BRILL *Behaviour (2022)* DOI:10.1163/1568539X-bja10160 **Behaviour** brill.com/beh

Constraints on population growth of blue monkeys (*Cercopithecus mitis*) in Kibale National Park, Uganda

Hannah Frogge [a], **Revee A. Jones** [b], **Samuel Angedakin** [c], **Richard Busobozi** [d], **Prime Kabagambe** [d], **Felix O. Angwela** [d,e], **Nicole Thompson González** [a] and **Michelle Brown** [a,f,g,*]
[a] Department of Anthropology, University of California, Santa Barbara, CA, USA
[b] Division of Solid Tumor Oncology, Memorial Sloan Kettering Cancer Center, New York, NY, USA
[c] Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[d] Makerere University Biological Field Stations, Kampala, Uganda
[e] School of Agriculture and Environmental Science, Mountains of the Moon University, Fort Portal, Uganda
[f] Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany
[g] Department of Biology, University of Konstanz, Konstanz, Germany
[*]Corresponding author's e-mail address: mbrown@anth.ucsb.edu
ORCID iDs: Frogge: 0000-0003-0949-3051; Angedakin: 0000-0002-7471-3332;
Angwela: 0000-0001-5495-0974; Thompson González: 0000-0002-3195-1277;
Brown: 0000-0002-2995-1745

Received 9 October 2021; initial decision 14 December 2021; revised 23 January 2022; accepted 15 March 2022; published online 15 April 2022

Abstract
Changes in population size are driven by environmental and social factors. In spite of repeated efforts to identify the constraints on an unusually low-density population of blue monkeys (*Cercopithecus mitis*), it remains unclear why this generalist species fails to thrive in Kibale National Park in Uganda. While an unidentified disease may occasionally obstruct conception, it does not seem to limit overall reproductive rates. Infanticide at this site is infrequent due to the long tenures of resident males. Our analyses indicate that the single biggest constraint on blue monkey densities may be feeding competition with grey-cheeked mangabeys (*Lophocebus albigena*): across Kibale, the densities of these two species are strongly and negatively correlated. Though further analysis is needed to understand the timing and strength of feeding competition between them, we conclude that blue monkeys at Ngogo experience competitive exclusion from grey-cheeked mangabeys, possibly resolving the 50-year mystery surrounding this population.

DOI 10.1163/1568539X-bja10160

Keywords
competitive exclusion, resource competition, wildlife health.

1. Introduction

As primate populations decrease globally, identifying the factors that drive the distribution and abundance of primates is of central importance to conservation. Population size and change are shaped by births, deaths, and migration rates (Sibly et al., 2002), which are influenced by a number of external environmental factors (e.g., food availability, predation, human interference) as well as social factors (e.g., infanticide and territorial dynamics). As multiple factors can jointly affect population growth rates, determining the specific drivers for any one population can be a complex endeavour. This is particularly true in long-lived animals that require monitoring over extended periods (Packer et al., 2005; Chapman et al., 2010; Colchero et al., 2021), in which regular constraints are often interspersed with singular and dramatic events such as mass die-offs (Packer et al., 2005; Azeem et al., 2010; Milton & Giacalone, 2014). One result of this complexity is that many primate studies focus on a single environmental variable to explain population dynamics (e.g., food availability: Worman & Chapman, 2006; disease: Caillaud et al., 2006). Here, we evaluate several mechanisms simultaneously to investigate the potential causes for the persistently and unusually small population of blue monkeys (*Cercopithecus mitis*) at the Ngogo site in Kibale National Park, Uganda. Previous observations at this location led to three proposed mechanisms of population constraint: inter-species competition for food resources; disease; and infanticide (Butynski, 1990). We use demographic and behavioural data to evaluate each of these proposed mechanisms.

Although several factors usually commingle to influence population dynamics, food and nutrient availability are often primary drivers of population size. Across three continents, the biomass of diurnal, frugivorous primates increases with annual fruit abundance (Hanya et al., 2011). This trend is also apparent in studies of individual species (e.g., chimpanzees, *Pan troglodytes*: Balcomb et al., 2000). The specific nutritional content of food, such as the protein-to-fibre ratio (Gillespie et al., 2004) and the ratio of copper to total energy (Rode et al., 2006), may further constrain population size. The predictive power of food and nutrient availability for primate population size is not universal, however, and is sometimes stronger or more consistent for one species than for others within the same feeding guild (Chapman et al., 2010, 2015). Across sites within Kibale, blue monkey density corresponds with the density of food trees but grey-cheeked mangabey (*Lophocebus albigena*) density does not (Worman & Chapman, 2006). In contrast, long-term analyses restricted to the Kanyawara site in Kibale indicate that stable food availability corresponds with a decrease in blue monkey density and an increase in mangabey density (Chapman et al., 2010). Such inconsistent patterns indicate that other factors may moderate the effects of food availability on population size.

Though rarely documented, disease has potentially powerful effects on primate population dynamics (Daszak & Cunningham, 1999). Viral epidemics have been responsible for decimating certain populations, such as Ebola virus in western lowland gorillas (*Gorilla gorilla gorilla*: Caillaud et al., 2006), and human-origin rhinoviruses and paramyxoviruses in chimpanzees (Scully et al., 2018; Negrey et al., 2019; Köndgen et al., 2008). Many such diseases are exacerbated by human disturbance, but on rare occasions, zoonotic pathogens and naturally occurring parasites wreak similar outcomes. Parasites have the potential to cause population decline in primates via their profound effects on survival and reproduction (Nunn, 2012). For example, adult mortality from botfly infection led to a $>$20 year plateau in the population size of Panamanian howler monkeys (*Alouatta palliata*: Milton, 1996). Similarly, in non-primates, parasite load is a primary constraint on population size via its effects on female fertility (Clutton-Brock & Coulson, 2002; Hudson et al., 2002).

Infanticide is commonly identified as a selective force on female social behaviour and reproductive strategies (Sterck et al., 1997), but may also strongly influence group demography and consequent population growth (Fedigan et al., 2021). Indeed, in some mammalian populations, infanticide is the primary cause of infant mortality (Lukas & Huchard, 2014) and may operate as a strong constraint on population size. In white-faced capuchins (*Cebus capucinus imitator*), infanticide negatively affects female lifetime reproductive success (Fedigan et al., 2021). In mountain gorillas (*Gorilla beringei beringei*), high population density led to more frequent intergroup encounters and subsequent infanticides, which accounted for a 57% decline in population growth (Caillaud et al., 2020). Alternatively, infanticide can operate as a secondary constraint: at low population densities, female Hanuman langurs (*Presbytis entellus*) form groups that are smaller and easier for a single male to monopolize, and for another to take over (Moore, 1999). These male takeovers are the context in which infanticide typically occurs, reducing infant survival and slowing recruitment into older age cohorts.

Although predation often limits population growth, it is not thought to be a strong constraint for blue monkeys at the Ngogo research site in Kibale National Park: studies of predator diets indicate that blue monkeys are rarely consumed, and victims are typically solitary or peripheral males (Struhsaker & Leakey, 1990; Watts & Mitani, 2015). Additionally, while population density tends to be lower at the edge of a species' range than in the center (Brown, 1984), leading to stronger Allee effects at the edge of the range (Caughley et al., 1988), this pattern does not explain why the Ngogo deme is far less dense than other peripheral demes. Compared to the nearby Kanyawara site, just 15 km away, where the density of blue monkeys was 52 individuals/km^2, Ngogo contained just 4 individuals/km^2 in 1984 (Butynski, 1990). This is especially striking in comparison with the Isecheno site in Kakamega Forest, Kenya, another peripheral deme, where the density of blue monkeys was recorded as 220 individuals/km^2 (Fashing & Cords, 2000). While low densities are to be expected in small, heavily encroached forest fragments (Plumptre & Cox, 2006), the low density of blue monkeys at the food-rich, high-quality, old-growth Ngogo site has stumped researchers for nearly 50 years (Lwanga et al., 2011; Butynski, 1990; Angedakin & Lwanga, 2011; Chapman & Lambert, 2000). To add to the mystery, blue monkeys are entirely absent from the southern half of the park (Figure 1). Yet the sites with few or no blue monkeys are thought to be ideal habitat for this dietary and habitat generalist, evidenced by the growing numbers of red-tailed monkeys (*Cercopithecus ascanius*), grey-cheeked mangabeys, and chimpanzees (Lwanga et al., 2011; Chapman et al., 2018), which consume many of the same foods as blue monkeys (Struhsaker & Leland, 1979; Conklin-Brittain et al., 1998).

