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Exploring multiple dimensions of conservation success: Long-term wildlife trends, anti-poaching efforts and revenue sharing in Kibale National Park, Uganda

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Abstract

Parks are essential for protecting biodiversity and finding ways to improve park effectiveness is an important topic. We contributed to this debate by examining spatial and temporal changes in illegal activities in Kibale National Park, Uganda between 2006 and 2016 and used existing data to evaluate how the changes were correlated with the living conditions of people in neighboring communities, as well as patrolling effort. We explore the effectiveness of conservation strategies implemented in Kibale, by quantifying changes in the abundance of nine animal species over two to five decades. While uncertainty in such animal survey data are inherently large and it is hard to generalize across a 795-km^2 area that encompasses diverse habitat types, data suggest an increase in animal abundance in the National Park. An increase in patrolling effort by park guards over the decade was correlated with a decline in the number of traps and snares found, which suggests patrolling helped limit resource extraction from the park. The park's edge was extensively used for illegal forest product extraction, while the setting of snares occurred more often deeper in the forest. Perhaps counter-intuitively, increased community wealth or park-related employment in a village next to the park were positively correlated with increased illegal forest product extraction. Overall, our results suggest that the portfolio of conservation strategies used over the last two to five decades were effective for protecting the park and its animals, although understanding the impact of these efforts on local human populations and how to mitigate any losses and suffering they sustain remains an important area of research and action. It is evident that complex social, political and economic drivers impact conservation success and more interdisciplinary studies are required to quantify and qualify these dimensions.

Introduction

Human actions have severely impacted biodiversity and have had a major impact on both the flora and fauna of the world's forest, particularly in the tropics. Extinction rates are estimated to be ~1000 times above the rate that would have occurred without anthropogenic impacts (Dirzo *et al*. 2014; Pimm *et al*. 2014; Ceballos *et al*. 2015). Habitat degradation was the major cause of biodiversity loss and between 2000 and 2012, 2.3 million km^2 of forest were lost globally, with

loss in the tropics increasing by 3% a year (Hansen *et al*. 2013). To put this in perspective, an area of forest larger than the islands of New Guinea, Borneo and Madagascar combined was lost in 12 years. In addition, even when habitat is maintained, hunting can decimate animal populations. For example, since 2007, illegal ivory trade is estimated to have doubled (Bennett, 2015) and forest elephant populations declined by 62% between 2002 and 2011 (Maisels *et al*. 2013). Illegal wildlife trade has become the fourth biggest international organized crime and solutions to reduce it are elusive (Pires & Moreto, 2011; Wasser *et al*. 2015; Moreto & Pires, 2018).

With over half of the world's plant and animal species found in the tropics (Scheffers *et al*. 2012), the establishment of protected areas (PAs) represent a valuable tool for protecting the world's tropical biodiversity. Since 1992, the global network of PAs has grown steadily, increasing yearly by an average of 2.5% in total area (Butchart *et al*. 2010; Rands *et al*. 2010). In 2018, terrestrial PAs covered 14.7% of the earth surface (World Bank, 2020). However, in a global analysis of 60 PAs, Laurance *et al*. (2012) found that researchers considered only ~50% of these PAs to have been effective over the last 20–30 years, while the remaining were experiencing alarming biodiversity erosion (see also Tranquilli *et al*. 2014).

Biodiversity loss within PAs is often linked to illegal resource extraction (Bennett, 2002; Critchlow *et al*. 2015; Stirnemann *et al*. 2018). Thus, taking protective measures to patrol and guard wildlife are often a critical components of conservation strategy (Ripple *et al*. 2015). Determining patterns of illegal activities can enable more effective patrolling (Critchlow *et al*. 2015). However, limiting poaching must involve more than enforcement (Challender & MacMillan, 2014; Moreto *et al*. 2017); understanding the socioeconomic drivers of resource extraction, how this varies spatially in relation to the stakeholders perceived threat from wildlife and law enforcement, and how those drivers change with development is also needed (Kahler *et al*. 2013; Moreto *et al*. 2017; Moreto & Pires, 2018). By studying the socioeconomic needs associated with illegal resource extraction, conservation and development projects can be designed to achieve the most appropriate and effective outcomes to meet the goals of the park and those of the surrounding human community.

Community-based conservation projects or integrated conservation-development projects that aim to also meet the needs of the local communities have been advocated as ethical and effective conservation tools (Western & Pearl, 1989; Robinson, 1993, 2011; Hulme & Murphree, 2001). However, empirical evidence regarding the claim that community projects are effective at conservation as well as meeting the needs of local communities remains scarce (Hackel, 1999; Berkes, 2004; Eklund *et al*. 2016; Cetas & Yasué, 2017). A comparison of PAs in Uganda using community-based approaches to those that did not, documented no difference in threat reduction (Mugisha & Jacobson, 2004), though likely the situation improved for the community around the park. Similarly, the establishment of a research field stations which increased community engagement in conservation activities through a research station, as well as provide health services through a clinic and mobile clinic for people living next to the park led to people viewing the park more positively (Chapman *et al*. 2015; Sarkar *et al*. 2016, 2019a, 2019b; Kirumira *et al*. 2019). However, the improvement in park–people relations, the livelihood of people and access to healthcare did not correspond to a decrease in illegal activities (Songorwa *et al*. 2000; Dickman *et al*. 2011; Kirumira *et al*. 2019). A 7-year study in Lake Mburo National Park, Uganda found that a community conservation project helped the local people recognize the positive aspects of the park but did not reduce levels of poaching and illegal grazing (Infield & Namara, 2001). A review of financial incentives to reduce illegal hunting, that included cases in Nepal, Kenya, Namibia, Mexico and Sweden, concluded that the benefits provided by projects were usually outweighed by the losses incurred and thus rarely reduced illegal hunting (Dickman *et al*. 2011). These findings suggest that community-based conservation projects may not be a universally effective tool for conservation, though if they improve the welfare of local communities, there is an ethical imperative to continue such approaches. Such findings point to the need to more fully evaluate strategies to promote park effectiveness by integrating long-term data from different disciplines.

Here, we examine spatial and temporal changes in illegal activities in Kibale National Park, Uganda between 2006 and 2016 and use existing data to evaluate how changes were correlated to changes in the living conditions of people in neighboring communities and patrolling effort. We explore the effectiveness of these conservation strategies for wildlife by quantifying changes in abundance of nine animal species over 23–49 years and found all of the species increased in abundance. Kibale embodies challenges faced by many forested PAs and their surrounding communities. Human population density on the periphery of the park is high and increasing, and the region is experiencing economic growth (Hartter *et al*. 2015). Associated with these changes, human-wildlife conflicts are on the rise (Naughton-Treves *et al*. 1998; Mackenzie, 2012a; Omeja *et al*. 2014). Within the park, illegal activities target trees used as fuel wood for cooking and poles for building, grasslands used for grazing livestock, wild animals hunted for meat, plants collected for traditional treatments and wetlands are used for collecting reeds (Chapman *et al*. 2006; Naughton-Treves *et al*. 2007; Salerno *et al*. 2018). The key questions this study set out to assess were whether: (1) the edge of the park or the core area is more vulnerable to resource extraction; (2) incidence of forest product extraction and hunting related to community wealth; and (3) long-term conservation policies and associated changes in encroachment behaviors were linked to changes in animal abundance.

Materials and methods

Study site

Kibale is a 795-km^2 National Park located in western Uganda (0° 13' to 0° 41' N and 30° 19' to 30° 32' E) near the foothills of the Rwenzori Mountains (Chapman &

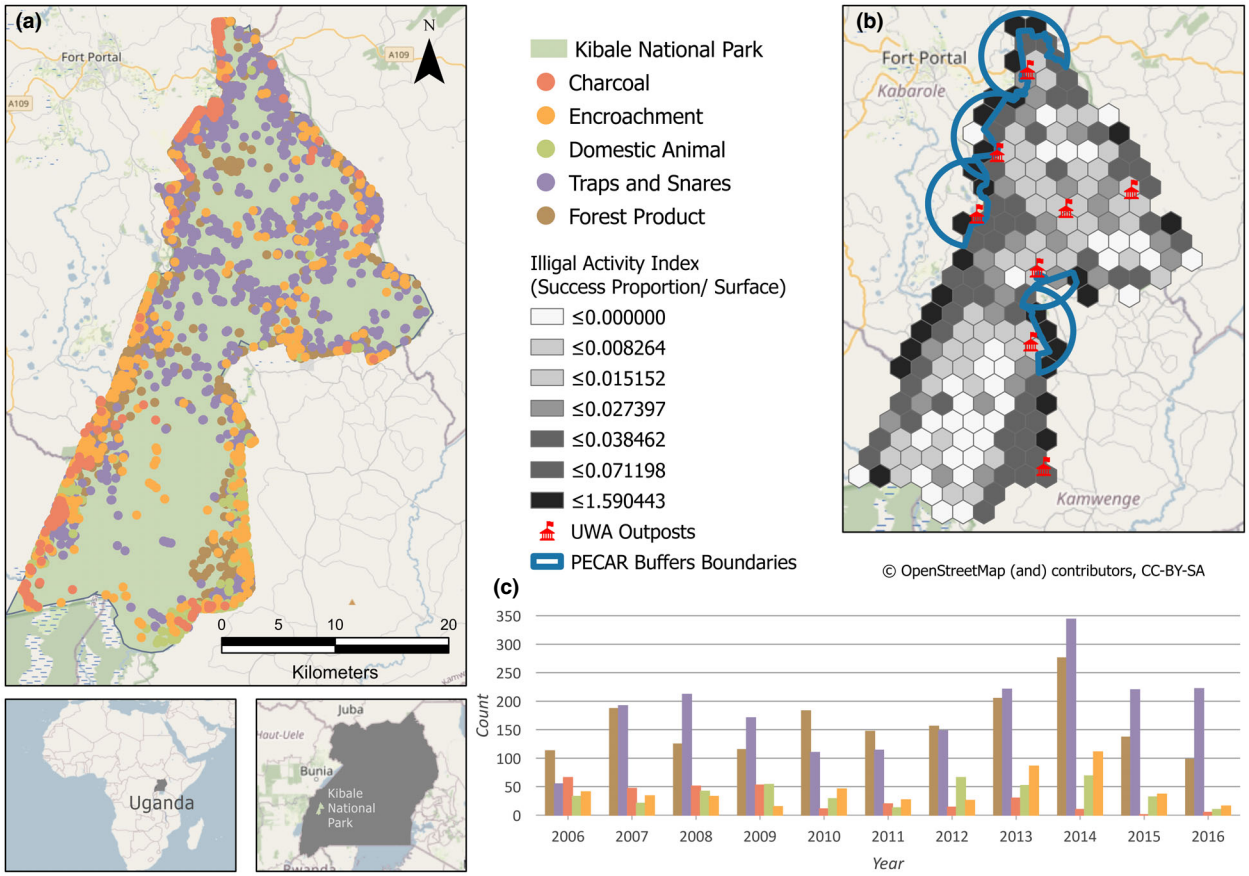

Figure 1 (a) Locations of Kibale National Park and records of illegal activities between 2006 and 2016, (b) Hexagons and Illegal activity Index (IAI) used for analysis, (c) Counts of five types of illegal activities per year over the study period. The activities in the legend are shown according to rendering order.

