

Wildlife Crime and Monitoring:
Applications for Ranger-Collected Data

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Abstract

Anthropogenic factors such as habitat loss, over-harvesting and the introduction of non-native species are causing declines in global biodiversity. In sub-Saharan Africa, illegal hunting for bushmeat or high-value products such as rhino horn and ivory is threatening many mammal populations. Monitoring these populations is vital to ensuring their survival, yet professional scientific monitoring programs are costly and logistically difficult. Ranger-based monitoring, where rangers record evidence of illegal activities or wildlife sightings when on patrol is becoming increasingly popular.

Here, we use maps of occurrence probability of bushmeat poaching derived from ranger-collected data in Queen Elizabeth National Park (QENP), Uganda, to determine the direct impacts of illegal hunting on herbivore populations. We found that the main target species for bushmeat poaching, Uganda kob, showed declines in areas predicted to have high poaching risk, reporting population level impacts of illegal hunting in a savannah for the first time.

We go on to document how ranger-collected elephant sightings data can be used to predict their spatial distribution within QENP, using Bayesian hierarchical occupancy modelling to address the non-systematic method of data collection. We also attempt to create a time series model of elephant abundance in order to predict rapid declines that can occur in elephant populations.

We conclude by highlighting the potential for ranger-based monitoring and ranger-collected data, suggesting ways it might be incorporated to continually monitor vulnerable populations in light of a rapidly expanding human population.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author.

This work has not previously been presented for an award at this, or any other,

University. All sources are acknowledged as References.

Chapter 1. Introduction

1.1 Commercial and subsistence bushmeat hunting in protected areas

Global biodiversity is in decline, due to anthropogenic factors such as habitat loss, over-harvesting and the redistribution of species around the planet. In tropical countries, the primary threats to vertebrates are over-harvesting and habitat loss, and strategies to combat this include the creation of protected areas and law enforcement. Wildlife crime has become a topic of international concern in recent years, due to the dramatic rise in elephant and rhino poaching to meet international demands for rhino horn and ivory. The term wildlife crime, however, covers a much wider range of activities, from bushmeat hunting and illegal fishing, to firewood and medicinal plant collection, all of which can affect both populations and biodiversity. Smaller-scale wildlife crimes, such as subsistence bushmeat hunting, are often driven by poverty, in particular during times of economic hardship (Rogan *et al.* 2017). Commercial bushmeat hunting might occur when larger species, such as buffalo, are hunted and the meat sold to generate funds which are then used as currency. Illegal harvesting of animals for bushmeat, either for subsistence, or commercial for markets can have negative impact on populations in protected areas. Commercial bushmeat hunting typically involves larger mammals, such as buffalo or hippopotamus, due to their high value, with meat ending up in regional markets. Subsistence bushmeat hunting involves smaller, lower value animals, such as smaller antelope, and typically ends up in local markets (Harrison *et al.* 2015). Cases of negative ecological impacts from illegal bushmeat poaching have been well documented in African rainforest regions (Noss 1998, Fa *et al.* 2002, Brashares *et al.*

2004, Jachmann 2008, Fa & Brown 2009, Laurance 2012, Watson *et al.* 2013), but are less common for savannah ecosystems.

Bushmeat is a significant contributor to food security, often being the primary source of protein in rural communities, as well as providing funds for healthcare and education (Loibooki *et al.* 2002, Nielsen 2006, Lindsay *et al.* 2013). The human population is increasing rapidly in much of sub-Saharan Africa (Hall *et al.* 2017), and populations bordering protected areas are growing faster than those in other rural areas (Wittemeyer *et al.* 2008). This suggests that people perceive the benefits of protected areas, either from the share of income generated from protected areas to local communities, or the opportunity to carry out illegal activities (Hofer *et al.* 1996). The authors suggest that levels of bushmeat poaching are likely to increase while its benefits are sufficient to encourage people to migrate close to protected areas.