In this study, we re-evaluate the factors proposed to constrain the growth of the blue monkey deme at Ngogo: inter-species feeding competition, disease, and infanticide have all been proposed as potential explanations for the unusually small number of blue monkeys at this site (Butynski, 1990; Angedakin & Lwanga, 2011). As is the custom for studies at multiple sites within a single forest or region, we refer to the distinct communities at each site in Kibale as a 'deme' (Chapman & Chapman, 2000; Chapman et al.,

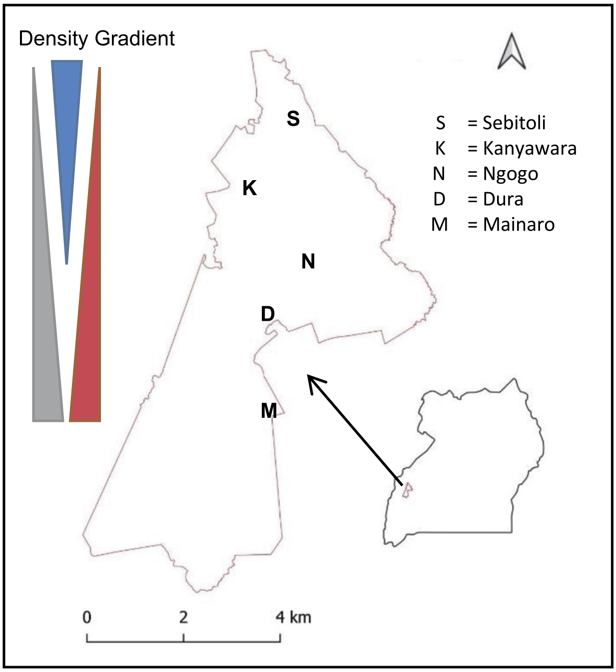

Figure 1. Research sites (letters) in Kibale National Park (red outline) in western Uganda (black outline), where monkey populations were censused from 1975 through 2018 (Butynski, 1990; Chapman et al., 2000, 2018; Chapman & Lambert, 2000; Teelen, 2007; Lwanga et al., 2011; Brown, 2013; this study). Grey, blue, and red wedges indicate the north-to-south gradient in population density for grey-cheeked mangabeys, blue monkeys, and red-tailed monkeys.

2002), e.g., the Kanyawara blue monkey deme versus the Ngogo blue monkey deme. We begin with an update on the size and composition of the Ngogo and Kanyawara demes, and compare these to earlier reports to calculate the changes in deme size. For Ngogo, we also calculate the historical density trends of competing red-tailed monkeys, grey-cheeked mangabeys, and chimpanzees for comparison with the blue monkeys. We then consider how our recent observations of these groups pertain to the three potential constraints described above. To evaluate whether inter-species feeding competition might explain the low numbers of Ngogo blue monkeys (H1), we test for correlations in the density of blue monkeys versus red-tails, mangabeys, and chimpanzees at sites throughout Kibale National Park. We also take a more focused approach by evaluating dietary overlap among these species within the Ngogo site. To determine whether a persistent disease is responsible for the small deme size (H2), we discuss the patterning of disease symptoms and whether these correspond with decreased reproduction or survival. Finally, to examine the role of infanticide (H3), we qualitatively discuss the frequency with which resident males are replaced in groups, the disappearance of unweaned infants, and any presumed infanticides.

2. Methods

2.1. Study site and species

Kibale National Park (0°13–41′N, 30°19–32′E) is located in western Uganda and consists largely of old-growth rainforest of varying elevation and slope, interspersed with smaller patches of grassland, woodland, and swamp (Struhsaker, 1997). Kibale experiences two wet and two dry seasons each year, with annual rainfall averaging 1689 mm (Chapman et al., 2017). The Ngogo research station (0°29′N, 30°25′E) is located in the center of the northern portion of Kibale, while the Kanyawara station (0°33′N, 30°21′E) is on the north-western boundary of the park and is adjacent to a village. Elevation ranges from 1250–1525 m at Ngogo and from 1400–1650 m at Kanyawara. Each research station is overlaid by a dense network of trails, generally spaced 50-100 m apart, to facilitate observations of wild primates.

Blue monkeys live in permanent, mixed-sex groups consisting of one adult male and multiple adult females, subadults, juveniles, and infants (Rudran, 1978). The average size of blue monkey groups varies within and across forests, with a group size of 14.3 (7.9 adult females) in Kibale (Lwanga, 1987; Butynski, 1990; Angedakin & Lwanga, 2011; Gorgaten et al., 2015; this study), and 32.6 (10.9 adult females) in Kakamega (Cords, 1987; Gao & Cords, 2020). Females are philopatric, begin reproducing at 6–7 years old, give birth approximately every 24–36 months, and can live >20 years in the wild, which means that groups are composed of multi-generational matrilines (Cords & Chowdhury, 2010). Though blue monkeys appear to prefer to eat ripe fruit, their diet consists of large fractions of unripe fruit, young leaves, and insects, as well as smaller fractions of many other plant parts and small vertebrates (Rudran, 1978). They are described as territorial in Kenya (Cords & Rowell, 1986; Cords, 1987; but not in South Africa: Lawes & Henzi, 1995), where adjacent groups enforce strict boundaries and generally win intergroup conflicts initiated on their side of the boundary.

Because of the multi-generational nature of social groups and their pattern of spatial defence, a group occupies the same home range for many years — even decades (Cords & Rowell, 1986; Cords & Chowdhury, 2010).

2.2. Behavioural observations

We followed blue monkey groups intermittently at the Ngogo and Kanyawara research stations from October 2013 through August 2019, in the context of three different research projects. Several primary groups were followed at each site (Table 1), with an additional three groups at Ngogo tracked for short periods for the purpose of establishing the density of groups, their composition, and home range size. Every individual in each group is uniquely identifiable on the basis of scars, stiff fingers, tail shape, and the size and colour of nipples (for adult females). All observers carried Apple iPods with labelled photos of each blue monkey to facilitate reliable identifications.

After an initial assessment period (October 2013 through May 2014) in which we identified groups and individuals at the two sites, we began intensive observations of group dyads at Ngogo, each consisting of one blue monkey group and one matching group of grey-cheeked mangabeys whose home range overlapped extensively with the blue monkey group. We followed the two groups in each dyad simultaneously, for periods lasting from 7 to 12 months, starting in October 2015 and ending in July 2019. At Kanyawara, we followed only one blue monkey group at a time from September 2018 through August 2019.

In each observation month, we followed a group for several consecutive days (mean 5.5 ± SD 2.5 days). We tracked groups from dawn until dusk on observation days and recorded the presence or absence of each group member, whether they exhibited disease symptoms, and whether an unweaned, dependent infant accompanied each adult female. We recorded the location of the group centre-of-mass using a handheld GPS unit every 30 minutes, as well as the presence of other primate species within 50 m of the focal group. Monkeys in African rainforests often travel together in polyspecific associations (Struhsaker, 1981), which could intensify the feeding competition among them. In the period spanning October 2015 through March 2018, we recorded all foraging activity during the first 5 min of each group scan that occurred every 30 min: we noted the identity of foraging individuals, the plant species consumed (or we recorded ‘insect’ if the animal was foraging on invertebrates), and the plant part (fruit, flowers, young or mature leaves, or ‘other’).

Table 1.

The size, composition, and number of blue monkey study groups at the Ngogo and Kanyawara research sites in Kibale National Park in western Uganda.