Lambert, 2000) (Fig. 1). Kibale is dominated by mid-altitude (920–1590 m), moist-evergreen forest that receives a mean annual rainfall of 1667 mm (1990–2019), in two rainy seasons (Stampone *et al*. 2011).

Kibale received National Park status in 1993. Prior to this, it was a Forest Reserve and a Game Corridor, gazette between 1926 and 1932, with the stated goal of providing sustained hardwood timber production and game (Osmaston, 1959; Struhsaker, 1997; Chapman *et al*. 2005). Prior to the 1920s, it was a hunting reserve for nobility (Mackenzie, 2012a). Today, hunting and poaching are strictly prohibited, but persist none-the-less (MacKenzie *et al*. 2011). Snares primarily target bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus harveyi*), blue duiker (*Cephalophus monticola*), bushpig (*Potamochoerus larvatus*) and other small game, but can seriously injure other species, including chimpanzees (*Pan troglodytes*) and elephants (forest elephants – *Loxodonta cyclotis*, savanna elephants – *Loxodonta africana* and their hybrids) (Wrangham & Mugume, 2000; Krief *et al*. 2013). Animals often raid crops in neighboring farms, creating conflict with local people (Naughton-Treves, 1999; Mackenzie & Ahabyona, 2012; Mackenzie, 2012a; Sarkar *et al*. 2016). The boundary between the park and community own land is now well demarcated, though historically was a major point of contention. In the early 1990s the Forest Service and subsequently Uganda Wildlife Authority (UWA) planted marker trees and placed permanent markers and increased enforcement efforts to avoid people settling inside the park boundaries.

Human population density surrounding Kibale increased 10.5 times between 1959 and 2002 (Hartter *et al*. 2015), with density exceeding 270 people/km^2 at the western edge – more than double the national average (Hartter, 2010). Between 2000 and 2020, the population within 1-km of the park's boundary almost doubled going from 123 to 229 people/km^2 (MacKenzie *et al*. 2017; WorldPop, 2020). Many of the people neighboring Kibale are recent immigrants to the area; 56% of households migrated to the park borders in the last generation (MacKenzie, 2012b). Local people are typically smallhold farmers, cultivating less than 5 ha, to grow staple foods, such as bananas, maize, beans and cassava. Some people also cultivate cash crops, such as tea, eucalyptus and coffee, while others find work in tea plantations, as research assistants at the various field stations, in the tourism

industry, with the reforestation project, as casual laborers or commute to the nearest large town to work (Mackenzie, 2012a; Mackenzie & Hartter, 2013b; Sarkar *et al*. 2019a, 2019b). Wood is used for cooking and heating, as well as charcoal, alcohol production, brick production and construction (Naughton-Treves & Chapman, 2002; Naughton-Treves *et al*. 2007), and residents depend on Kibale for craft materials, medicinal plants and places to put beehives for honey production (MacKenzie *et al*. 2011).

The areas to the south of the park were influenced by land conflict. During the governments of Idi Amin and Milton Obote, the difficult conditions for rural people and breakdown of civil institutions led to people moving into the south of the PA and converting about 70 km^2 of forest to agricultural land (Hamilton, 1984; Naughton-Treves, 1999). Estimates of the number of people residing in this area vary dramatically. One estimate is given by van Orsdol (1986), who, based on aerial and ground surveys, estimated that 8800 people were living in the PA. The Makerere University Institute for Social Research report (MISR Makerere University Institute for Social Research, 1989) estimated that between 42 000 and 57 000 people resided in the area, with some of these people having primary residence outside the reserve. Finally, the National Environmental Management Authority (1997) estimated that 30 000 households, or approximately 170 000 people, were residing in Kibale. Regardless of the exact numbers, the resettlement worsened relationships with the people to the south (L'Roe & Naughton-Treves, 2017; MacKenzie, 2018). The level of resentment in the area may be slight tempered by the fact that many of the evicted knew they were encroaching on protected land and many had agricultural plots and homes both inside and outside of the park (MISR Makerere University Institute for Social Research, 1989; Struhsaker, 1997). Resource use in this area may have been restricted for many generations (since the 1800s), which complicate views about entitlements over the resources in the park (Nampindo & Plumptre, 2005).

In addition to a well-documented history, Kibale hosts one of the longest continuously running research field stations in Africa (Sarkar *et al*. 2019b). Kibale provided the ideal study site for this research due to the great wealth of long-term interdisciplinary data available.

Uganda Wildlife Authority ranger patrols and illegal activity records

Kibale is managed by the UWA that was established in 1996 through the union of the Uganda National Parks and the Game Department, and the enactment of the Uganda Wildlife Statute. UWA's mandate is multidimensional and their mission statement is 'To conserve, economically develop and sustainably manage the wildlife and Protected Areas of Uganda in partnership with neighboring communities and other stakeholders for the benefit of the people of Uganda and the global community'. To sustainably manage wildlife, UWA must prevent overexploitation. In Kibale, bushmeat hunting is driven predominantly by local consumption and does not involve large-scale commercial sales (Hartter & Goldman, 2009). To limit poaching, patrols are conducted out of eight UWA outposts that were established between 1932 and 2011, with new outposts being constructed based on need and the availability of funds. During patrols rangers record illegal activities using their GPS, noting type and location. These data were entered into either MIST, SMART or Earth Ranger systems, but not consistently and without provenance origin in the database. So, we extracted lines that were consistent throughout the study period (dates, illegal activity types).

From the UWA patrols, we obtained records of 4952 illegal activities between January 2006 and December 2016 (Fig. 1a) with patrols occurring in 128 out of the 132 months. All the illegal activities have been classified into five classes: (1) extraction of forest products, which includes mostly fuelwood, but also medicinal plants, thatch for roofing and craft material, (2) setting snares and traps for bushmeat, (3) charcoal production, (4) domestic animal grazing within the park and (5) encroachment – farming in the park. All of these categories of illegal activities are displayed in Fig. 1; however, since charcoal production and farming inside the park were rarely observed, and animal grazing was also rare and occurred primarily to the very south of the park, these categories are not considered in subsequent statistical analyses. Patrols often started from the ranger posts; however, when transport was available efforts were made to take rangers to distant locations throughout the park. This was done so that encroachers could not predict where the chances of being discovered by rangers were the highest.

Local communities surveys

Indices of wealth, perceived benefits and losses associated with living near the park and demographic information were collected from communities along the park's edge in three surveys (2006, 2009 and 2012) (MacKenzie *et al*. 2017). Although not designed for longitudinal comparison, these three surveys did spatially overlap in five circular areas of 5 km radius centered on Kibale entrance gates from which ranger patrols often started (Fig. 1). These areas were in close proximity to the areas where the relative abundance of animal populations were assessed (see below). For more information on how these data were collected, ethics permissions and exact questions asked see MacKenzie *et al*. (2017). Here we aggregate categories considered in these previous studies in MacKenzie *et al*. (2017): all types of park-associated employment (i.e. tourism, field station, trail cutters, reforestation) under employment benefit, all other park-associated benefits (i.e. ecosystem services, support to local schools, revenue sharing, resource access agreements) under nonemployment benefits, trouble living near the park (primarily crop raiding) and lack of access to resources under losses, and owning cows, chickens, sheep, goats, pigs, house construction standard and land ownership under wealth. For sociodemographic analysis, we focused on a 9-year period from January 2006 to December 2014 for which UWA patrol records were available for 107 of the 108 months, with 4174 activities recorded. We compiled all variables collected in 2006, 2009 and 2012 with illegal

activity data collected by UWA for 3-year periods centered on the survey years. The 2006 survey was associated with UWA illegal activity data from 2006, 2007 and 2008, 2009 was associated with illegal activity data from 2009, 2010 and 2011 and 2012 with data for 2012, 2013 and 2014. The survey data were annotated with the population density data of people living within 5 km of the park (WorldPop, 2020).

Land cover and land use

Data from *OpenStreetMap* (www.openstreetmap.org) were collected and analyzed in ArcGIS Pro. Two major roads pass through the park crossing both edges. Road length, closest distance to a major road and closest distance to an edge of each illegal activity points were calculated to represent access to the forest for poaching and to the market for poached resources. The surface of six land cover classes was used to estimate the role of the type of agricultural activity and the nature of the remaining habitat outside the park on poaching activities (following Hartter, 2007).

Changes in animal abundance

We assess changes in the populations of 11 mammal species between 49 years (from 1970 to 2019, for six independent censuses) and 23 years (from 1996 to 2019, 23 years, for four independent censuses) during daytime surveys. This assessment involved four species that are hunted – red duiker (*Cephalophus harveyi*), blue duiker (*Cephalophus moniticola*), bushbuck (*Tragelaphus scriptus*) and bushpig (*Potamochoerus larvatus*). We also monitored elephant populations (forest elephants – *Loxodonta cyclotis*, savanna elephants – *Loxodonta africana* and their hybrids) as they have been hunted in the past, but are now rarely killed (Brooks & Buss, 1962; Omeja *et al*. 2014). We also considered five primate species (redtail monkeys – *Cercopithecus ascanius*, blue monkeys – *C. mitis*, mangabeys – *Lophocebus albigena*, Ashy red colobus – *Piliocolobus tephrosceles* and black-and-white colobus – *Colobus guereza)*, as how these species respond to habitat disturbance is well documented (Struhsaker, 1997; Chapman *et al*. 2010b, 2018a). The species considered are all long-lived mammals, thus their populations change slowly. Providing a longer duration illustrates clearly how the populations are being affected over time by changing conservation efforts.

