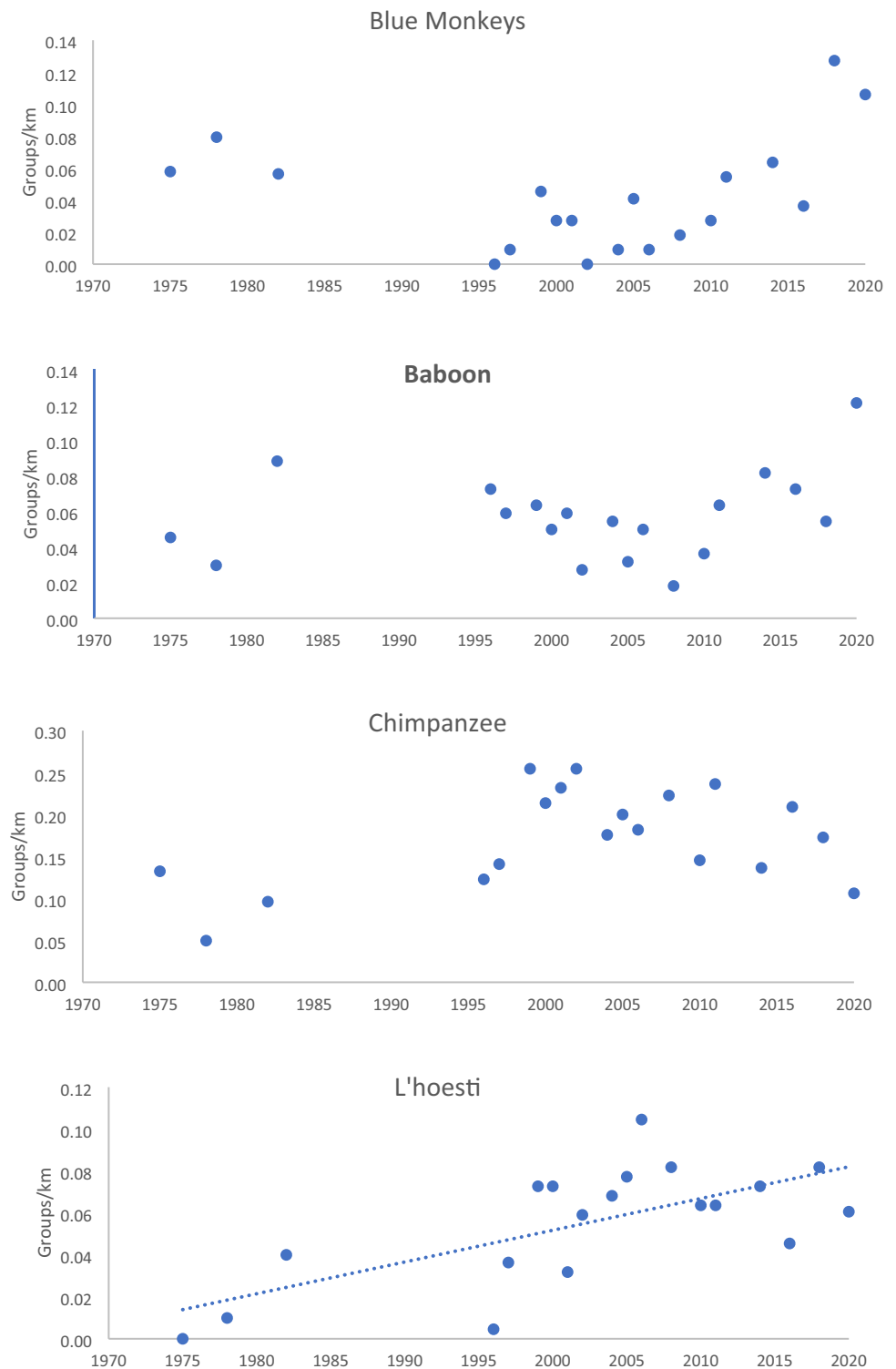


should be viewed with caution, as the number of encounters is relatively small, and it is possible that these shy animals were becoming more habituated and, therefore, easier to detect. Similarly, the abundance of chimpanzees appeared to increase marginally between the 1970s/80s and the late

1990s onward. These changes might also reflect increasing habituation.