The impacts of bushmeat poaching in protected areas can be extreme. It is estimated that up to 10% of the Serengeti-Mara wildebeest population is poached for bushmeat each year (Rentsch and Packer 2015). Buffalo populations have declined in Serengeti National Park where illegal bushmeat hunting takes place, and levels of poaching are unsustainable with the accelerated population growth around the park's borders (Hofer *et al.* 1996, Metzger *et al.* 2010, Hilborn *et al.* 2006)

Along with a reduction in food quality, bushmeat hunting was found to be a contributing factor in the decline in the Serengeti Masai giraffe (*Giraffa camelopardalis tippelskirchi*) population (Sinclair 1995, Campbell & Borner 1995, Stauss *et al.* 2015). Serengeti giraffe density is estimated to have fallen by 80% since 1970 (Stauss *et al.* 2015). Furthermore, giraffe poaching may be male-biased, as

males spend more time in dense woodland and browse higher in the canopy, where snares are often set (Young & Isbell 1991). Male-biased hunting has led to a reduction in female fecundity in several species (Ginsberg & Milner-Gulland 1994).

Hunting of impala in Serengeti buffer zones not only significantly reduces their density, but also their demography (populations are more likely to be female-skewed) and behaviour (Setsaas *et al.* 2007). Buffer zone populations have demonstrate higher alertness levels, as well as longer flight initiation distance to approaching humans. This suggests bushmeat hunting has impacts other than merely reducing population densities.

Hunting for bushmeat also significantly reduces mammal species richness. A less strictly protected forest reserve in Tanzania was found to have 40% fewer mammal species than a national park (Hegerl *et al.* 2017). The main difference between these two protected areas is the level of protection, suggesting that ineffective or non-existent law enforcement can lead to uncontrolled hunting, which in turn has a significant impact on local fauna.

Bushmeat hunting may also have indirect effects on non-target species. Brodie *et al.* (2009) found significantly reduced mammal-dispersed tree recruitment in areas with high levels of bushmeat poaching for primates and ungulates in Southeast Asia. In the highest poached protected areas, the extinction of a key canopy species *Choerospondias axillaris* is a real possibility, although it may take several decades.

As well as threatening wild herbivore populations, illegal bushmeat hunting causes competition between humans and other apex predators for limited prey species and reduces the ecosystem's carrying capacity for large carnivores (Rogan *et al.* 2017).

The above literature certainly suggests that bushmeat poaching has a significant impact on both abundances and distributions of animals within protected areas, as well as non-target organisms such as trees and predators. It is also evident that bushmeat poaching is more intense and has much greater effects in areas with insufficient law enforcement. In order to conserve biological diversity within protected areas, it is therefore important to improve law enforcement where possible, preferably without increasing strain on already small budgets.

Although there is a growing body of evidence pointing to the scale and negative impacts of illegal bushmeat hunting in savannah ecosystems, there have been no studies to date which have looked at the direct impacts of bushmeat hunting on herbivore populations. It remains unclear whether the scale of bushmeat poaching in protected areas is sustainable or not, and if offtake falls below or exceeds surplus productivity. In order to properly study this, it is important to understand both the spatial and temporal trends of illegal bushmeat hunting inside protected areas.

Critchlow *et al.* (2015) used ranger-collected data on a variety of illegal activities from Queen Elizabeth National Park (QENP) in Uganda to model these trends.

Using these models, the authors were able to predict where each illegal activity is most likely to occur, and suggest alternative ranger patrol routes (Critchlow *et al.*

2017), which increased detections of illegal activities by up to 250%. In chapter 2 of this thesis, I modelled the spatial and temporal trends in abundance of three key herbivore species in QENP, using the probability of illegal bushmeat hunting from Critchlow *et al.* (2015) as a covariate, in order to investigate the direct impacts of bushmeat hunting on herbivore species.

1.2 Illegal hunting of African elephant for ivory

The iconic African elephant plays a number of important ecological, economic and cultural roles in sub-Saharan Africa. Elephants are a keystone species, meaning they have a disproportionately large effect on the community and ecosystem processes within savannahs. Elephants act as ecosystem engineers, shaping the landscape and vegetation structure around them (Laws 1970, Fritz 2017). In savannah ecosystems, elephants clear young trees, maintaining open savannah grassland whilst dispersing seeds of many plant species (Wilby *et al.* 2001). This has profound trophic effects, providing and improving habitat for invertebrates (Romero *et al.* 2015), reptiles and amphibians (Pringle 2008, Nasser *et al.* 2011) and other herbivores (Rutina *et al.* 2005).