The hunted species, as well as elephants, are cryptic and hide or avoid approaching observers, thus we elected to count tracks and dung. We used the same methods each year and walked the same 4-km transects once per month for 12 months in the year of sampling (Table 1). A single set of tracks in a line was counted as one sighting. Both dung and tracks were removed after they were counted to ensure that they were not repeatedly counted.

We assessed primate abundance through 6-year long census efforts conducted between 1970 and 2019 (1970 (Struhsaker, 1975), 1980 (Skorupa, 1988), 1996, 2005, 2014, 2019 (Chapman *et al*. 2010b; Chapman *et al*. 2018a, Chapman 2019 unpublished data). We used the same transects as described above. It was not possible to obtain accurate group counts during a census walk because some species form groups of over 150 animals, while others can remain hidden or immobile in the canopy for long periods. Thus, we established an independent effort to estimate the sizes of groups and evaluated group size in three periods (July 1996–May 1998, July 2010–May 2011, May 2017–May 2018, $N = 220$ group counts; (see Gogarten *et al*. 2015 for an analysis of the first two periods). These estimates were used in the analysis for this paper.

It is possible that changes in the animal abundance are related to forest change, but no clear relationship between chances in abundance and changes in forest structure (Chapman *et al*. 2010a; Chapman *et al*. Submitted), phenology (Chapman *et al*. 2005; Chapman *et al*. 2018b; Chapman *et al*. (Submitted)), food nutritional content (Rothman *et al*. 2015) or climate change (Chapman *et al*. 2005; Chapman *et al*. 2019; Chapman *et al*. (Submitted)) are discernable.

Analysis

All data were imported into ArcGIS Pro, and georeferenced. The park was tessellated into 203 hexagons of 5 km^2 to optimize illegal activities analysis (Fig. 1). Hexagons are used to aggregate the data into spatial bins. Hexbinning was preferred over creating square-based fishnets as it is a tessellation method which closely approximates circles and thus results in more efficient data aggregation around the center (Carr *et al*. 1987). The size of the hexagon was chosen such that they was not so small that they only encompassed a few points and that toward the edge there are many hexagons which overspill the park boundary, while not so large that regional trends were lost because of aggregation. Most of the hexagons fell completely within the park with 42.86% hexagons ($N = 87/203$) located near the edge. The overlap area of these fringe hexagons with the park ranged from 0.0003 to 4.9989 km^2. We quantified the proportion of successful patrols (number of patrols that found evidence of illegal resource extraction/total patrols) in each hexagon (Fig. 1). Since some of the hexagons included areas outside the park, we normalized the success rate by surface area of each hexagon within the park. The prepared data were imported into R for analysis using Spearman's correlation.

An *illegal activity index* (IAI) was calculated dividing the number of illegal activity records by the number of days a patrol track crossed the hexagon. This was then weighted by the amount of park per hexagon to avoid edge effects. The IAI was used in all correlative analyses. For monthly analysis, we divided the number of records of illegal activities by the number of patrol tracks.

Results

Spatial distribution of illegal activity records between 2006 and 2016

Illegal activities were located an average of 1012 m from the park's edge (Fig. 1a). But half of illegal activities were located between the park's edge and 439 m. Therefore, high

Table 1 Data collection for each datasets: animal abundance, local communities surveys and illegal activities record in Kibale National Park, Uganda (K denoted forestry compartments near Makerere Biological Field Station (Chapman *et al.* 2018a)

Data type	Location	70	80	96	97	98	99	2000 0	1	2	3	4	5	6	7	8	9	2010 10	11	12	13	14	15	16	17	18	19
Animal Abundance	K30																										
	K14																										
	K15																										
	Sebitoli																										
	Dura River																										
	Mainaro																										
	Nyakatojo																										
	Restoration Area 1																										
Social Assessment	See Fig 1																										
Extraction Assessment	See Fig 1																										

The grey areas highlight when the surveys were conducted.

IAI scores (N = 27 hexagons; IAI >0.07) are all at the forest edge (Fig. 1b). Most (69.7%) records of illegal activity were within 5 km of an UWA outpost (see also Plumptre *et al.* 2014).

Traps and snares represented 40.6% of the records and was the dominat incident further from the park's edge (mean = 1.56 km, median = 0.92 km) than vegetation-related illegal activities (mean = 0.66 km, median = 0.302 km; Fig. 2, Wilcoxon signed-rank test $P < 0.001$). Overall, 80.94% of the extraction of forest products were within a 1-km of the park's edge, while 52.61% of the traps and snares were within a kilometer of the edge. Both forest product ($r_{sp} = -0.415$, $P < 0.001$) and trap and snare ($r_{sp} = -0.078$, $P = 0.0603$) incidence declined with distance from the edge. Forest products ($r_{sp} = -0.262$, $P < 0.001$) and marginally traps and snares ($r_{sp} = -0.080$, $P = 0.055$) were also negatively related to distance from the road. This suggests that proximity to roads (ease of transportation, access to markets and forest) plays a role in where people decide to extract resources.

Interestingly, the extraction of forest products was positively related to the distance from tea plantations ($r_{sp} = -0.258$, $P < 0.001$), thus it was lowest near tea plantations, but finding traps and snares were independent of distance from tea ($r_{sp} = -0.063$, $P = 0.129$). The map highlights that domestic animal-related infringements were more common in the south where it is drier and grassland is more common.

Temporal distribution of adjusted illegal activity records between 2006 and 2016

The incidents of illegal activities of different types and the effort to deter them (number of patrol tracks) varied over time (Figs 1c and 3). The number of traps and snares found generally appeared to decrease between 2006 and 2016 ($r_{sp} = 0.651$, $P < 0.05$), while the number of patrols conducted by UWA appeared to increase ($r_{sp} = 0.824$, $P < 0.01$; Fig. 3).

There was considerable monthly variation in IAI (Fig. 4). This variation did not appear to be centered on holidays (Easter – April and Christmas – December), times when school fees are due (January, May, August), harvest/crop raiding periods (May–July, November–March; (Mackenzie & Ahabyona, 2012), or during school breaks (evaluated as months with more than 1 week or longer of holidays, i.e. not March, June, July, September, October, November).

Social factors linked to resource extraction between 2006 and 2014

There appeared to be a positive, though weak, relationships between the wealth of the community and the extent to which forest products were extracted ($r_{sp} = 0.090$, $P < 0.05$). There was also a positive correlation between wealth and the setting of traps and snares for bushmeat ($r_{sp} = 0.160$, $P < 0.001$).

The setting of traps and snares was also positively correlated with employment ($r_{sp} = 0.116$, $P < 0.01$) or perceived

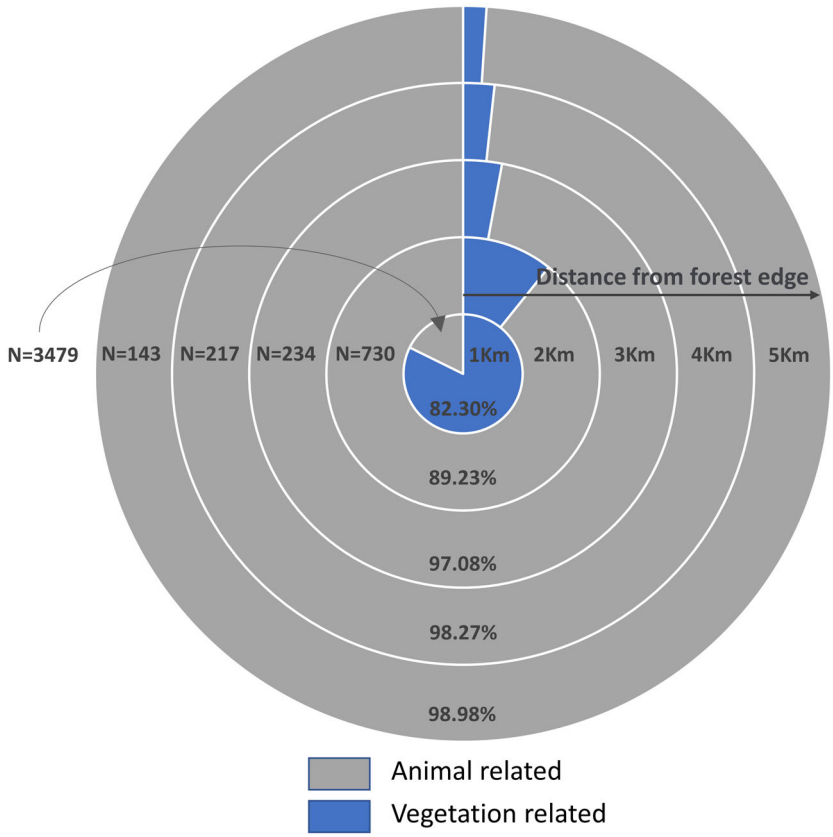

Figure 2 The proportion of encroachment activities that involved vegetation extraction (forest products) and animal-related (traps and snares) illegal activities at different distances from the edge of Kibale National Park Uganda.

benefits, such as ecosystem services or help (e.g. scaring off elephants, digging elephant trenches; $r_{sp} = 0.134$, $P < 0.001$). The harvesting of forest products and the rate at which communities received park-associated employment ($r_{sp} = 0.077$, $P = 0.065$) or nonemployment-related benefits ($r_{sp} = 0.078$, $P = 0.060$) did not show statistically significant correlations. Peoples' perception that living close to the park caused them more losses increased incidences of traps and snares ($r_{sp} = 0.155$, $P < 0.001$) and forest product extraction ($r_{sp} = 0.083$, $P < 0.05$). The increase in population density around the park correlates positively with increased harvesting of forest products ($r_{sp} = 0.101$, $P = 0.015$). We did not detect a correlation between population density and hunting ($r_{sp} = -0.006$, $P = 0.892$).

Changes in animal abundance between 1996 and 2019

Despite conducting 506 surveys covering 2010 km at eight sites (Table 2), there remains considerable uncertainty in the size of animal populations across the park, though broad patterns do appear across sites. With respect to the ungulates and elephants (Fig. 5), all species at the six sites (24 comparisons) seemed to exhibit an initial increase in abundance between 1996 and 2005, with the exception of bushbuck at three sites (Mainaro, Dura River and Sebitoli) which appeared to exhibit only a slight increase and duiker at two sites (Mainaro and Sebitoli) that also had a slight increase. There were also declines in some species at some sites in the last decade. The largest decline in abundance appeared to be in the elephants at Sebitoli; given the large ranging patterns and foraging behavior of elephants and the fact that the killing of elephants very rarely occurs in Kibale, we expect that the herds probably used other areas in the park to the south. There appeared to be recent declines in bushpig in the three sites near the field station (K-15, K-14 and K-30), despite being a site of frequent patrols and having researchers frequently in the forest. All species were found in the early regenerating forest of P1 and Nyakatojo.