Few studies document long-term population dynamics of primates in protected areas that were not significantly disturbed prior to receiving protection. Barelli et al. (2023)

Fig. 1 (continued)



provide an 18-year record of the abundance of Udzungwa red colobus (*Piliocolobus gordonorum*), Peters' Angola colobus (*Colobus angolensis palliatus*), and Moloney's monkey (*Cercopithecus mitis moloneyi*) in the Udzungwa Mountains, Tanzania. They document relative stability in abundance for all three species in the protected Udzungwa

Mountains National Park, but a decline in Angola colobus and red colobus in the unprotected Udzungwa Scarp Nature Reserve, while Moloney's monkey remained stable. Thus, their results from the protected area for Angola colobus and Moloney's monkey are similar to ours for black and white colobus and blue monkeys. While the Udzungwa red colobus

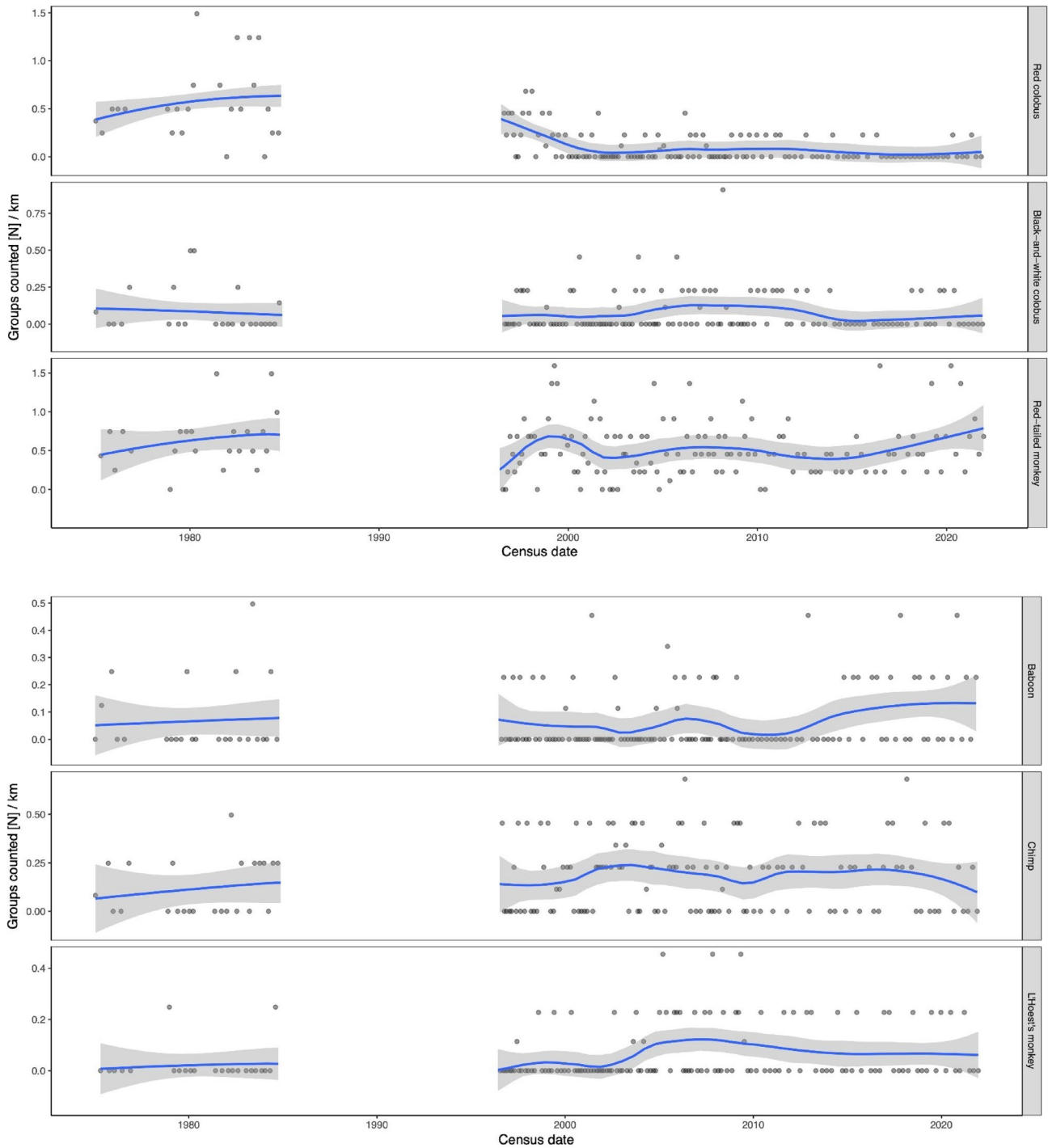


Fig. 2 Relative abundance (groups/km) of eight diurnal primate species at Ngogo, Kibale National Park, Uganda, between 1975 and 2021. Each dot represents the value from a census. The shaded intervals denote the 95% confidence intervals for the LOESS regressions, with the regression masked for the large gap in data collection