	Ngogo*				Kanyawara**	
	1978–1984[1]	1984–1985[1,2]	2009[3]	2013–2019[4]	1973–1984[1,5]	2013–2019[4]
Group name	33	33-1	1	BN1	1	BK1
			2	BN2	2	BK2
				BN5	3	BK3
				BN6	4	
No. of observation months	64	21	6	13	72	8
			6	27	70	6
				17	61	4
				6	71	
Mean group size[a] (adult females)	13.0 (12.0)	9.3 (6.0)	13.0 (12.0)	6.4 (3.2)	8.5 (7.5)	14.0 (11.0)
			15.0 (14.0)	4.8 (2.8)	6.6 (5.3)	7.0 (5.0)
				8.7 (5.7)	16.0 (15.0)	9.0 (6.5)
				6.0 (4.0)	10.8 (9.5)	
Mean birth rate (infants per female per year)	0.42	0.40	0.08	0.75	0.30	0.25
				0.20	0.31	0.20
				0.50	0.11	0.33
				0.33	0.22	
# resident male takeovers	2	2	0	1	0	0
			0	1	0	1
				0	1	0
				0	1	
Home range size[b] (km^2)	2.53	1.74	0.91	0.76	0.44	0.32
			0.48	1.29	0.27	0.22
				1.09	0.30	0.22
				0.39	0.45	

[1] Butynski (1990); [2] Lwanga (1987); [3] Angedakin & Lwanga (2011); [4] this study; [5] Rudran (1978).

*Group 33 split into 33-1 and 33-2 in 1984 and soon after, 33-2 left the study site (Butynski, 1990). Group 1 is suspected to have split into BN1 and BN2 between 2009 and 2013, and group 2 split into BN5 and BN6 between 2014 and 2016.

**The groups were initially mis-identified in the current study so Butynski's groups 1, 2, and 3 correspond with BK3, BK2, and BK1, respectively.

[a] Group size is the number of adults and subadults, excluding juveniles and infants.

[b] Calculated as the summed area of the 50 m × 50 m grid cells used by the study group.

2.3. Historical density trends

To generate current estimates of deme size, we first calculated group density for the Ngogo and Kanyawara blue monkey demes from 2008 through

2019 by generating home ranges as 95% kernel density polygons using the mean squares smoothing function in Biotas v2.0a3.8 (Ecological Software Solutions, Naples, FL, USA) from the 30 min group scans. We then determined the percentage of each home range that fell within a 1 km^2 portion of the study site and summed these proportions to calculate the group density. The difference between our estimates of group density versus those listed in Brown & Waser (2018) arises from the different methods for generating home ranges (i.e., 100% minimum convex polygons versus 95% kernel density polygons).

To compare the changes in density of other demes of arboreal, frugivorous primates at Ngogo, we multiplied group density estimates by group size to generate estimates of the number of individuals/km^2. We calculated group size as the sum of adults and subadults, excluding juveniles and infants, because the latter exhibit much higher mortality rates and their numbers fluctuate more quickly than those of the independent individuals. In addition, we are interested in measures of the reproductive capacity of the demes and dependent individuals should not be included in such a measure. Some authors only report total group size, however, so in these cases we multiplied this number by the expected ratio of independents to total group size using group composition data from a comparable study in Kibale of the same species, from the period closest to the study of interest. At Kanyawara, we only used group size and group density estimates for the K30 (unlogged) and K14 (lightly logged) compartments (and not from the heavily logged K15 compartment), as this is where most of the study groups occurred. We then calculated the annual population growth as the change in group size, divided by the original group size, and then divided by the number of years between consecutive studies. We also report the percent change in population size from the first study to the most recent population estimate. While these estimates are useful for identifying general trends, it should be remembered that they are hyper-local in nature. For instance, data on the density of red-tailed monkeys at Ngogo is largely confined to one river valley south of the camp site (an area of approx. 3 km^2) and it is unknown whether this portion is representative of the entirety of the Ngogo site (approx. 33 km^2).

2.4. *Testing hypotheses*

To determine whether blue monkey populations are adversely affected by feeding competition from other primate species (H1), we used population estimates from the literature for blue monkeys, red-tailed monkeys, chimpanzees, and grey-cheeked mangabeys across all research sites within Kibale (1973–2020, see Table A1 in the Appendix at 10.6084/m9.figshare.19368716). As chimpanzee densities are typically reported as the number of new nests per km walked, we converted this to a population estimate by dividing by a correction factor for the number of nests built per day per individual (1.09), and multiplying by a correction factor (1.2) to account for the fact that juveniles and infants do not build their own nests (Plumptre & Cox, 2006). Most sites in Kibale were censused in multiple years. To reduce auto-correlation among the census results for a particular site, we used census records separated by approx. 10 years. Due to the small sample size, there was insufficient power to conduct a multi-level analysis, so the results should be interpreted with caution. Authors reported their results using one of several measures of population density (groups or individuals per km^2) or relative abundance (groups or individuals encountered per kilometre of census transect). In some cases, we were able to convert into other units where mean group sizes had been reported for the site. Finally, although Chapman et al. (2018) divide the Kanyawara site into compartments based on their logging intensity, we averaged across these compartments because they are adjacent and compartments are sometimes smaller than the primate home ranges. We then analysed the data using linear regressions in Stata v17 (StataCorp, College Station, TX, USA) to test for correlations in species densities. We chose not to use a Bonferroni correction for multiple testing because this is a preliminary analysis, meant to guide further research rather than serve as a definitive test of a hypothesis (Nakagawa, 2004; Garamszegi, 2006).

To evaluate feeding competition on a smaller spatial scale, we compare the foraging and space use of blue monkey-grey cheeked mangabey group dyads (where a dyad is composed of one group of each species whose home ranges overlap extensively; data from the Ngogo Monkey Project, 2015-2018). For the foraging data, we compiled all records of feeding on plant parts and tallied them by plant species and blue monkey group ID. We considered a plant species to be an important part of the diet if it constituted $\geqslant 1\%$ of the annual diet of at least one group. We then determined the spatial overlap per monkey dyad using the home range polygons and the ‘merge’ and ‘dissolve’ functions in QGIS v3.10.12. We determined the amount of time each blue monkey group spent in association with their overlapping mangabey group as the percent of 30 min scans in which the two groups were within 50 m of each other.

To assess the extent to which the Kibale blue monkey communities exhibit signs of active disease (H2; symptoms are described in the Results section), we tally the number of symptomatic versus total individuals per group and per month (data from the Ngogo Monkey Project, 2013–2019), and from this we calculate the prevalence of disease symptoms (where total group size consists of adults and subadults only). If the symptoms are caused by a parasite species, we expect the likelihood of symptoms to increase with rainfall because the latter can influence host condition and host-parasite interactions. As no more than two individuals per group were symptomatic at a given time, we scored symptoms as present or absent per group-month. We tested this prediction using the lme4 package (glm function, binomial family) in R v1.4.1717 (R Core Team, 2021) with presence or absence of symptoms per month as the response variable, mean monthly rainfall as the predictor, and group identity as a random intercept. We conducted a Hosmer-Lemeshow goodness-of-fit test using the performance package to check model quality.

To evaluate whether the frequency of male takeovers and infanticide might constrain population growth (H3), particularly at Ngogo, we qualitatively discuss the frequency of births per female, infant disappearances, the size of the juvenile cohort, and male turnover (data from the Ngogo Monkey Project, 2013–2019). Where possible, we tally the number of infants who disappeared within 6 months after birth and note whether their disappearance coincided with the replacement of the resident male.

2.5. *Ethical statement*

The data collection protocols for this study were approved by the Institutional Animal Care and Use Committee at the University of New Mexico (approval No. 11-100661-MCC, for field work that occurred in 2013–2014) and deemed exempt by the IACUC at the University of California, Santa Barbara, CA, USA (2015–2019). Permissions to conduct the studies were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Uganda Office of the President. All research activities were conducted in compliance with Ugandan national laws, in adherence with the ASAB/ABS Guidelines for the Use of Animals in Research, and all institutional guidelines. The non-invasive field observations were conducted within Kibale National Park, a public entity managed by the Uganda Wildlife Authority. The IUCN conservation status of blue monkeys is ‘least concern’ and no monkeys were handled, captured or otherwise manipulated during this study.