All of the primate species seemed to increase in abundance over the 26 years of monitoring and the pattern of increase was similar among the sites (Fig. 6). The largest increase in numbers were for red colobus, but since their numbers were high to begin with the per cent increase (36.5%) is not as high as the other folivore, black-and-white colobus, that increased by 53.4%. Blue monkeys are relatively rare in Kibale and are only found in measurable numbers at the northern sites, but at these locations they showed a large percentage increase (51.4%). The frugivorous mangabey populations increased by 25.6%, while the frugivorous

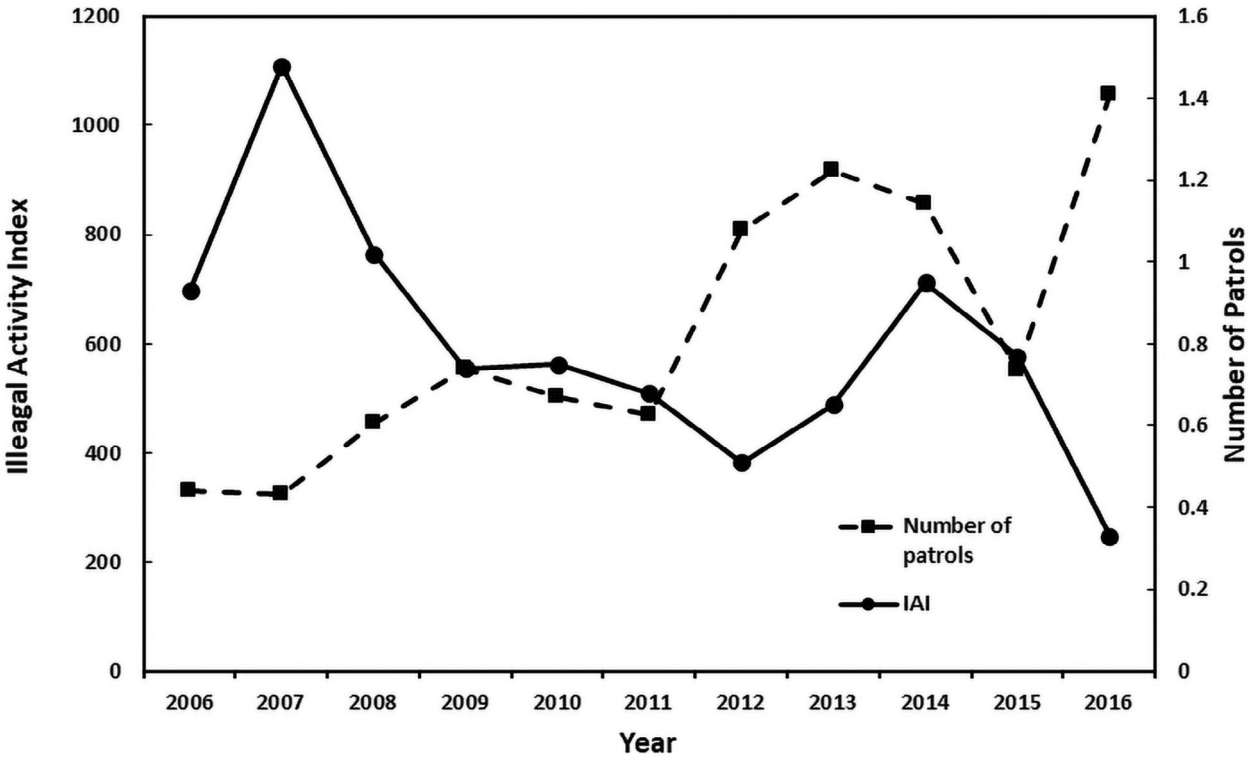

Figure 3 Changes in the Illegal Activity Index (IAI) and the number of patrols between 2006 and 2016 during the monitoring conducted by the Uganda Wildlife Authority for Kibale National Park, Uganda.

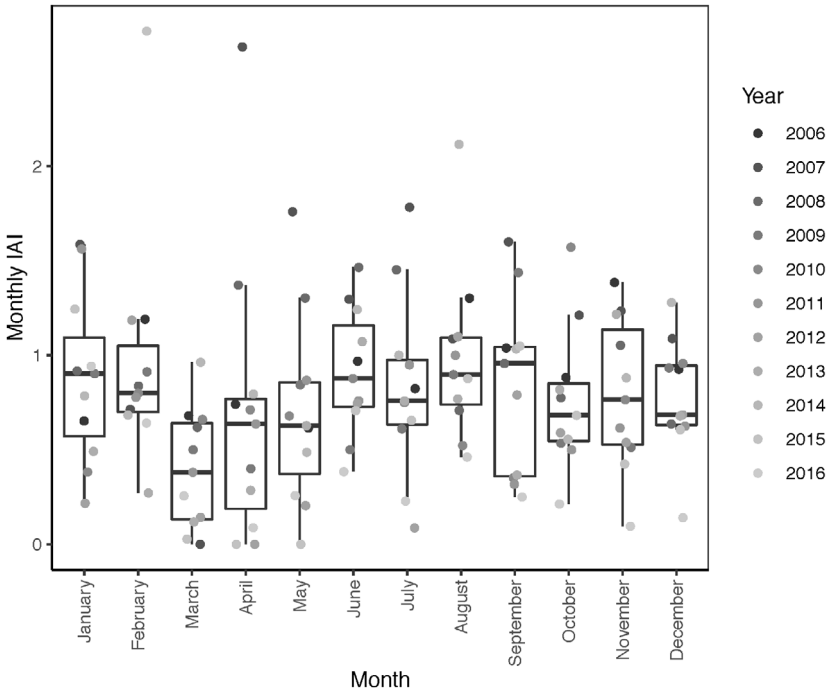

Figure 4 Monthly variation of Illegal Activity Index (IAI) between 2006 and 2016 in Kibale National Park, Uganda. The ends of the box are the upper and lower quartiles, the median is indicated by the vertical line inside the box and the whiskers are the two lines outside the box that extend to the highest and lowest observations. Each year is illustrated by a point.

Table 2 Characteristics of the censuses that were conducted at different locations in Kibale National Park, Uganda (ordered from North to South)

Area	Forest type	Logging intensity	Size (ha)	Census Period	Transect length (m)	No. of transects	Total distance(km)
Sebitoli	Logged	50%	Unknown	05/08/14/19	4200	38	160
K-15	Logged	50%	347	80/96/05/08/14/19	4000	102	408
K-14	Logged	25%	405	80/96/05/08/14/19	3600	96	346
K-30	Old growth	<1%	282	70/80/96/05/08/14/19	4000	161	644
Nyakatojo	Regenerating	100%	60	05/14/19	4000	23	92
Dura	Old growth	<1%		05/08/14/19	4450	35	156
Mainaro	Old growth	<1%		05/08/14/19	4000	30	120
Plantation 1	Regenerating	100%	~120	05/14/19	4000	21	84
Total						506	2010

Logging intensity is an estimate of the number of stems (>30 cm DBH) killed. The Dura and Mainaro areas are part of the continuous forest, thus no size is given. The total distance surveyed was 2010 km. The surveys at Nyakatojo and Plantation 1 were only included to determine if the species considered were using these regenerating areas.

redtail monkeys only showed a modest 9.0% increase. It is surprising to note that for all of the primates the size of the groups increased (average increase = 93.1%, N = 339 groups counted), with the red colobus average group size more than doubling (167.9%, N = 97).

Discussion

Environmental degradation (Hansen *et al*. 2013; Scheffers *et al*. 2019), the loss of biodiversity (Pimm *et al*. 2014) and the fact that PAs are often ineffectual (Laurance *et al*. 2012), has generated considerable debate among conservation and development researchers and practitioners about the best ways forward. Some scholars discuss the alienation of local rural people from nature and the failure of PAs (Pimbert & Pretty, 1997; Schwartzman *et al*. 2000), while others indicate the need of the rural poor for food and forest products (Gibson & Marks, 1995), or that weak institutions (Barrett *et al*. 2001, 2011) are responsible. It is clear that this situation is complex and new insights and information are needed (Robinson, 2011; Junker *et al*. 2020).

Our research reveals interesting findings that we hope contribute to this debate. We collate data from several sources to build a long-term, multifaceted portrayal of conservation outcomes in Kibale. Data for such modelling are rare and thus a data fusion was done to evaluate the various correlations between different influences and outcomes. First, the results point to potential efficacy of patrolling in this particular socio-economic and ecological context; this deterrence may be effective in that people encroaching into the park are then at risk of being caught and criminally charged, facing hefty fines and prison sentences. We found that the increased patrolling done by UWA correlated with a decrease in the use of snares over our decade of monitoring, though clearly many factors have changed in the region that we could not control for. At the same time, in Kibale, there appeared to be a general increase of animal populations, though there was considerable variation across the park and accurately estimating animal abundance at this spatial scale remains challenging. Broadly, our findings lend support to the wildly held view that law enforcement measures, such as ranger patrolling, are one way to ensure adherence to restrictions imposed on local communities around PAs in a way that allows flora and fauna to thrive (Tranquilli *et al*. 2012, 2014; Gandiwa *et al*. 2013; Critchlow *et al*. 2015). A study in Taï National Park, Côte d'Ivoire, similarly suggested that increases in patrolling allowed animal populations to increase (Kablan *et al*. 2019).

Second, we add further support to the hypothesis that park's edges are particularly vulnerable to resource extraction, a pattern observed in many PAs (Woodroffe & Ginsberg, 1998; Jenks *et al*. 2012). The extraction of forest products, particularly fuel wood, was observed most often near the forest edge and thus close to residences (see also Naughton-Treves & Chapman, 2002; MacKenzie *et al*. 2011). This may reflect the fact that cost of walking long distances into the forest to obtain these resources outweigh the benefits. These offenses, while illegal in this PA, rarely go enforced if done on the small household scale. This finding though, may also be related to the pattern observed that most records of illegal activities were detected in the proximity of the outposts. It is important to note that we were not able to control for ranger movements in our analyses as these records were not kept; it is thus also possible that rangers simply spent most time patrolling and detecting illegal activity near their outposts. All but one of the ranger outpost were at the edge of the park, suggesting that the edge effects could also be driven by the position of rangers in the park. The collection of detailed track logs of rangers in addition to the data on where illegal activities were detected, would be extremely helpful for future analysis. This edge effect supports the long held belief that to prevent species losses large protected areas provide the best option as they have a smaller surface area to volume ratio (Wilcox & Murphy, 1985; Arroyo-Rodríguez *et al*. 2020).