(September 1984 to July 1996). Smaller periods when data were not collected are indicated by no points associated with the month (e.g., November 1976 and October 1978). Note that the y-axis is on different scales for the different species, reflecting large differences in observation rates among species during this census

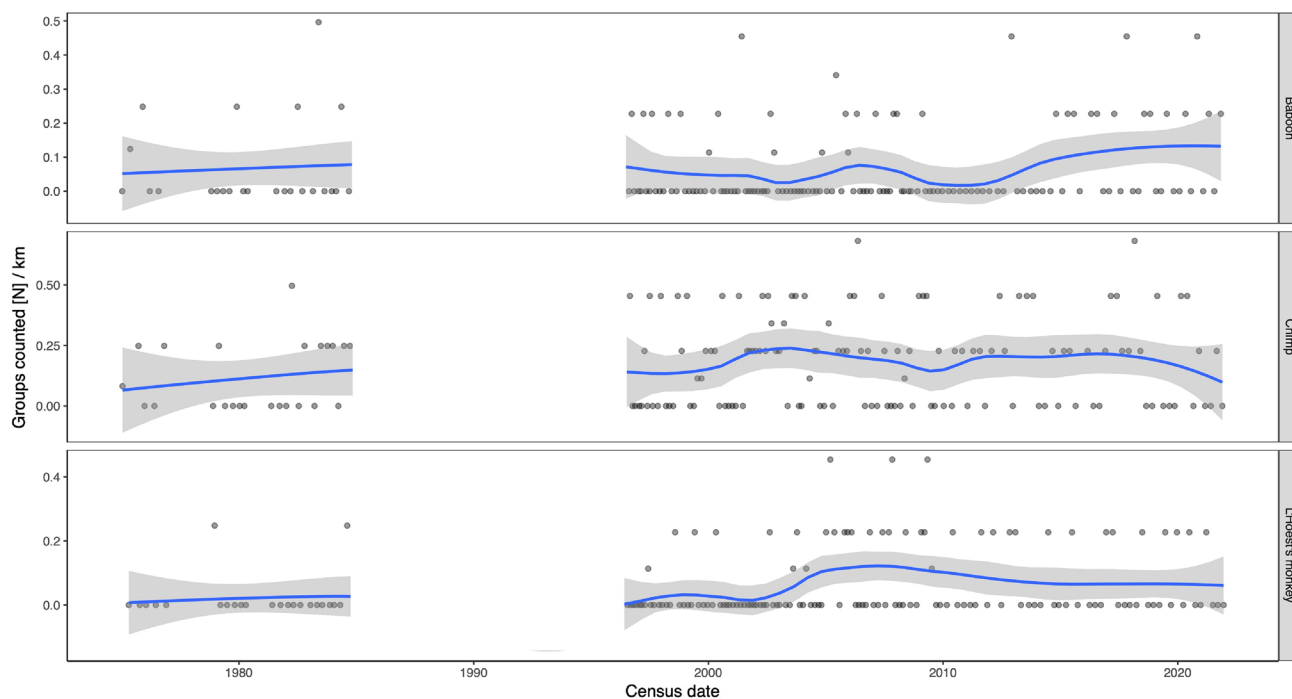


Fig. 2 (continued)

population was stable, red colobus at Ngogo declined dramatically due to chimpanzee predation.

An improved understanding of population trends can be obtained by augmenting data derived from censuses with observations of specific groups of known individuals over time. We are fortunate, as several observational studies have been conducted on the primates at Ngogo. Detailed studies of specific redbtail groups show an increase in abundance (Frogge et al. 2022). This is supported by Lwanga et al. (2011) and marginally by our data. At least two new groups of redbtail monkeys formed as the result of group fission in the vicinity of the census transect (Struhsaker and Leland 1988; Windfelder and Lwanga 2002). Frogge et al. (2022) report an increase of 27% in redbtail group density between 1981 and 2016 in the Ngogo study area. This is reflected to some extent in our results over a longer period. However, some of the new groups used areas that did not overlap our census transect. These areas were covered in grassland during the early years of research at Ngogo, but with protection against fires set by poachers, forest regeneration progressed with time, providing additional habitat for redbtails (Lwanga 2003, 2006). By contrast, the census transect described here took place in old growth forest.