Elephants also have large economic value across much of Africa. Photographic tourism is a huge global market (Moorhouse *et al.* 2017), the revenue from which can be re-invested in conservation programs, such as the creation of protected areas and the implementation of range patrols (Ballantyne *et al.* 2009). Tourism revenue is also often re-invested in local communities as incentives for conserving wildlife (Ahebwa *et al.* 2009, Sandbrook, 2010), facilitating local employment and the construction of schools, clinics and infrastructure (Archibald & Naughton-Treves 2001). The benefits of photographic tourism are not always perceived by, or well invested in, local communities. Naidoo *et al.* (2016) suggest that in many protected areas, local people see poaching as a more rational and consistent source of income.

Prior to European colonisation of Africa, there may have been as many as 20 million elephants across the continent, and 1 million as recently as 1970 (Douglas-Hamilton 1987, Milner-Gulland & Beddington 1993). During the 1970's and 1980's, wide scale

poaching of elephant for ivory, as well as habitat loss and fragmentation caused severe declines in the majority of populations (Wittemyer *et al.* 2014, Craigie *et al.* 2010). Between the late 1980's, elephant populations had recovered considerably, until a sharp rise ivory prices in the last decade led to a spike in elephant poaching. (Wittemyer *et al.* 2014) It is unclear quite how many elephants remain in the wild today, with current estimates around 350,000 (Chase *et al.* 2016). Despite some populations remaining stable or increasing (Morrison *et al.* 2018, Van Aarde & Jackson 2007), the continent wide population of elephants is shrinking by 8% per year (Chase *et al.* 2016).

As well as illegal hunting of elephant for ivory, declines in populations have also been attributed to habitat loss and fragmentation, and conflict with humans (Ripple *et al.* 2015, Lobora *et al.* 2017). Since 1970, the amount of suitable elephant habitat has fallen by as much as 60% (Blanc *et al.* 2007, UNEP 2013). At the same time, the human population of Africa is increasing rapidly, with more elevated growth around protected areas (Wittemeyer *et al.* 2008). As elephants are migratory and often travel long distances (Thouless 1995), this inevitably leads to conflict between humans and elephants, leading to illegal killings to protect livelihoods.

The increasing demand for ivory in Asian countries such as China, Japan and Hong Kong has caused the price of ivory on the black market to increase dramatically over the past 15 years (Stiles 2004, Gibson *et al.* 2018). This has resulted in many more elephants being poached, with an estimated population decrease of 144,000 between 2007 and 2014 (Chase *et al.* 2016), a trend which has continued in recent years (Kyando *et al.* 2017, Beale *et al.* 2018, Schlossberg *et al.* 2018).

Conservation efforts to prevent the illegal hunting of elephants generally consist of the creation of protected areas, wildlife corridors to facilitate migrations and surveillance patrols by law enforcement agencies. Although 84% of elephants can be found in protected areas (Chase *et al.* 2016), poaching is still common. Effective law enforcement has been shown to reduce numbers of elephants poached in protected areas (Leader-Williams *et al.* 1990, Milner-Gulland & Leader Williams 1992, Jachmann & Billiouw 1997, Martin 2010, Moore *et al.* 2017), although it remains unclear whether ranger patrols act as a deterrent to poachers (Beale *et al.* 2018). In order to conserve the remaining African elephants, at both global and continental scales, close monitoring of existing populations is vital.

1.3 Ranger-based monitoring and ranger-collected data

The monitoring of biodiversity is crucial in assessing trends in vulnerable species and assigning conservation priorities (Balmford *et al.* 2005). Likewise, monitoring of populations is vital in order for conservation scientists and policy makers to assess the impacts of their interventions (Kremen *et al.* 1994). Although scientifically robust, professional monitoring programs carried out by trained scientists, such as large mammal aerial surveys, are often highly costly and logistically difficult, especially for conservation agencies in developing countries. This high cost can result in monitoring programs being discontinued or carried out so infrequently that rapid declines in key populations can be missed (Danielsen *et al.* 2005b).