Despite the potential evidence supporting high rates of illegal activities at the forest edge, the forest boundary has not been severely eroded since park establishment (Hartter, 2010; Hartter & Goldman, 2011; Hartter *et al*. 2016). In contrast to

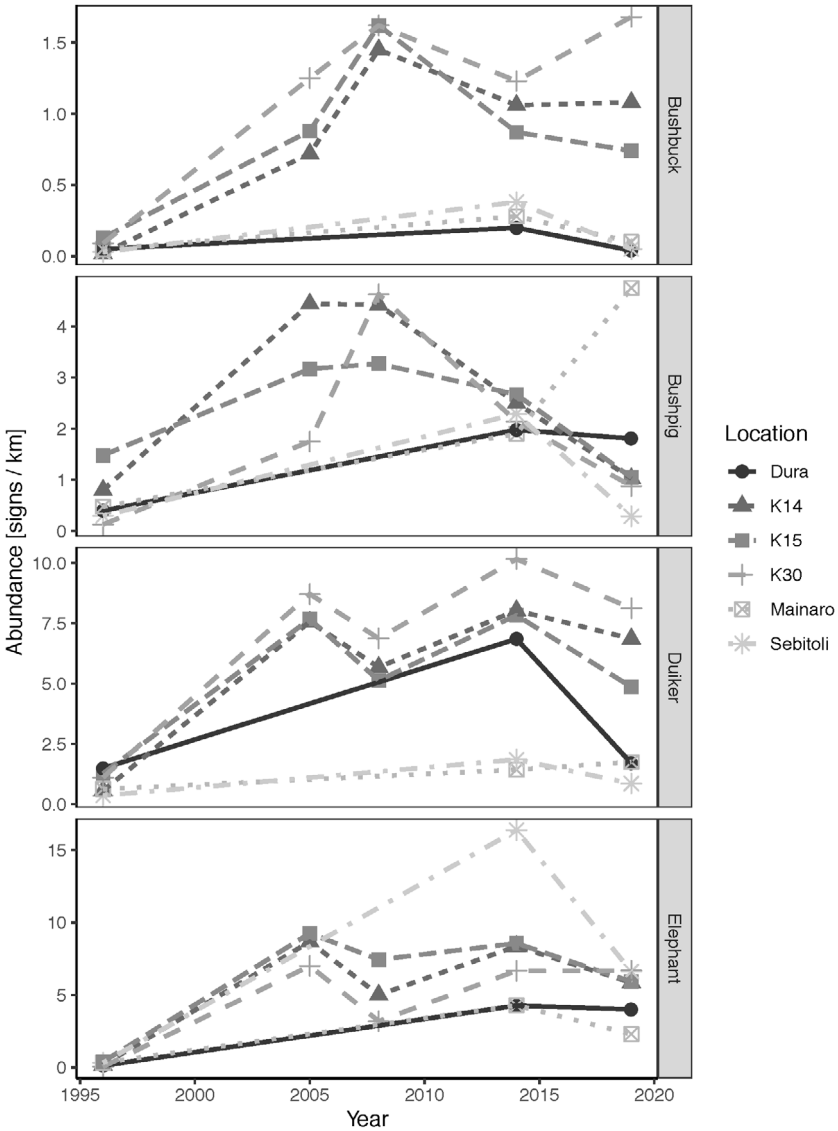

Figure 5 The abundance (sightings/km of transect walked) of bushbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus larvatus*), duiker (red duiker – *Cephalophus harveyi)* and blue duiker – *Cephalophus moniticola*; combined) and elephants (forest elephants – *Loxodonta cyclotis*, savanna elephants – *Loxodonta africana*, and their hybrids) in Kibale National Park Uganda between 1996 and 2019.

general encroachment, the setting of snares was detected more often deeper in the forest. This does not seem to reflect the abundance of animals within Kibale (Worman & Chapman, 2006); rather this may reflect the fact that the chances of being caught is higher near the edge or that traps are more frequently checked and removed at the park edge. Hunters have been observed to catch animals toward the center of the park, carry them toward the edge, but only bring them out of the park under the cover of darkness. People may alter behavior in relation to how they perceive risk of detection (Kahler & Gore, 2015, 2017).

Third, we found a positive correlation between the wealth of the community in proximity to a forest area and the incidence of forest product extraction. Some reports suggest that many Ugandans consider bushmeat to taste better and be better nutritionally than domestic meat (Olupot *et al*. 2009). While the drivers of poaching in Uganda are likely related to food insecurity and tradition, poachers are also able to generate significant wealth by engaging in illegal resource extraction from national parks (Moreto & Lemieux, 2015). During conversations with local community members, we were told that 'poachers sell bushmeat to people and it is very delicious', indicating a healthy market for bushmeat within local communities. As wealth increases in local communities, primarily through agricultural profits from food and cash crops (MacKenzie & Hartter, 2013a), the market for bushmeat may also be increasing. There is considerable unexplained variation in the setting of snares and as the

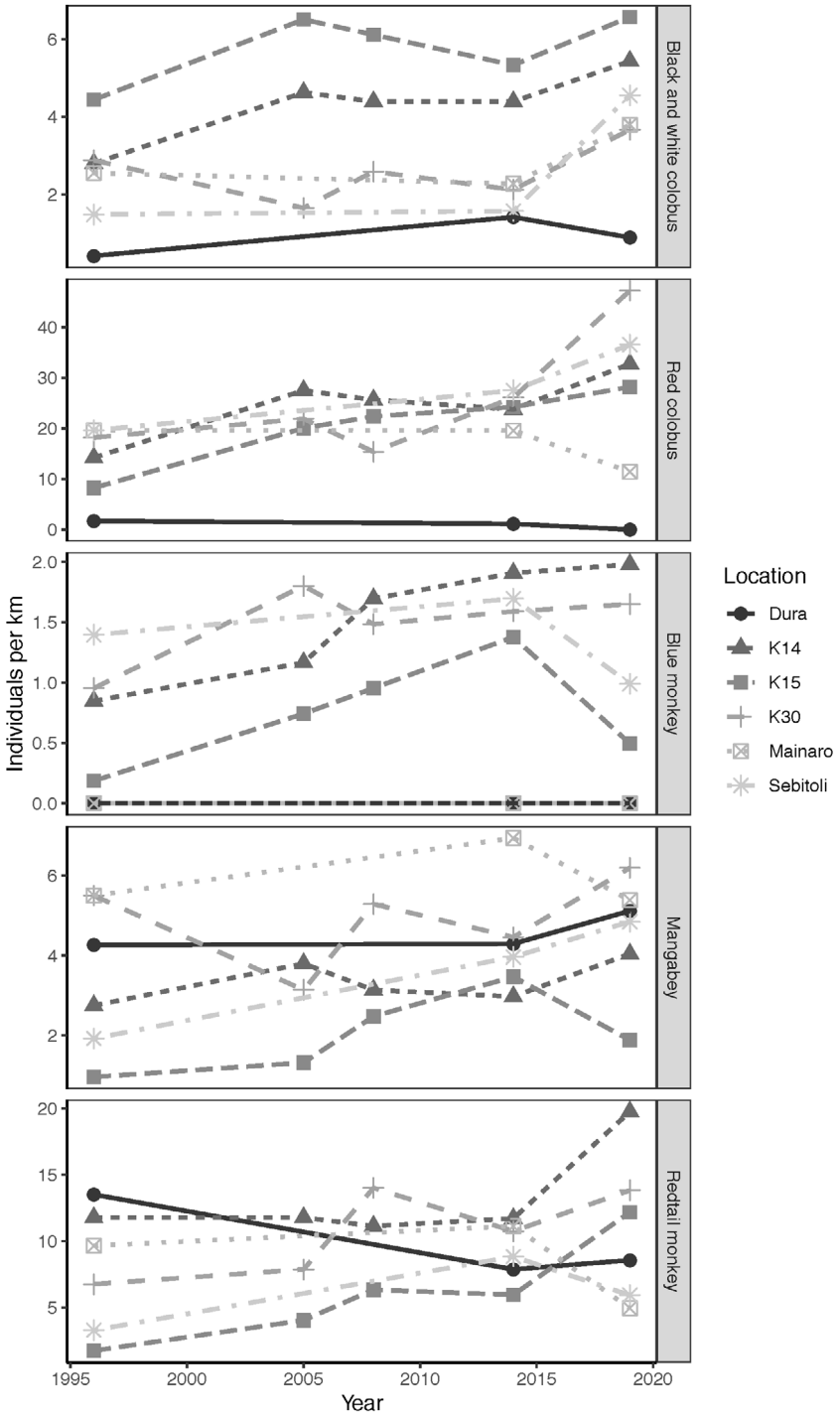

Figure 6 The abundance (individual / km walked) of five primate species (black-and-white colobus – *Colobus guereza;* red colobus – *Procolobus (Piliocolobus) rufomitratus tephrosceles;* blue monkeys – *Cercopithecus mitis*; mangabeys – *Lophocebus albigena*; and redtail monkeys – *Cercopithecus ascanius* in Kibale National Park, Uganda. Abundance changes were determined using line transect methods involving the walking 506 transect and covering 2010 km.

strongest predictor of setting traps and snares was the distance from the edge, suggesting that the relationship of illegal activities with particular communities living at the edge should be considered with an abundance of caution.

We also found that park-based employment in tourism, research and carbon sequestration operations and the receipt of other conservation benefits was weakly positively correlated with illegal resource extraction in an area. This finding

corroborates results of prior studies linking admitted extraction of timber, firewood and non-forest products to the receipt of park-based benefits (Mackenzie, 2012a, 2018; Solomon *et al*. 2012). Similar statements, while not common, have been made by people neighboring other parks around the world. For example, Rasolofoson *et al*. (2015) examined the conservation value of Community Forest Management programs in Madagascar that were designed to allow local communities to benefit from resources harvested from the forest. They investigated the effectiveness of these programs at reducing deforestation from 2000 to 2010 in Madagascar, but could not detect an effect (see Mugisha & Jacobson, 2004 for a similar example).