3. Results

3.1. Deme status

The density of all arboreal, frugivorous primate demes (blue monkeys, red-tailed monkeys, grey-cheeked mangabeys, and chimpanzees) at Ngogo increased from the 1970s through the 2010s but the magnitude of change differed dramatically across species and years (Figure 2, Table A1 in the Appendix at 10.6084/m9.figshare.19368716). Red-tailed monkeys exhibited the largest total increase in density (+109% over 35 years, for a mean percent change of +3.1%), followed by grey-cheeked mangabeys (+88% ÷ 42 years = +2.1% change). The size of the resident chimpanzee community also increased within the much narrower range of years in which these records were collected (+52% ÷ 17 years = +3.0% change). By comparison, the density of blue monkeys at Ngogo and Kanyawara increased very little (Ngogo: +17% ÷ 40 years = +0.4% change; Kanyawara: +9% ÷ 47 years = +0.2% change). The Kanyawara deme of blue monkeys remains larger than the Ngogo deme (1981-1982: 14.2 times larger; 2018-2019: 8.2 times larger) and is characterized by larger group sizes and smaller home ranges (Table 1).

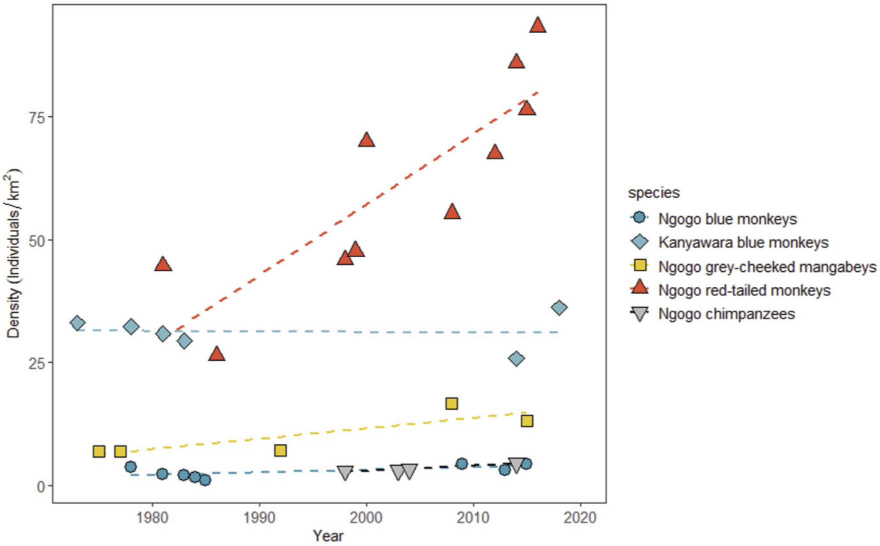

Figure 2. Changes in deme density of red-tailed monkeys, grey-cheeked mangabeys, chimpanzees, and blue monkeys at the Ngogo and Kanyawara research sites. See Table A1 in the Appendix at 10.6084/m9.figshare.19368716 for details.

The small size of the Ngogo groups appears to be the product of recent group fissions. The two groups studied by Angedakin & Lwanga (2011) split between 2009 and 2013, resulting in four daughter groups and in the disappearance of some adults (Table 1). In spite of the higher birth rates, there was no recruitment from the juvenile to the adult age classes via maturation in the Ngogo groups. There were no subadult or juvenile females in BN2 to mature into the adult age category, and the one subadult female and two unsexed juveniles who were present in BN1 in 2014 disappeared before observations resumed in 2015. However, an adult female immigrated into BN2 in October 2015, an event that is considered highly unusual for this female-philopatric species (Lawes et al. 2013).

3.2. H1: feeding competition

Across all sites in Kibale, the population size of blue monkeys is strongly and negatively correlated with that of grey-cheeked mangabeys, but not with chimpanzees or red-tailed monkeys (Table 2). At locations where the relative abundance of grey-cheeked mangabeys is relatively high, blue monkeys are absent (Figure 3). In contrast, the abundances of red-tailed monkeys and mangabeys correlate positively with each other.

We explored the potential for between-species feeding competition at the Ngogo site (2015–2018). Fruit feeding by blue monkeys constitutes 61–91% of the foraging records on plant-based foods, and the diet of blue monkeys overlaps more closely with grey-cheeked mangabeys than with other frugivorous primates, confirming older reports from a nearby site (Struhsaker,

Table 2.
Linear regression analyses of the relationships between deme sizes of frugivorous primates sampled at five sites and over 45 years, within Kibale National Park.

Species pair	Measurement unit	Coefficient	p	R^2	N
BL vs. RT	groups/km walked	−0.20	0.195	0.06	15
BL vs. MY	groups/km walked	−0.62	0.004*	0.45	*15*
BL vs. CH	individuals/km^2	−2.79	0.185	0.24	6
RT vs. MY	groups/km walked	1.01	0.011*	0.35	*15*
RT vs. CH	individuals/km^2	18.17	0.297	0.08	6
MY vs. CH	individuals/km^2	−0.64	0.909	0.00	6

BL, blue monkey; RT, red-tailed monkey; MY, grey-cheeked mangabey; CH, chimpanzee.
*Significant relationships ($p < 0.05$).

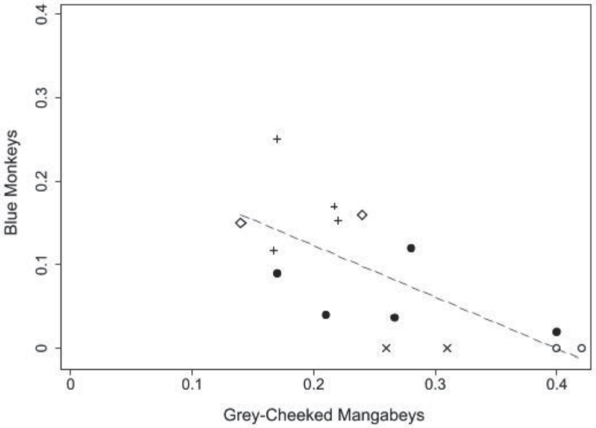

Figure 3. Deme relative abundance (groups/km walked) for blue monkeys and grey-cheeked mangabeys across five sites in Kibale National Park, sampled intermittently from 1975 through 2018. Legend: (●) Ngogo; (+) Kanyawara; (○) Mainaro; (◇) Sebitoli; (×) Dura.

1978; Conklin-Brittain et al., 1998). We identified 34 important food species for blue monkeys (i.e., species that were ⩾1% of the annual sum of plant foraging records for at least two groups), many of which were also important foods for the other primate frugivores: 85% of these foods were also important for mangabeys in 2015–2018, 65% for red-tailed monkeys in 2008 (Brown, 2013), and 44% for chimpanzees (Watts et al., 2012; Table A2 in the Appendix at 10.6084/m9.figshare.19368716). While a high degree of dietary overlap suggests a strong potential for inter-species competition, it does not explain why competitive exclusion only occurs between blue monkeys and mangabeys, and not with the other primate species. For instance, in 270 days of observing blue monkey-mangabey group dyads, there were only eight observations of interspecies agonism: the instigator was a mangabey in five instances, and a blue monkey in three instances. There were nine agonistic incidents between blue monkeys and red-tailed monkeys, and 27 incidents between mangabeys and red-tailed monkeys.