Studies of blue monkeys described only one group at Ngogo along the census transect during 1978 through 1984 (Butynski 1990). Group density along and in the general vicinity of the census transect increased from one in 2009 to four in 2018. This change was due, in part, to group fission

(Angedakin and Lwanga 2011; Frogge et al. 2022), and is reflected by our data, though later in time. This increase is not more strongly indicated in our results because some of the new groups resulting from the fissions were using areas that overlapped our census transect very little (Frogge et al. 2022).

Focal studies of mangabeys at Ngogo report a significant increase in the number of groups (Frogge et al. 2022) due in part to group fission (Lysa Leland, pers. comm.) and, as with redbtails, an increase in habitat due to forest regeneration (Lwanga 2006). This increase is consistent with our findings. Frogge et al. (2022) also report an increase in group size both for mangabeys and redbtails.

The chimpanzee population at Ngogo has increased steadily over the last 2+ decades (yearly population size 1998–2022, $r=0.977$, $p<0.001$; cf. Mitani 2021). This increase is not strongly revealed in our census results because the number of chimpanzees at Ngogo expanded mainly in an area to the west of the census transect. This increase resulted, in part, from the fission of the chimpanzee community forming a splinter group that resides primarily to the west of our census transect (Sandel and Watts 2021).

The continuing decline in red colobus encounters at Ngogo supports the conclusions of earlier studies that this decline is primarily due to unusually high predation rates by chimpanzees (Mitani and Watts 1999; Watts and Mitani 2015). Such high rates have not been observed elsewhere in Kibale. Currently, few red colobus monkeys occur near

the Ngogo census transect. Chimpanzees in the two communities at Ngogo hunt these monkeys primarily around the peripheries of each of the chimpanzee's territories and in the territories of their chimpanzee neighbors (Ngogo Chimpanzee Project, unpublished data). These areas are far from the census transect, which now lies in an area of overlap between the two chimpanzee communities. If there is a reduction in chimpanzee numbers, or if the rates of predation upon red colobus decline, the population of red colobus at Ngogo is expected to increase. This suggestion is supported by the rapid rate at which red colobus have increased in other areas of the park. In some areas of Kibale, red colobus have colonized regenerating forest and reached high densities in just over a decade, but in these areas predation by chimpanzees is not thought to be a significant factor affecting population growth. For example, we quantified red colobus abundance in two areas of regenerating forest after they were cleared. Now, 24 years later, red colobus abundance in these areas is just 5% less than in adjacent old growth forest (Chapman et al. Submitted). Given the potential for rapid recoveries of red colobus populations in protected areas following a perturbation, it is striking that the population at Ngogo has not recovered from its collapse three decades ago. This suggests that chimpanzee predation is still limiting the recovery of this population.

Our results also support an earlier conclusion that the Ngogo primate community is in a non-equilibrium state (Lwanga et al. 2011). The species composition is continuously changing, with some species increasing, others decreasing, and some appearing to be stable. A similar non-equilibrium primate community is described for Kanyawara farther north within Kibale (Chapman et al. Submitted; Chapman et al. 2010a, b).

Our results highlight that extrapolating population trends to larger areas based on censuses at single locations should be done with caution. For example, while blue monkeys are relatively rare at Ngogo, they were about tenfold more common 10 km to the north at Kanyawara (Butynski 1990), while the reverse is true for mangabeys (Struhsaker 1997; Frogge et al. 2022). Red colobus are now very rare at Ngogo but are common and even increasing elsewhere in Kibale (Chapman et al. 2021). Even at Ngogo, Teelen (2007) found differences in group encounter frequencies for four of six primate species among five census transects.

Line transect censuses are a central tool of primate ecologists and conservationists. They are generally designed and used in areas where detailed studies of wildlife are absent. They are meant to provide a rough approximation of relative abundance in broad surveys covering large areas, but they are also used for a variety of other purposes including assessing population change. Studies such as ours, where data from line transect censuses can be compared with detailed focal-group studies conducted over decades, allow

an evaluation of the degree to which census results are consistent with the more detailed and accurate findings of focal studies. This provides insights into the effectiveness of transect censuses and raises important methodological issues.