These findings are in contradiction to the narrative that nature preservation can be helped primarily by alleviating poverty and reducing the need for the resources in PAs (Adams & Hutton, 2007). This perspective emerged from the 1982 World Parks Congress in Bali, and there was consensus that PAs 'in developing countries will survive only insofar as they address human concerns' (Western & Pearl, 1989 p134). The integration of biodiversity conservation with sustainable development became a widely supported conservation strategy following the report issued by the World Commission on Environment and Development in 1987 (the Brundtland Commission (Brundtland, 1987). This led to an approach that became known as community-based conservation, which claimed that conservation goals could be achieved by aiding the development and wealth accumulation of the local communities (Berkes, 2004). Our results in Kibale, like those of others (Songorwa *et al*. 2000; Mugisha & Jacobson, 2004; Rasolofoson *et al*. 2015), may not perhaps entirely support that poverty alleviation in and of itself, increases biodiversity protection. Globally, as populations get richer, meat consumption appears to increase before showing trends of reduction (Cole & McCoskey, 2013). Here, as with other PAs, it is perhaps a similar process playing out at a smaller local scale (Fa *et al*. 2009; Chaves *et al*. 2017, 2019). The remit of conservation plans need to broaden to ensure access to quality food and resources, ideally in a way that reduces the reliance on (bush)meat (Chaves *et al*. 2017). Alleviating poverty and improving access to healthy resources is clearly an ethical and important goal, regardless of the conservation implications; if conservation efforts can assist in this goal without harming their efficacy, this approach likely remains an ethical and effective solution. Moral and ethical considerations clearly justify improving the livelihood of the local communities; perhaps rather, efforts should be made to further improve the conservation outcomes of such initiatives (Robinson, 2011).

While we have generated extensive long-term datasets on illegal human activities, animal abundance and social factors, even longer-term data collection is needed to properly assess the impact of different conservation initiatives, especially those aimed at local communities. Many of the conservation programs in Kibale have improved the wealth of neighboring communities, but these programs may only result in conservation benefits after a considerable period of time; these benefits are not realized equally and equitably by all living near the park. For example, the effect of education programs will only be seen when school children of today are adults and choose to use forest products and/or eat bushmeat or not. Similarly, despite the large number of people the clinic and mobile clinic treats each year, it will be years until a large proportion of the densely populated communities have received medical care, as well as health and conservation education (Chapman *et al*. 2015). Further, the non-hostile attitude about Kibale does not directly translate into conservation-friendly local human–environment interactions (Ryan *et al*. 2015).

While these results are intriguing, we strongly encourage further long-term research to better assess complex human-environment interactions in PAs. To achieve this, conservation data must be made open, accessible and comparable between sites. Such large scale efforts will require the investment of significant amounts of resources, but new technologies may also help in the collection, integration and analysis of such data. However, care must be taken to avoid over-automation of conservation activities as people are an integral part of the solution and over reliance on technology can undo years of progress in reconciling biodiversity conservation goals with the requirements of the community (Sarkar & Chapman,2021a, 2021b).

Parks face unprecedented, varied challenges, thus data must be integrated across multiple disciplines and over a wide range of spatiotemporal scales (König *et al*. 2019). Open science and the re-use of data is called for by groups such as the European Commission High Level Expert Group on Scientific Data 2010, National Institutes of Health, National Science Foundation, and the Organization for Economic Co-operation and Development (Pasquetto *et al*. 2017, 2019). Conservation efforts must embrace policies for sharing, releasing and the data should be made available with precautions to both to in-country institutions, and in international data repositories.

In the end, conservation programs must, at least in part, be evaluated with respect to how well they conserve biodiversity. Unfortunately, this is rarely done as long-term monitoring of animal populations is difficult, expensive and are receiving a declining amount of funding (Chapman *et al*. 2017; Hughes *et al*. 2017). For Kibale, we have collected a suite of long-term data characterizing changes in the social and economic environment, park encroachment and the abundance of key animal species and we hope that putting together this information has provided some useful insights into the complex factors influencing the success of conservation initiatives. The efforts that UWA and their collaborators used over the last two and a half decades with respect to patrolling and community outreach appear to have contributed to protecting the park and its animals. Our results suggest that poverty alleviation programs in the region may need to be integrated more closely with a holistic conservation approach that meets appropriate moral and ethical considerations.

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Conflict of interest

The authors declare that they have no conflict of interest.

References

Adams, W. & Hutton, J. (2007). People, parks and poverty: political ecology and biodiversity conservation. *Conserv. Soc.* **5**, 147–183.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, A.J. & Tscharntke, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* **23**, 1404–1420.

Barrett, C.B., Brandon, K., Gibson, C. & Gjertsen, H. (2001). Conserving tropical biodiversity amid weak institutions. *Bioscience* **51**, 497–502.

Barrett, C.B., Tavis, A.J. & Dasgupta, P. (2011). On biodiversity conservation and poverty traps. *Proc. Natl Acad. Sci. USA* **108**, 13907–13912.

Bennett, E.L. (2002). Is there a link between wild meat and food security? *Conserv. Biol.* **16**, 590–592.

Bennett, E.L. (2015). Legal ivory trade in a corrupt world and its impact on African elephant populations. *Conserv. Biol.* **29**, 54–60.

Berkes, F. (2004). Rethinking community-based conservation. *Conserv. Biol.* **18**, 621–630.

Brooks, A.C. & Buss, I.O. (1962). Past and present status of the elephant in Uganda. *J. Wildl. Manage.* **26**, 38–50.

Brundtland, G.H. (1987) Our common future, report of the World Commission on Environment and Development, World commission on environment and development, 1987. *Published as Annex to General Assembly document A/42/427, development and international Co-operation: Environment August,* **2,** 1987.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C. & Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168.

Carr, D.B., Littlefield, R.J., Nicholson, W. & Littlefield, J. (1987). Scatterplot matrix techniques for large N. *J. Am. Stat. Assoc.* **82**, 424–436.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human–induced species losses: entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253.

Cetas, E.R. & Yasué, M. (2017). A systematic review of motivational values and conservation success in and around protected areas. *Conserv. Biol.* **31**, 203–212.

Challender, D.W. & MacMillan, D.C. (2014). Poaching is more than an enforcement problem. *Conserv. Lett.* **7**, 484–494.

Chapman, C.A., Bortolamiol, S., Matsuda, I., Omeja, P.A., Paim, F.P., Reyna-Hurtado, R., Sengupta, R. & Valenta, K. (2018*a*). Primate population dynamics: variation in abundance over space and time. *Biodivers. Conserv.* **27**, 1221–1238.

Chapman, C.A., Chapman, L.J., Jacob, A.L., Rothman, J.M., Omeja, P.A., Reyna-Hurtado, R., Hartter, J. & Lawes, M.J. (2010*a*). Tropical tree community shifts: implications for wildlife conservation. *Biol. Conserv.* **143**, 366–374.

Chapman, C.A., Chapman, L.J., Struhsaker, T.T., Zanne, A.E., Clark, C.J. & Poulsen, J.R. (2005). A long-term evaluation of fruiting phenology: importance of climate change. *J. Trop. Ecol.* **21**, 31–45.

Chapman, C.A., Corriveau, A., Schoof, V.A., Twinomugisha, D. & Valenta, K. (2017). Long-term simian research sites: significance for theory and conservation. *J. Mammal.* **98**, 652–660.

Chapman, C.A., Galán-Acedo, C., Gogarten, J.F., Guo, S., Kalbitzer, U., Hou, R., Omeja, P.A., Anna Sugiyama, A. & Struhsaker, T.T. (Submitted) Drivers of rainforest change: a 40-year evaluation.

Chapman, C.A., Hou, R. & Kalbitzer, U. (2019). What will climate change mean for primates? *Primatology, bio-cultural diversity and sustainable development in tropical forests. A global perspective*. 137–151. Mexico City, Mexico: UNESCO.

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., Lawes, M.J. & Eeley, H.A.C. (2006). What hope for African primate diversity? *Afr. J. Ecol.* **44**, 1–18.

Chapman, C.A., Lawes, M.J., Gogarten, J.F., Hou, R., Omeja, P., Sugiyama, A. & Kalbitzer, U. (Submitted) A 50-year fruiting phenology record reveals different responses among rainforest tree species to changing climate. https://assets.researchsquare.com/files/rs-414446/v1/836a5223-98df-4967-b13fd47de36973aa.pdf?c=1631881483

Chapman, C.A., Struhsaker, T.T. & Lambert, J.E. (2005). Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. *Int. J. Primatol.* **26**, 539–555.

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

Chapman, C.A., Valenta, K., Bonnell, T.R., Brown, K.A. & Chapman, L.J. (2018*b*). Solar radiation and ENSO predict fruiting phenology patterns in a 16-year record from Kibale National Park, Uganda. *Biotropica* **50**, 384–395.

Chapman, C.A., van Bavel, B., Boodman, C., Ghai, R.R., Gogarten, J.F., Hartter, J., Mechak, L.E., Omeja, P.A., Poonawala, S., Tuli, D. & Goldberg, T.L. (2015). Providing health care to improve community perceptions of protected areas. *Oryx* **49**, 636–642.

Chaves, W.A., Monroe, M.C. & Sieving, K.E. (2019). Wild meat trade and consumption in the Central Amazon, Brazil. *Hum. Ecol.* **47**, 733–746.

Chaves, W.A., Wilkie, D.S., Monroe, M.C. & Sieving, K.E. (2017). Market access and wild meat consumption in the central Amazon. *Brazil. Biol. Conserv.* **212**, 240–248.

Cole, J.R. & McCoskey, S. (2013). Does global meat consumption follow an environmental Kuznets curve? *Sustain. Sci. Pract. Policy* **9**, 26–36.

Critchlow, R., Plumptre, A., Driciru, M., Rwetsiba, A., Stokes, E., Tumwesigye, C., Wanyama, F. & Beale, C. (2015). Spatiotemporal trends of illegal activities from ranger-collected data in a Ugandan national park. *Conserv. Biol.* **29**, 1458–1470.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proc. Natl Acad. Sci. USA* **108**, 13937–13944.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the anthropocene. *Science* **345**, 401–406.

Eklund, J., Blanchet, F.G., Nyman, J., Rocha, R., Virtanen, T. & Cabeza, M. (2016). Contrasting spatial and temporal trends of protected area effectiveness in mitigating deforestation in Madagascar. *Biol. Conserv.* **203**, 290–297.