There is also a surprisingly high degree of alignment in the placement of blue monkey and grey-cheeked mangabey home ranges (Figure 4; 2015–2019). In the four dyads that we studied, the species' home ranges were similar in size (blue: 1.64 ± 0.60 km^2; mangabey: 1.42 ± 0.28 km^2) and much of the home range area was shared; within the combined area of a blue and mangabey dyad, the blue monkey ranges constituted 77–100% of

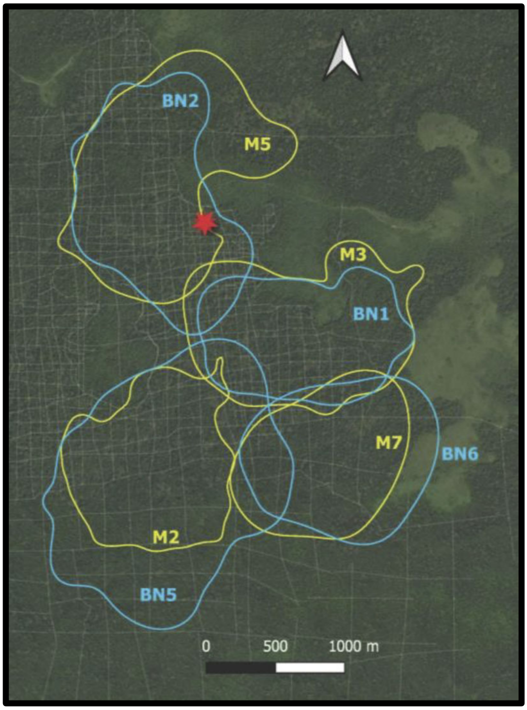

Figure 4. Home ranges of paired blue monkey (blue polygons and text) and grey-cheeked mangabey (yellow polygons and text) study groups, overlaid on the trail system. Red star indicates the location of the Ngogo camp site. Home ranges are drawn as 95% kernel density estimates.

the combined area. Yet this spatial alignment is unlikely to be achieved by traveling together: blue monkeys spend only (mean ± SD) 36 ± 21% of their time in association with mangabeys.

3.3. H2: infectious disease

During observations conducted on blue monkey groups at Ngogo from 2013 through 2019, multiple male and female members from groups BN2 and BN1 exhibited symptoms suggestive of infectious disease. When symptomatic, an individual drags its anus along branches (‘butt-scooting’) and frequently licks its hand and then uses the hand to apply saliva onto its unusually red and hairless anogenital area. Males also apply saliva to the penis. The symptoms are not accompanied by coughing, sneezing, vomiting, or diarrhoea. Symptoms are observed a few or many times per day, which we score as moderate or intense severity, respectively. When the symptoms are intense, individuals often interrupt feeding bouts to rub the fruit or leaf being consumed against the inflamed area.

We consider these behaviours to be highly unusual within the Ngogo and Kanyawara research sites because they are limited to a few blue monkey groups and other primates do not exhibit these symptoms. Within the Ngogo groups with symptomatic individuals (BN1 and BN2), only a few animals were afflicted and only in some months. The monthly prevalence of symptomatic individuals was (mean ± SD) 0.01 ± 0.04 for BN1 ($N = 10$ months) and 0.19 ± 0.17 for BN2 ($N = 23$ months). The symptomatic individuals were a subadult male and a juvenile in BN1, and three adult females and one subadult male in BN2. Though some studies find correlations between helminth or viral infections and rainfall, there was no such correlation between symptoms and rainfall for the Ngogo blue monkey deme (generalized linear mixed model: $N = 33$, $p = 0.155$, $Z = 1.42$; goodness-of-fit-test: $\chi^2 = 3.417$, $p = 0.491$).

In addition to the individuals with active symptoms, there was one adult female in BN2 and one in BK2 who presented with perianal alopecia and hyperpigmentation. We never observed these individuals butt-scooting or applying saliva to the afflicted area, but we interpret their physical characteristics as potentially indicating a history of disease that had either been resolved or which was dormant during the years in which we observed blue monkeys.

The location of the inflamed area(s) is suggestive of a sexually transmitted infection and we suspect that the underlying pathogen interferes with reproduction because symptomatic females were never accompanied by dependent offspring ($N = 3$ females). When females in BN1 or BN2 had infants, it was only after their symptoms subsided. The one female in BN2 who frequently exhibits intense (rather than moderate) symptoms has never been accompanied by dependent offspring, nor have we seen evidence, such as an enlarged abdomen, that she might be pregnant. This female was the 2015 immigrant and exhibited neither active symptoms nor evidence of a history of symptoms in her first year in the BN2 study group.

3.4. H3: infanticide and male turnover

We counted 11 unweaned infants in the blue monkey study groups at Ngogo and 6 infants in the Kanyawara groups between 2013-2019. We observed 9 of the Ngogo infants for sufficiently long that we could determine their proximate fates: 7 survived to become juveniles and 2 disappeared. One of these disappearances coincided with a resident male replacement in group BN1 that occurred during a gap in observations between late November 2013 and early February 2014. The second infant disappeared from group BN5 during a 2-month gap in observations between February and May 2017; when we resumed observations, the mother of the missing infant was intermittently absent from the group for the subsequent 5 months (i.e., within each 2-week observation period per month, she was present in the group on some days and absent on others) before resuming full-time residency in October. There was no change in male residency in BN5 during this time. In sum, we suspect that the BN1 infant was killed by the new male resident whereas the death of the BN5 infant was not attributable to infanticide.

Due to the intermittent nature of group observations, we cannot determine the exact length of male tenure. However, male replacements occurred in 2 of the Ngogo study groups during a 2 month-long observation gap in December 2013 and January 2014, and the new males continued to be present for several years afterward: the BN1 male was still present 31 months later, and the BN2 male was present 79 months later. These multi-year tenures are much longer than the mean tenure of 5.8 months reported by Butynski (1990) for the Ngogo study group in the 1970s–1980s. At Kanyawara, the resident male in BK1 was present for at least 63 months. Based on this limited number of males, we can at least say that some males have multi-year tenures at both sites.

Resident male replacement and subsequent infanticides are often preceded by multi-male influxes during mating seasons (Cords & Fuller, 2010), yet we rarely observe influxes in Kibale blue monkey groups. We observed all or part of 7 mating seasons for 5 Ngogo groups and 3 seasons for 3 Kanyawara groups. Only one of these mating seasons involved a multi-male influx: in this case, 2 additional males joined BN4 in August 2019.

4. Discussion

The Ngogo deme of blue monkeys grew very little over the last 40+ years — far less than sympatric species with similar diets (Figure 2), less than other blue monkey demes (Fashing & Cords, 2000; Cords & Chowdhury, 2011), and far less than their reproductive capacity (Rowell, 1970; Bronikowski et al., 2016). Our analyses indicate that the single biggest constraint on blue monkey populations appears to be competitive exclusion with grey-cheeked mangabeys, because deme sizes of these species are strongly and negatively correlated across sites. Disease and infanticide may also have some effect on blue monkey demographics, though to a moderate and minor extent, respectively.

Competitive exclusion between blue monkeys and grey-cheeked mangabeys initially appears bi-directional because each species is at a low abundance when the other is at a high abundance (Figure 3). However, an alternative possibility is that this relationship is driven by a third, hidden factor, which we propose to be the amount of seasonally inundated swamp forest, i.e., the area flanking small streams within the forest. Mangabeys prefer these swampy areas because many of their important foods are concentrated in this habitat (Olupot & Waser, 2013; Brown, 2013). Moreover, mangabeys are larger than, and dominant to, blue monkeys and can evict them from feeding sites (Houle et al., 2006, 2010). Thus within Kibale, mangabey abundance increases along a north-to-south gradient, as does the proportion of swamp forest (i.e., inversely in relation to the hilliness of the terrain). Our proposal is that, where swamps are abundant, mangabeys will also be abundant and blues will be rare; where swamps are rare, mangabeys will also be rare while blues will be abundant. A spatially explicit analysis across the Albertine Rift is needed to test this hypothesis on a broader scale. Competitive exclusion between these two primate species also explains why blue monkeys are very abundant at sites like Budongo and Kakamega (where mangabeys are absent) but not in Kibale, which would otherwise be an ideal habitat for blue monkeys. Notably, previous analyses were unsuccessful in attributing changes in monkey populations to changes in food availability: e.g., whereas the basal area of food trees increased, the abundance of blue monkeys and grey-cheeked mangabeys did not (Chapman et al., 2002, 2005; Worman & Chapman, 2005, 2006). The discovery of competitive exclusion between these primates, which went undiagnosed in a macro-ecological examination of competitive exclusion among primates (Kamilar & Ledogar, 2011), indicates that analyses of population trends would be greatly improved by accounting for inter-species competition, not just food availability.