Given the importance of transect census data to conservation, we encourage research into how this method of collecting data can be improved. For example, when we conducted censuses on consecutive days, we found appreciable variation, as we did between months and even years, but censusing on consecutive days may over-represent groups that are repeatedly returning to a preferred food tree or groups with short-day ranges. By typically sampling once a month, our precision curves only start to asymptote after 25 months. However, over long periods such as this, important population changes could occur. These considerations indicate that additional research is needed to determine the optimal interval between censuses. The goal would be to minimize biases, such as those associated with repeatedly finding the same group at the same site, while simultaneously maximizing the amount of data collected, resulting in increased precision. The most appropriate interval will vary depending on the diet of the species and its typical day range. In this context, it would be instructive to determine whether conducting censuses once a week is appropriate for a range of species and examine how quickly precision curves asymptote. Such a study promises to yield important results but will be difficult to implement because it would involve intensive sampling over a long time and require considerable funding. Finally, our results also demonstrate the limitations of conducting censuses in only one area if one wants to extrapolate to larger areas. This raises questions regarding the number of transects required for a given locale and how far apart they need to be to represent an area beyond the immediate vicinity of the transect.

Research in Kibale has been conducted widely over the park for more than five decades, providing detailed ecological data that can be matched with long-term monitoring of primate populations. This research shows that most primate populations are negatively affected by logging (Struhsaker 1997), but that predicting its influence on primate populations is challenging (Gogarten et al. 2012). Furthermore, many factors have been implicated in playing a role in influencing primate population dynamics in Kibale, including: changes in food availability (Chapman et al. 2021); fluctuations in food availability and quality related to climate change (Potts et al. 2020; Rothman et al. 2015); invasive plant species (e.g., *Lantana camara*) (Barahukwa et al. 2023; Omeja et al. 2016); predator prey-switching, and changes in elephant abundance. Dramatic increases in elephant numbers, following a significant decline in the 1970s, resulted in the alteration of vegetation and forest tree community structure (Chapman et al. 2010a, b; Kalbitzer et al. 2019; Omeja et al. 2014, 2012). None of these processes are likely to have

direct effects on primates (e.g., there may be thresholds, or processes may be episodic, such as droughts or disease outbreaks). These processes will change at different rates, and they will likely combine in unexpected ways. As a result, finding a clear causal relationship for such changes is problematic. We can, however, at least monitor trends in primate populations through a combination of detailed studies of groups and line transect censuses, as demonstrated by the studies at Ngogo and Kanyawara. Results from these studies provide park managers with information on shifting patterns of vegetation and animal population dynamics that can be useful in conservation planning (Sarkar et al. 2021). If a species is shown to be in decline across a park or regionally, efforts can be made to protect new areas or restore habitats that are useful to that species. This may become possible with new commitments being made to conserve areas. For example, in the UN Kunming-Montreal Global Biodiversity Framework (COP15) in 2022, delegates from 188 countries agreed to put 30% of the planet under protection by 2030. Uganda has committed to halt and reverse forest loss and land degradation by 2030 and to increase forest cover from an estimated 12.5% in 2020 to 21% in 2030. In addition, the country launched a 40 million tree planting campaign on March 2, 2021, focusing on forest restoration using indigenous trees (Updated Nationally Determined Contribution 2022).

Our studies at Ngogo demonstrate that most species of primates are increasing or stable, affirming the effectiveness of the Uganda Wildlife Authority and its collaborators. Evidence from studies elsewhere in Kibale support this conclusion and suggest that primate abundance in the park is increasing. This increase is due to several factors: primates have colonized over 15 km² of regenerating forest consisting of trees replanted as part of a carbon offset program; areas have been protected from fire; former pine plantations have been replaced by regenerating natural forest; and forests have also regenerated in the center of the park and in southern areas previously occupied by grasslands (Chapman et al. Submitted; Sarkar et al. 2021; more research in the south and east of Kibale is needed).

Despite the largely positive picture of primate conservation in this region of the park that emerged from our long-term datasets, the threats to animals in Kibale National Park might change in the future, and we do not suggest complacency. Between 2000 and 2020, the human population within 1 km of the edge of the park almost doubled, increasing from 123 to 229 individuals per km², with further rapid population growth predicted for this region (MacKenzie et al. 2017; WorldPop 2020). While our data suggest that the management of the park and considerable efforts of researchers and conservation biologists in the region have so far been able to cope with the large human population growth, at least in terms of primate conservation, the impact of climate change,

changing human lifestyles, and predicted continued population growth, are unknown and expected to bring with them new challenges. Given these expected increasing pressures on the park, every effort must be made to gain support from the neighboring communities for the conservation of Kibale National Park and continue funding conservation initiatives and raising the voices of the next generation of conservation biologists in the region.

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Data Availability Not Applicable.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Ethical standards The research complies with the ethical standards of our field and animals were only observed from a distance to cause as little disturbance as possible. Permission for this research was given by the Uganda National Council for Science and Technology, Uganda Forest Department, Uganda Wildlife Authority, and Makerere University Biological Field Station.

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