Fa, J.E., Albrechtsen, L., Johnson, P.J. & Macdonald, D.W. (2009). Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. *Anim. Conserv.* **12**, 599–610.

Gandiwa, E., Heitkönig, I.M.A., Lokhorst, A.M., Prins, H.H.T. & Leeuwis, C. (2013). Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: a case study of northern Gonarezhou National Park and adjacent areas. *J. Nat. Conserv.* **21**, 133–142.

Gibson, C.C. & Marks, S.A. (1995). Transforming rural hunters into conservationists: an assessment of community-based wildlife management programs in Africa. *World Dev.* **23**, 941–957.

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.

Hackel, J.D. (1999). Community conservation and the future of Africa's wildlife. *Conserv. Biol.* **13**, 726–734.

Hamilton, A.C. (1984). *Deforestation in Uganda*. Oxford, UK: Oxford University Press.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013). High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853.

Hartter, J.N. (2007). *Landscape change around Kibale National Park, Uganda: Impacts on land cover, land use, and livelihoods*. Gainesville, FL: University of Florida.

Hartter, J. (2010). Resource use and ecosystem services in a forest park landscape. *Soc. Nat. Res.* **23**, 207–223.

Hartter, J., Dowhaniuk, N., MacKenzie, C.A., Diem, J.E., Palace, M.W., Ryan, S.J. & Chapman, C.A. (2016). Perceptions of risk in communities near parks in an African biodiversity hotspot. *Ambio* **45**, 692–705.

Hartter, J. & Goldman, A.C. (2009). Life on the edge: Balancing biodiversity, conservation, and sustaining rural livelihoods around Kibale National Park, Uganda. *FOCUS Geogr.* **52**, 11–17.

Hartter, J. & Goldman, A. (2011). Local responses to a forest park in western Uganda: alternate narratives on fortress conservation. *Oryx* **45**, 60–68.

Hartter, J., Ryan, S.J., MacKenzie, C.A., Goldman, A., Dowhaniuk, N., Palace, M., Diem, J.E. & Chapman, C.A. (2015). Now there is no land: a story of ethnic migration in a protected area landscape in western Uganda. *Popul. Environ.* **36**, 452–479.

Hughes, B.B., Beas-Luna, R., Barner, A.K., Brewitt, K., Brumbaugh, D.R., Cerny-Chipman, E.B., Close, S.L., Coblentz, K.E., de Nesnera, K.L., Drobnitch, S.T., Figurski, J.D., Focht, B., Friedman, M., Freiwald, J., Heady, K.K., Heady, W.N., Hettinger, A., Johnson, A., Karr, K.A., Mahoney, B., Moritsch, M.M., Osterback, A.-M., Reimer, J., Robinson, J., Rohrer, T., Rose, J.M., Sabal, M., Segui, L.M., Shen, C., Sullivan, J., Zuercher, R., Raimondi, P.T., Menge, B.A., Grorud-Colvert, K., Novak, M. & Carr, M.H. (2017). Long-term studies contribute disproportionately to ecology and policy. *Bioscience* **67**, 271–281.

Hulme, D. & Murphree, M. (2001). *African wildlife and livelihoods: the promise and performance of community conservation*. London, UK: James Currey Ltd.

Infield, M. & Namara, A. (2001). Community attitudes and behaviour towards conservation: an assessment of a community conservation programme around Lake Mburo National Park, Uganda. *Oryx* **35**, 48–60.

Jenks, K.E., Howard, J. & Leimgruber, P. (2012). Do ranger stations deter poaching activity in national parks in Thailand? *Biotropica* **44**, 826–833.

Junker, J., Petrovan, S.O., Arroyo-RodrÍguez, V., Boonratana, R., Byler, D., Chapman, C.A., Chetry, D., Cheyne, S.M., Cornejo, F.M., CortÉs-Ortiz, L., Cowlishaw, G., Christie, A.P., Crockford, C., Torre, S., De Melo, F.R., Fan, P., Grueter, C.C., GuzmÁn-Caro, D.C., Heymann, E.W., Herbinger, I., Hoang, M.D., Horwich, R.H., Humle, T., Ikemeh, R.A., Imong, I.S., Jerusalinsky, L., Johnson, S.E., Kappeler, P.M., Kierulff, M.C.M., KonÉ, I., Kormos, R., Le, K.Q., Li, B., Marshall, A.J., Meijaard, E., Mittermeier, R.A., Muroyama, Y., Neugebauer, E., Orth, L., Palacios, E., Papworth, S.K., Plumptre, A.J., Rawson, B.M., Refisch, J., Ratsimbazafy, J., Roos, C., Setchell, J.M., Smith, R.K., Sop, T., Schwitzer, C., Slater, K., Strum, S.C., Sutherland, W.J., Talebi, MaurÍcio, Wallis, J., Wich, S., Williamson, E.A., Wittig, R.M. & KÜhl, H.S. (2020). A severe lack of evidence limits effective conservation of the world's primates. *Bioscience* **70**, 794–803.

Kablan, Y.A., Diarrassouba, A., Mundry, R., Campbell, G., Normand, E., Kühl, H.S., Koné, I. & Boesch, C. (2019). Effects of anti-poaching patrols on the distribution of large mammals in Taï National Park, Côte d'Ivoire. *Oryx* **53**, 469–478.

Kahler, J.S. & Gore, M.L. (2015). Local perceptions of risk associated with poaching of wildlife implicated in human-wildlife conflicts in Namibia. *Biol. Conserv.* **189**, 49–58.

Kahler, J.S. & Gore, M.L. (2017). Conservation crime science. *Conserv. Criminol.*. **27**, https://onlinelibrary.wiley.com/doi/10.1002/9781119376866.ch2

Kahler, J.S., Roloff, G.J. & Gore, M.L. (2013). Poaching risks in community-based natural resource management. *Conserv. Biol.* **27**, 177–186.

Kirumira, D., Baranga, D., Hartter, J., Valenta, K., Tumwesigye, C., Kagoro, W. & Chapman, C.A. (2019). Evaluating a union between health care and conservation: a mobile clinic improves park-people relations, yet poaching increases. *Conserv. Soc.* **17**, 51–62.

König, C., Weigelt, P., Schrader, J., Taylor, A., Kattge, J. & Kreft, H. (2019). Biodiversity data integration—the significance of data resolution and domain. *PLoS Biol.* **17**, e3000183.

Krief, S., Cibot, M., Bortolamiol, S., Lafosse, S., Seguya, A. & Guillot, J. (2013). Proximités géographiques et phylogénétiques entre les chimpanzés et les humains et conséquences sanitaires. Exemple du parc national de Kibale en Ouganda. *Bull. Acad. Vet. Fr.* **166**, 276–285.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M.O., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H.-B., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J.O., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharntke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Verea, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L.U., Yonzon, P. & Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**, 290–294.

L'Roe, J. & Naughton-Treves, L. (2017). Forest edges in western Uganda: from refuge for the poor to zone of investment. *For. Policy Econ.* **84**, 102–111.

Mackenzie, C.A. (2012*a*). Accruing benefit or loss from a protected area: location matters. *Ecol. Econ.* **76**, 119–129.

MacKenzie, C.A. (2012*b*). Trenches like fences make good neighbours: revenue sharing around Kibale National Park, Uganda. *J. Nat. Conserv.* **20**, 92–100.

MacKenzie, C.A. (2018). Risk, reciprocity and retribution: choosing to extract resources from a protected area. *Ecol. Econ.* **143**, 314–323.

Mackenzie, C.A. & Ahabyona, P. (2012). Elephants in the garden: financial and social costs of crop raiding. *Ecol. Econ.* **75**, 72–82.

MacKenzie, C., Chapman, C.A. & Sengupta, R. (2011). Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. *Environ. Conserv.* **39**, 38–50.

MacKenzie, C. & Hartter, J. (2013*a*). Demand and proximity: drivers of illegal forest resource extraction. *Oryx* **47**, 288–297.

Mackenzie, C.A. & Hartter, J. (2013*b*). Demand and proximity: drivers of illegal forest resource extraction. *Oryx* **47**, 288–297.

MacKenzie, C.A., Salerno, J., Chapman, C.A., Reyna-Hurtado, R., Tumusiime, D.M. & Drake, M. (2017). Changing perceptions of protected area benefits and troubles around Kibale National Park, Uganda. *J. Environ. Manage.* **200**, 217–228.

Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba'a, R., Abitsi, G., Ambahe, R.D., Amsini, F., Bakabana, P.C., Hicks, T.C., Bayogo, R.E., Bechem, M., Beyers, R.L., Bezangoye, A.N., Boundja, P., Bout, N., Akou, M.E., Bene, L.B., Fosso, B., Greengrass, E., Grossmann, F., Ikamba-Nkulu, C., Ilambu, O., Inogwabini, B.-I., Iyenguet, F., Kiminou, F., Kokangoye, M., Kujirakwinja, D., Latour, S., Liengola, I., Mackaya, Q., Madidi, J., Madzoke, B., Makoumbou, C., Malanda, G.-A., Malonga, R., Mbani, O., Mbendzo, V.A., Ambassa, E., Ekinde, A., Mihindou, Y., Morgan, B.J., Motsaba, P., Moukala, G., Mounguengui, A., Mowawa, B.S., Ndzai, C., Nixon, S., Nkumu, P., Nzolani, F., Pintea, L., Plumptre, A., Rainey, H., de Semboli, B.B., Serckx, A., Stokes, E., Turkalo, A., Vanleeuwe, H., Vosper, A. & Warren, Y. (2013). Devastating decline of forest elephants in Central Africa. *PLoS One* **8**, e59469.

MISR Makerere University Institute for Social Research (1989). *Settlement in forest reserves, game reserves, and National Parks*. Kampala, Uganda: Makerere University.

Moreto, W.D., Brunson, R.K. & Braga, A.A. (2017). 'Anything we do, we have to include the communities': law enforcement rangers' attitudes towards and experiences of community–ranger relations in wildlife protected areas in Uganda. *Br. J. Criminol.* **57**, 924–944.

Moreto, W.D. & Lemieux, A.M. (2015). Poaching in Uganda: perspectives of law enforcement rangers. *Deviant Behav.* **36**, 853–873.

Moreto, W.D. & Pires, S.F. (2018). *Wildlife crime: an environmental criminology and crime science perspective*. Durham, NC: Carolina Academic Press.