We found greater dietary overlap between blues and mangabeys than with red-tailed monkeys or chimpanzees, but it remains unclear exactly how exclusion arises because agonism among them is rare. One possibility, yet to be tested, is that the monkey species rely on the same foods during periods of resource scarcity, yet mangabeys are able to consume these resources earlier or more completely than blue monkeys (Houle et al., 2006). Such periods would be especially problematic for blue monkeys if they routinely avoid the larger-bodied and physically dominant mangabeys (Houle et al., 2010), which is a strategy made possible by eavesdropping on the long-distance vocalizations of mangabey males (Brown & Waser, 2018). However, any explanation for the intense competition between blues and mangabeys would also have to explain why competition with red-tailed monkeys and chimpanzees does not result in exclusion. To our knowledge, the mechanisms of competitive exclusion have never been examined closely among sympatric primates — despite the fact that it is quite common, especially among African frugivores (Kamilar & Ledogar, 2011) — and merits serious investigation. Many primates will be forced into sub-optimal habitat fragments due to anthropogenic effects and climate change, and it is crucial to understand the competitive dynamics that shape population-level processes to ensure that they have a future.

The most important effect of feeding competition is reduced energy intake, which results in reduced expenditure on metabolism, daily activities, reproductive effort, and immune function (Barton & Whiten, 1993; Owen et al., 2021). In turn, a weakened immune response allows normally asymptomatic parasites to increase in number and to exert detrimental effects on host fitness. We suspect that this causal chain may account for the disease symptoms observed among some Ngogo blue monkeys, but further analysis is needed to determine whether the symptomatic groups (BN1 and BN2) are more energetically stressed than the non-symptomatic groups (BN5 and BN6), and whether blue monkeys are more energetically stressed than the grey-cheeked mangabeys and red-tailed monkeys, which exhibit much larger percent changes in population size. Moreover, it is unclear which parasite species causes the symptoms and whether it is unique to blue monkeys, or common among primates but symptomatic only under pervasive energetic stress and reduced immune function. A previous analysis found that Ngogo blue monkeys and mangabeys are infected with many of the same gastrointestinal parasites, though the blues carried one amoeba (*Iodamoeba*) and four nematodes (*Anatrichosoma*, *Necator*, *Strongyloides*, and *Trichostrongylus*) not seen in the mangabey samples (Ochieng et al., 2020).

Viruses and other, non-gastrointestinal parasites have not been examined for Ngogo monkeys but could also cause the observed symptoms. For instance, ano-genital inflammation was observed in Ngogo red colobus monkeys (*Procolobus rufomitratus tephrosceles*) from 1970–1988 and was, in some individuals, also associated with facial inflammation and scab-like lesions, with necrosis around the mouth and eyes in extreme cases (Struhsaker, 2010; Struhsaker et al., 2019). Though the causal agent(s) in red colobus remain undiagnosed, they are thought to potentially be a virus (herpes, measles, monkeypox), bacterial infection, and/or environmental toxins. Whereas the red colobus monkeys exhibit a wide array of symptoms and several deaths were attributed to the mystery infections, we see a limited range of symptoms among Ngogo blue monkeys and no clear link to mortality. Instead, the blue monkey symptoms correspond with reduced reproductive activity. Both the Ngogo blue and red colobus monkeys provide an important opportunity to study how persistent, long-term infection affects population demographics. By comparison, most of the documented disease-related changes in primate populations have been catastrophic outbreaks due to yellow fever, anthrax, ebola, or tuberculosis (Leendertz et al., 2004; Sapolsky & Share, 2004; Caillaud et al., 2006; Almeida et al., 2014). Ngogo is also unusual in that the proposed links between food availability, immune function, and population trends are due to interactions with naturally occurring competitors, rather than anthropogenically caused habitat loss.

The final proposed mechanism — infanticide by newly immigrated males who replace the previous resident male — may still occur at Ngogo but at a low frequency, in part because males now enjoy much longer tenures than in previous decades (Butynski, 1990). As a result, infant survival rates do not appear to be a major component of slow deme growth. As for the influence of birth rates, we observed similar or even higher reproductive rates at Ngogo than were previously documented at Kanyawara in the 1970s–1980s. In contrast, there is very low recruitment from juvenile to adult age classes. Further research is needed to determine whether juveniles and subadults die because of the energetic constraints of feeding competition from mangabeys. Reduced energy would lead to stunted growth and/or lack of investment in the immune system, rendering individuals more vulnerable to secondary infections, chronic anaemia, and insufficient nutrient retention (Owen et al., 2021). Before we began observations in 2013, however, it seems that several adult females disappeared from the Ngogo groups, possibly related to the fissioning of Angedakin & Lwanga's (2011) groups. It is not unusual for adults to disappear shortly after a group fission (Struhsaker & Leland, 1988; Windfelder & Lwanga, 2004; Cords, 2012), and for these fissions to be initiated by bachelor males attempting to establish their own groups (Cords & Rowell, 1986; Lwanga, 1987).

Together, feeding competition, disease and infanticide appear to coalesce into a 'perfect storm' of factors that constrain the growth of the Ngogo blue monkey deme, with the strongest element likely to be competitive exclusion by mangabeys. This presents a feasible resolution to the decades-old mystery of why the blue monkeys at this site remain at such low numbers, and provides useful information to conserve this species across its increasingly fragmented and human-dominated range.

Acknowledgements

This manuscript is dedicated to the memory of Dr. Jeremiah Lwanga, who mentored and cheered many of us and whose enduring love of blue monkeys inspired us to study the Kibale population. We thank the staff of the Ngogo Monkey Project for their assistance in the field and the many funding agencies whose financial support made this research possible. Grants awarded to M.B. were from the Leakey Foundation; the US National Science Foundation (grant Nos 0333415, 0742450, 1103444 and 2127253); Columbia University; the International Primatological Society; the American Association of Physical Anthropologists; the Hellman Family Foundation; the University of California, Santa Barbara (grants from the Academic Senate and the Institute for Social, Behavioural, and Economic Research); and an anonymous donor. The UC Global Health Institute supported the research of H.F. and the Conservation, Research, and Educational Opportunities International supported the research of R.A.J. Research by S.A. was funded by the US National Science Foundation through a grant (# IOB-0516644) awarded to John Mitani (David Watts and Linda Vigilant as co-PIs) for the Ngogo Chimpanzee Project. Logistical support was provided to M.B. by the Alexander von Humboldt Foundation (in the framework of the Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research and awarded to Margaret Crofoot). Any opinions, findings, and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of the funding agencies. The data used in these

analyses are archived and freely available on the Data Dryad website (https://doi.org/10.25349/D9CG7F).

References

Almeida, M.A.B., Cardoso, J.D.C., dos Santos, E., da Fonseca, D.F., Cruz, L.L., Faraco, F.J.C., Bercini, M.A., Vettorello, K.C., Porto, M.A., Mohrdieck, R., Ranieri, T.M.S., Schermann, M.T., Sperb, A.F., Paz, F.Z., Nunes, Z.M.A., Romano, A.P.M., Costa, Z.G., Gomes, S.L. & Flannery, B. (2014). Surveillance for Yellow Fever virus in non-human primates in southern Brazil, 2001–2011: a tool for prioritizing human populations for vaccination. — PLOS Neglect. Trop. Dis. 8: e2741.

Angedakin, S. & Lwanga, J. (2011). Changes in group size and composition of the blue monkeys (*Cercopithecus mitis stuhlmanni*) between 1984 and 2009 at Ngogo, Kibale National Park, Uganda. — Afr. J. Ecol. 49: 362-366.

Azeem, S., Bengis, R., Aarde, R.V. & Bastos, A.D.S. (2020). Mass die-off of African elephants in Botswana: pathogen, poison or a perfect storm? — Afr. J. Wildl. Res. 50: 149-156.

Balcomb, S.R., Chapman, C.A. & Wrangham, R.W. (2000). Relationship between chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. — Am. J. Primatol. 51: 197-203.

Barton, R.A. & Whiten, A. (1993). Feeding competition among female olive baboons, *Papio anubis*. — Anim. Behav. 46: 777-789.

Bronikowski, A., Cords, M., Alberts, S.C., Altmann, J., Brockman, D., Fedigan, L.M., Pusey, A., Stoinski, T., Strier, K.B. & Morris, W.F. (2016). Female and male life tables for seven wild primate species. — Sci. Data 3: 160006.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. — Am. Nat. 124: 255-279.

Brown, M. (2013). Food and range defense in group-living primates. — Anim. Behav. 85: 807-816.

Brown, M. & Waser, P.M. (2018). Group movements in response to competitors' calls indicate conflicts of interest between male and female grey-cheeked mangabeys. — Am. J. Primatol. 80: e22918.

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

Caillaud, D., Levréro, F., Cristescu, R., Gatti, S., Dewas, M., Douadi, M., Gautier-Hion, A., Raymond, M. & Ménard, N. (2006). Gorilla susceptibility to Ebola virus: the cost of sociality. — Curr. Biol. 16: 489-491.

Caillaud, D., Eckardt, W., Vecellio, V., Ndagijimana, F., Mucyo, J.-P., Hirwa, J.-P. & Stoinski, T. (2020). Violent encounters between social units hinder the growth of a high-density mountain gorilla population. — Sci. Adv. 6: eaba0724.

Caughley, G., Grice, D., Barker, R. & Brown, B. (1988). The edge of the range. — J. Anim. Ecol. 57: 771-785.

Chapman, C., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P. & Struhsaker, T.T. (2000). Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. — Conserv. Biol. 14: 207-217.

Chapman, C.A. & Chapman, L.J. (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. — Int. J. Primatol. 21: 565-585.

Chapman, C.A. & Lambert, J.E. (2000). Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. — Am. J. Primatol. 50: 169-185.

Chapman, C.A., Chapman, L.J., Cords, M., Gathua, J.M., Gautier-Hion, A., Lambert, J.E., Rode, K., Tutin, C.E.G. & White, L.J.T. (2002). Variation in the diets of Cercopithecus species: differences within forests, among forests, and across species. — In: The guenons: diversity and adaptation in African monkeys (Glenn, M.E. & Cords, M., eds). Kluwer Academic/Plenum Publishers, New York, NY, p. 319-344.

Chapman, C.A., Chapman, L.J., Zanne, A.E., Poulsen, J.R. & Clark, C.W. (2005). A 12-year phenological record of fruiting: implications for frugivore populations and indicators of climate change. — In: Tropical fruits and frugivores: the search for strong interactors (Dew, J.L. & Boubli, J.P., eds). Springer, Amsterdam, p. 75-92.

Chapman, C.A., Struhsaker, T.T., Skorupa, J.P., Snaith, T.V. & Rothman, J.M. (2010). Understanding long-term primate community dynamics: implications of forest change. — Ecol. Appl. 20: 179-191.

Chapman, C.A., Schoof, V.A.M., Bonnell, T.R., Gogarten, J.F. & Calmé, S. (2015). Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. — Phil. Trans. Roy. Soc. B: Biol. Sci. 370: 20140112.

Chapman, C.A., Bortolamiol, S., Matsuda, I., Omeja, P.A., Paim, F.P., Reyna-Hurtado, R., Sengupta, R. & Valenta, K. (2017). Primate population dynamics: variation in abundance over space and time. — Biodivers. Conserv. 27: 1221-1238.

Chapman, C.A., Omeja, P.A., Kalbitzer, U., Fan, P. & Lawes, M.J. (2018). Restoration provides hope for faunal recovery: changes in primate abundance over 45 years in Kibale National Park, Uganda. — Trop. Conserv. Sci. 11: 1940082918787376.

Clutton-Brock, T.H. & Coulson, T. (2002). Comparative ungulate dynamics: the devil is in the details. — Phil. Trans. Roy. Soc. B: Biol. Sci. 357: 1285-1298.

Colchero, F., Aburto, J.M., Archie, E.A., Boesch, C., Breuer, T., Campos, F.A., Collins, A., Conde, D.A., Cords, M., Crockford, C., Thompson, M.E., Fedigan, L.M., Fichtel, C., Groenenberg, M., Hobaiter, C., Kappeler, P.M., Lawler, R.R., Lewis, R.J., Machanda, Z.P., Manguette, M.L., Muller, M.N., Packer, C., Parnell, R.J., Perry, S., Pusey, A.E., Robbins, M.M., Seyfarth, R.M., Silk, J.B., Staerk, J., Stoinski, T.S., Stokes, E.J., Strier, K.B., Strum, S.C., Tung, J., Villavicencio, F., Wittig, R.M., Wrangham, R.W., Zuberbühler, K., Vaupel, J.W. & Alberts, S.C. (2021). The long lives of primates and the 'invariant rate of ageing' hypothesis. — Nature Commun. 12: 3666.

Conklin-Brittain, N.L., Wrangham, R.W. & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. macronutrients. — Int. J. Primatol. 19: 971-998.

Cords, M. (1987). Forest guenons and patas monkeys: male-male competition in one-male groups. — In: Primate societies (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 98-111.

Cords, M. (2012). The thirty-year blues: what we know and don't know about life history, group size and group fission of blue monkeys in the Kakamega forest, Kenya. — In: Long term studies of primates (Kappeler, P.M. & Watts, D.P., eds). Springer, Berlin, p. 289-312.

Cords, M. & Chowdhury, S. (2010). Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega forest, Kenya. — Int. J. Primatol. 3: 433-455.

Cords, M. & Fuller, J.L. (2010). Infanticide in *Cercopithecus mitis stuhlmanni* in the Kakamega forest, Kenya: variation in the occurrence of an adaptive behaviour. — Int. J. Primatol. 31: 409-431.

Cords, M. & Rowell, T.E. (1986). Group Fission in Blue Monkeys of the Kakamega forest, Kenya. — Folia Primatol. 46: 70-82.

Daszak, P. & Cunningham, A.A. (1999). Extinction by infection. — Trends Ecol. Evol. 14: 279.

Fashing, P.J. & Cords, M. (2000). Diurnal primate densities and biomass in the Kakamega forest: an evaluation of census methods and a comparison with other forests. — Am. J. Primatol. 50: 139-152.

Fedigan, L.M., Hogan, J.D., Campos, F.A., Kalbitzer, U. & Jack, K.M. (2021). Costs of male infanticide for female capuchins: when does an adaptive male reproductive strategy become costly for females and detrimental to population viability? — Am. J. Phys. Anthropol. 176: 349-360.

Gao, L. & Cords, M. (2020). Effects of female group size on the number of males in blue monkey (*Cercopithecus mitis*) groups. — Int. J. Primatol. 41: 665-682.

Garamszegi, L.Z. (2006). Comparing effect sizes across variables: generalization without the need for Bonferroni correction. — Behav. Ecol. 17: 682-687.

Gillespie, T.R., Greiner, E.C. & Chapman, C.A. (2004). Gastrointestinal parasites of the guenons of western Uganda. — J. Parasitol. 90: 1356-1360.

Gogarten, J.F., Jacob, A.L., Ghai, R.R., Rothman, J.M., Twinomugisha, D., Wasserman, M.D. & Chapman, C.A. (2015). Group size dynamics over 15+ years in an African forest primate community. — Biotropica 47: 101-112.

Hanya, G., Stevenson, P., Noordwijk, M. van, Wong, S.T., Kanamori, T., Kuze, N., Aiba, S., Chapman, C.A. & van Schaik, C. (2011). Seasonality in fruit availability affects frugivorous primate biomass and species richness. — Ecography 34: 1009-1017.

Houle, A., Vickery, W.L. & Chapman, C.A. (2006). Testing mechanisms of coexistence among two species of frugivorous primates. — J Anim Ecol 75: 1034-1044.

Houle, A., Chapman, C.A. & Vickery, W.L. (2010). Intratree vertical variation of fruit density and the nature of contest competition in frugivores. — Behav. Ecol. Sociobiol. 64: 429-441.

Hudson, P.J., Dobson, A.P., Cattadori, I.M., Newborn, D., Haydon, D.T., Shaw, D.J., Benton, T.G. & Grenfell, B.T. (2002). Trophic interactions and population growth rates: describing patterns and identifying mechanisms. — Phil. Trans. Roy. Soc. B: Biol. Sci. 357: 1259-1271.