Mugisha, A.R. & Jacobson, S.K. (2004). Threat reduction assessment of conventional and community-based conservation approaches to managing protected areas in Uganda. *Environ. Conserv.* **31**, 233–241.

Nampindo, S. & Plumptre, A. (2005). A Socio-economic assessment of community livelihoods in areas adjacent to corridors linking Queen Elizabeth National Park to other protected areas in Western Uganda. *Wildlife Conservation Society, Albertine Rift Programme*.

Naughton-Treves, L. & Chapman, C.A. (2002). Fuelwood resources and forest regeneration on fallow land in Uganda. *J. Sustain. For.* **14**, 19–32.

Naughton-Treves, L., Kammen, D.M. & Chapman, C. (2007). Burning biodiversity: woody biomass use by commercial and subsistence groups in western Uganda's forests. *Biol. Conserv.* **134**, 232–241.

Naughton-Treves, L., Treves, A., Chapman, C.A. & Wrangham, R.W. (1998). Temporal patterns of crop raiding by primates: linking food availability in croplands and adjacent forest. *J. Appl. Ecol.* **35**, 596–606.

Naughton-Treves, L. (1999). Whose animals? A history of property rights to wildlife in Tooro, Western Uganda. *Land Degrad. Dev.* **10**, 311–328.

Olupot, W., McNeilage, A. & Plumptre, A.J. (2009) An analysis of socioeconomics of bushmeat hunting at major hunting sites in Uganda. *WCS Working Paper 38*.

Omeja, P.A., Jacob, A.L., Lawes, M.J., Lwanga, J.S., Rothman, J.M., Tumwesigye, C. & Chapman, C.A. (2014). Changes in elephant density affect forest composition and regeneration? *Biotropica* **46**, 704–711.

Osmaston, H.A. (1959). *Working plan for the Kibale and Itwara Forests*. Entebbe, Uganda: Ugandan Forest Department.

Pasquetto, I.V., Borgman, C.L. & Wofford, M.F. (2019). Uses and reuses of scientific data: the data creators' advantage.

Pasquetto, I.V., Randles, B.M. & Borgman, C.L. (2017). On the reuse of scientific data. *Data Sci. J.* **16**, 8.

Pimbert, M.P. & Pretty, J.N. (1997). Parks, people and professionals: putting 'participation'into protected area management. *Soc. Change Conserv.* **16**, 297–330.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752.

Pires, S.F. & Moreto, W.D. (2011). Preventing wildlife crimes: Solutions that can overcome the 'Tragedy of the Commons'. *Eur. J. Crim. Policy Res.* **17**, 101–123.

Plumptre, A.J., Fuller, R.A., Rwetsiba, A., Wanyama, F., Kujirakwinja, D., Driciru, M., Nangendo, G., Watson, J.E. & Possingham, H.P. (2014). Efficiently targeting resources to deter illegal activities in protected areas. *J. Appl. Ecol.* **51**, 714–725.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J. & Vira, B. (2010). Biodiversity conservation: challenges beyond 2010. *Science* **329**, 1298–1303.

Rasolofoson, R.A., Ferraro, P.J., Jenkins, C.N. & Jones, J.P. (2015). Effectiveness of community forest management at reducing deforestation in Madagascar. *Biol. Conserv.* **184**, 271–277.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J. & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103.

Robinson, J.G. (1993). The limits to caring: sustainable living and the loss of biodiversity. *Conserv. Biol.* **7**, 20–28.

Robinson, J.G. (2011). Ethical pluralism, pragmatism, and sustainability in conservation practice. *Biol. Conserv.* **144**, 958–965.

Rothman, J.M., Chapman, C.A., Struhsaker, T.T., Raubenheimer, D., Twinomugisha, D. & Waterman, P.G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology* **96**, 873–878.

Ryan, S.J., Southworth, J., Hartter, J., Dowhaniuk, N., Fuda, R.K. & Diem, J.E. (2015). Household level influences on fragmentation in an African park landscape. *Appl. Geogr.* **58**, 18–31.

Salerno, J., Chapman, C.A., Diem, J.E., Dowhaniuk, N., Goldman, A., MacKenzie, C.A., Omeja, P.A., Palace, M.W., Reyna-Hurtado, R., Ryan, S.J. & Hartter, J. (2018). Park isolation in anthropogenic landscapes: land change and livelihoods at park boundaries in the African Albertine Rift. *Reg. Environ. Change* **18**, 913–928.

Sarkar, D., Andris, C., Chapman, C.A. & Sengupta, R. (2019*a*). Metrics for characterizing network structure and node importance in Spatial Social Networks. *Int. J. Geogr. Inf. Sci.* **33**, 1017–1039.

Sarkar, D. & Chapman, C.A. (2021*a*). Academic Incentives Should Not Promote the "Extinction of Nature Experience". *Tropical Conservation Science*, **14**, 194008292110573. http://dx.doi.org/10.1177/19400829211057335

Sarkar, D. & Chapman, C.A. (2021*b*). The Smart forest conundrum: contextualizing pitfalls of sensors and AI in conservation science for tropical forests. *Trop. Conserv. Sci.* **14**, 19400829211014740.

Sarkar, D., Chapman, C.A., Angom, S.C., Valenta, K., Kagoro, W. & Sengupta, R. (2019*b*). A tiered analysis of community benefits and conservation engagement from the Makerere University Biological Field Station, Uganda. *Prof. Geographer* **71**, 422–436.

Sarkar, D., Chapman, C.A., Kagoro, W. & Sengupta, R. (2016). Countering elephant raiding with Short Message Service: challenges of deploying public participation-based systems in a setting with sparse Information Communication Technologies resources. *Can. Geographer/Le Géographe Canadien* **60**, 493–504.

Scheffers, B.R., Joppa, L.N., Pimm, S.L. & Laurance, W.F. (2012). What we know and don't know about Earth's missing biodiversity. *Trends Ecol. Evol.* **27**, 501–510.

Scheffers, B.R., Oliveira, B.F., Lamb, I. & Edwards, D.P. (2019). Global wildlife trade across the tree of life. *Science* **366**, 71–76.

Schwartzman, S., Nepstad, D. & Moreira, A. (2000). Arguing tropical forest conservation: people versus parks. *Conserv. Biol.* **14**, 1370–1374.

Skorupa, J.P. (1988). *The effect of selective timber harvesting on rain forest primates in Kibale Forest, Uganda*. PhD Thesis. Davis, CA: University of California.

Solomon, J., Jacobson, S.K. & Liu, I. (2012). Fishing for a solution: can collaborative resource management reduce poverty and support conservation? *Environ. Conserv.* **39**, 51–61.

Songorwa, A.N., Bührs, T. & Hughey, K.F. (2000). Community-based wildlife management in Africa: a critical assessment of the literature. *Nat. Resour. J.* **40**, 603–643.

Stampone, M., Hartter, J., Chapman, C.A. & Ryan, S.J. (2011). Trends and variability in localized percipitation around Kibale National Park, Western Uganda, Africa. *Res. J. Environ. Earth Sci.* **3**, 14–23.

Stirnemann, R., Stirnemann, I., Abbot, D., Biggs, D. & Heinsohn, R. (2018). Interactive impacts of by-catch take and elite consumption of illegal wildlife. *Biodivers. Conserv.* **27**, 931–946.

Struhsaker, T.T. (1975). *The Red Colobus Monkey*. Chicago, IL: University of Chicago Press.

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

Tranquilli, S., Abedi-Lartey, M., Abernethy, K., Amsini, F., Asamoah, A., Balangtaa, C., Blake, S., Bouanga, E., Breuer, T., Brncic, T.M., Campbell, G., Chancellor, R., Chapman, C.A., Davenport, T.R.B., Dunn, A., Dupain, J., Ekobo, A., Eno-Nku, M., Etoga, G., Furuichi, T., Gatti, S., Ghiurghi, A., Hashimoto, C., Hart, J.A., Head, J., Hega, M., Herbinger, I., Hicks, T.C., Holbech, L.H., Huijbregts, B., Kühl, H.S., Imong, I., Yeno, S.-D., Linder, J., Marshall, P., Lero, P.M., Morgan, D., Mubalama, L., N'Goran, P.K., Nicholas, A., Nixon, S., Normand, E., Nziguyimpa, L., Nzooh-Dongmo, Z., Ofori-Amanfo, R., Ogunjemite, B.G., Petre, C.-A., Rainey, H.J., Regnaut, S., Robinson, O., Rundus, A., Sanz, C.M., Okon, D.T., Todd, A., Warren, Y. & Sommer, V. (2014). Protected areas in tropical Africa: assessing threats and conservation activities. *PLoS One* **9**, e114154.

Tranquilli, S., Abedi-Lartey, M., Amsini, F., Arranz, L., Asamoah, A., Babafemi, O., Barakabuye, N., Campbell, G., Chancellor, R., Davenport, T.R.B., Dunn, A., Dupain, J., Ellis, C., Etoga, G., Furuichi, T., Gatti, S., Ghiurghi, A., Greengrass, E., Hashimoto, C., Hart, J., Herbinger, I., Hicks, T.C., Holbech, L.H., Huijbregts, B., Imong, I., Kumpel, N., Maisels, F., Marshall, P., Nixon, S., Normand, E., Nziguyimpa, L., Nzooh-Dogmo, Z., Tiku Okon, D.T., Plumptre, A., Rundus, A., Sunderland-Groves, J., Todd, A., Warren, Y., Mundry, R., Boesch, C. & Kuehl, H. (2012). Lack of conservation effort rapidly increases African great ape extinction risk. *Conserv. Lett.* **5**, 48–55.

van Orsdol, K.G. (1986). Agricultural encroachment in Uganda's Kibale Forest. *Oryx* **20**, 115–117.

Wasser, S., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C. & Weir, B.S. (2015). Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science* **349**, 84–87.

Western, D. & Pearl, M.C. (1989). *Conservation for the twenty-first century*. Oxford, UK: Oxford University Press.

Wilcox, B.A. & Murphy, D.D. (1985). Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.* **125**, 879–887.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.

World Bank (2020). Terrestrial protected areas. https://data.worldbank.org/indicator/ER.LND.PTLD.ZS. Accessed April 24, 2020.

WorldPop (2020). Open spatial demographic data and research.

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.

Wrangham, R. & Mugume, S. (2000). Snare removal program in Kibale National Park: a preliminary report. *Pan Afr. News* **7**, 18–20.