Kamilar, J.M. & Ledogar, J.A. (2011). Species co-occurrence patterns and dietary resource competition in primates. — Am. J. Phys. Anthropol. 144: 131-139.

Köndgen, S., Kühl, H., N'Goran, P.K., Walsh, P.D., Schenk, S., Ernst, N., Biek, R., Formenty, P., Mätz-Rensing, K., Schweiger, B., Junglen, S., Ellerbrok, H., Nitsche, A., Briese, T., Lipkin, W.I., Pauli, G., Boesch, C. & Leendertz, F.H. (2008). Pandemic human viruses cause decline of endangered great apes. — Curr. Biol. 18: 260-264.

Lawes, M.J. & Henzi, S.P. (1995). Inter-group encounters in blue monkeys: how territorial must a territorial species be? — Anim. Behav. 49: 240-243.

Lawes, M.J., Cords, M. & Lehn, C. (2013). *Cercopithecus mitis* gentle monkey (diademed monkey, blue monkey, Syke's monkey). — In: Primates vol. II (Butynski, T.M., Kingdon, J. & Kalina, J., eds). Bloomsbury, London, p. 354-362.

Leendertz, F.H., Ellerbrok, H., Boesch, C., Couacy-Hymann, E., Mätz-Rensing, K., Hakenbeck, R., Bergmann, C., Abaza, P., Junglen, S., Moebius, Y., Vigilant, L., Formenty, P. & Pauli, G. (2004). Anthrax kills wild chimpanzees in a tropical rainforest. — Nature 430: 451-452.

Lukas, D. & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. — Science 346: 841.

Lwanga, J. (1987). Group fission in blue monkeys (*Cercopithecus mitis stuhlmanni*): effects on the socioecology in Kibale Forest, Uganda. — M.Sc. Thesis. Makerere University, Kampala.

Lwanga, J.S., Struhsaker, T.T., Struhsaker, P.J., Butynski, T.M. & Mitani, J.C. (2011). Primate population dynamics over 32.9 years at Ngogo, Kibale National Park, Uganda. — Am. J. Primatol. 73: 997-1011.

Milton, K. (1996). Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler monkey (*Alouatta palliata*) population in Panama. — J. Zool. 239: 39-63.

Milton, K. & Giacalone, J. (2014). Differential effects of unusual climatic stress on capuchin (*Cebus capucinus*) and howler monkey (*Alouatta palliata*) populations on barro Colorado island, Panama. — Am. J. Primatol. 76: 249-261.

Moore, J. (1999). Population density, social pathology, and behavioral ecology. — Primates 40: 1-22.

Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. — Behav. Ecol. 15: 1044-1045.

Negrey, J.D., Reddy, R.B., Scully, E.J., Phillips-Garcia, S., Owens, L.A., Langergraber, K.E., Mitani, J.C., Emery Thompson, M., Wrangham, R.W., Muller, M.N., Otali, E., Machanda, Z., Hyeroba, D., Grindle, K.A., Pappas, T.E., Palmenberg, A.C., Gern, J.E. & Goldberg, T.L. (2019). Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin. — Emerg. Microb. Infect. 8: 139-149.

Nunn, C.L. (2012). Primate disease ecology in comparative and theoretical perspective. — Am. J. Primatol. 74: 497-509.

Ochieng, J.R., Rwego, I.B., Kisakye, J.J.M. & Brown, M. (2020). Gastrointestinal parasites of blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Lophocebus albigena*) at the Ngogo research site in Kibale National Park, Uganda. — Afr. J. Ecol. 59: 489-496.

Olupot, W. & Waser, P.M. (2013). *Lophocebus albigena* (also *L. osmani*, *L. johnstoni*, *L. ugandae*) Grey-Cheeked Mangabey. — In: Primates, vol. II (Butynski, T.M., Kingdon, J. & Kalina, J., eds). Bloomsbury, London, p. 206-209.

Owen, J.C., Landwerlen, H.R., Dupuis, A.P., 2nd, Belsare, A.V., Sharma, D.B., Wang, S., Ciota, A.T. & Kramer, L.D. (2021). Reservoir hosts experiencing food stress alter transmission dynamics for a zoonotic pathogen. — Proc. Roy. Soc. Lond. B: Biol. Sci. 288: 20210881.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. — Science 307: 390-393.

Plumptre, A.J. & Cox, D. (2006). Counting primates for conservation: primate surveys in Uganda. — Primates 47: 65-73.

Rowell, T.E. (1970). Reproductive cycles of two *Cercopithecus* monkeys. — J. Reprod. Fertil. 22: 321-338.

Rudran, R. (1978). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale forest, Uganda. — Smith. Contrib. Zool. 249: 1-88.

Sapolsky, R.M. & Share, L.J. (2004). A Pacific culture among wild baboons: its emergence and transmission. — PLoS ONE 2: e106.

Scully, E.J., Basnet, S., Wrangham, R.W., Muller, M.N., Otali, E., Hyeroba, D., Grindle, K.A., Pappas, T.E., Thompson, M.E., Machanda, Z., Watters, K.E., Palmenberg, A.C., Gern, J.E. & Goldberg, T.L. (2018). Lethal respiratory disease associated with human rhinovirus C in wild chimpanzees, Uganda, 2013. — Emerg. Infect. Dis. 24: 267-274.

Sibly, R.M. & Hone, J. (2002). Population growth rate and its determinants: an overview. — Phil. Trans. Roy. Soc. B: Biol. Sci. 357: 1153-1170.

Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. — Behav. Ecol. Sociobiol. 4: 291-309.

Struhsaker, T.T. (1978). Food habits of five monkey species in the Kibale forest, Uganda. — In: Recent advances in primatology. 1. Behaviour. (Chivers, D.J. & Herbert, J., eds). Academic Press, London, p. 225-248.

Struhsaker, T.T. (1981). Polyspecific associations among tropical rain-forest primates. — Z. Tierpsychol. 57: 268-304.

Struhsaker, T.T. (1997). Ecology of an African rainforest: logging in Kibale and the conflict between conservation and exploitation. — University Press of Florida, Gainesville, FL.

Struhsaker, T.T. (2010). The red colobus monkeys: variation in demography, behavior, and ecology of endangered species. — Oxford University Press, Oxford.

Struhsaker, T.T. & Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale forest, Uganda. — In: Advances in the study of behavior (Rosenblatt, J., Hinde, R.A., Beer, C. & Busnel, M.C., eds). Academic Press, New York, NY, p. 158-228.

Struhsaker, T.T. & Leland, L. (1988). Group fission in redtail monkeys (*Cercopithecus ascanius*) in the Kibale forest, Uganda. — In: A primate radiation: evolutionary biology of the African guenons (Gautier-Hion, A., Bourliere, F., Gautier, P. & Kingdon, J., eds). Cambridge University Press, Cambridge, p. 364-388.

Struhsaker, T.T. & Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale forest, Uganda. — Behav. Ecol. Sociobiol. 26: 435-443.

Struhsaker, T.T., Angedakin, S. & Landsmann, A. (2019). Facial and genital lesions in baboons (*Papio anubis*) of Kibale National Park, Uganda. — Primates 60: 109-112.

Teelen, S. (2007). Primate abundance along five transect lines at Ngogo, Kibale National Park, Uganda. — Am. J. Primatol. 69: 1-15.

Watts, D.P. & Mitani, J.C. (2015). Hunting and prey switching by chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. — Int. J. Primatol. 36: 728-748.

Watts, D.P., Potts, K.B., Lwanga, J.S. & Mitani, J.C. (2012). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. diet composition and diversity. — Am. J. Primatol. 74: 114-129.

Windfelder, T. & Lwanga, J. (2004). Group fission in red-tailed monkeys (*Cercopithecus ascanius*) in Kibale National Park, Uganda. — In: The guenons: diversity and adaptation in African monkeys (Glenn, M.E. & Cords, M., eds). Kluwer Academic/Plenum Publishers, New York, NY, p. 147-159.

Worman, C.O. & Chapman, C.A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. — J. Trop. Ecol. 21: 689-697.

Worman, C.O. & Chapman, C.A. (2006). Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. — Int. J. Primatol. 27: 203-225.