Recently, monitoring programs carried out by untrained members of the community have risen in popularity. This locally-based monitoring can be carried out by local resource users monitoring harvests, hunters monitoring catch rates or censuses by local rangers (Danielsen *et al.* 2005b). When carrying out surveillance patrols,

employed rangers often record the location of any signs of illegal activities and notable wildlife sightings. This ranger-collected data can serve a variety of functions. Gray & Kalpers (2005) outline a successful monitoring program carried out by rangers in the Virunga-Bwindi region of East-Central Africa. The data collected provided information on illegal activities in the area, as well as locations and behavioural patterns of habituated and unhabituated groups of mountain gorillas (*Gorilla beringei beringei*). This allowed park managers to make rapid decisions in response to threats to the ecosystem. Brashares & Sam (2005) analysed data from a 33 year ranger-based monitoring program from savannah ecosystems in Ghana, West Africa to identify the minimum level of monitoring to be able to detect trends in abundance of wildlife over 5 year intervals. These methods of assessing ranger-collected data to assess trends in animal populations can lead to highly biased results, as analyses assume random or uniform survey effort across the area. Conversely, rangers focus on where they feel they are most likely to encounter illegal activities when planning their patrol routes. Recently, methods have been developed to address this bias by estimating the probability of detecting an event (in this case, a wildlife sighting) independently from the processes that drive the distribution of the events (Beale *et al.* 2014).

Rangers in QENP have been recording details of illegal activities and wildlife sightings since 1999, using the SMART (spatial monitoring and reporting tool) software and its predecessor MIST (management information system).

If implemented correctly, there are obvious benefits to ranger-based monitoring and ranger-collected data. Most importantly, the rangers' primary objective is detect and deter illegal activities within protected areas, therefore collecting data passively adds minimal additional costs to already strained resources.

While ranger-based monitoring has the potential to generate useful, low-cost data, many scientists are sceptical about its ability to detect true trends in abundance of wildlife compared with professional monitoring (Penrose & Call 1995). Rangers, such as those in QENP, are not actively looking for wildlife, and are not following set transects. Rangers set patrol routes based on where they feel they are most likely to encounter illegal activities, and therefore any wildlife sightings data collected will be heavily biased.

To date, there have been no published studies which directly compare ranger-collected data with professionally-collected data. In chapter 3 of this thesis, I used a novel method, adapted from Critchlow *et al.* (2015) for removing the bias in the ranger-collected data from QENP. I then attempted to infer the spatial distribution and temporal trends in abundance of elephant within the area, and compared this to a long running professional monitoring program.

Chapter 2. Herbivore Population Declines Associated With Bushmeat Poaching in a Ugandan National Park: A Modelling Approach.

2.1 Introduction

In protected areas illegal activities such as commercial poaching for ivory and rhino horn, non-commercial poaching for bushmeat, cattle encroachment, illegal timber harvesting and illegal fishing account for the majority of biodiversity loss (Geldmann *et al.* 2013, Laurance *et al.* 2012). In African savannah ecosystems, the commercial poaching of elephant and rhino gets much media attention, yet the ecological effects of illegal bushmeat hunting should not be underestimated (Lindsey *et al.* 2013, van Velden *et al.* 2018). While the majority of scientific literature on the ecological impacts of bushmeat hunting focuses on forest ecosystems in West Africa, the rich vertebrate communities of savannah ecosystems are both ecologically and economically valuable and are also exploited for bushmeat (Nuno *et al.* 2013, Rentsch and Packer 2015). Photographic tourism within African protected areas provides valuable income to economies, meaning bushmeat hunting is often an inefficient use of wildlife resources (Lindsey *et al.*, 2015). The human population of Africa is increasing rapidly, and with almost twice the rate of growth around protected areas (Wittemeyer *et al.* 2008), there is increased demand for bushmeat products.

Poaching is known to have negative effects on animal abundances in savannah ecosystems, for example, it is estimated that up to 10% of the Serengeti wildebeest population is poached for bushmeat each year (Rentsch and Packer 2015).

Population declines in buffalo, giraffe and impala have also been attributed to illegal bushmeat hunting (Setsaas *et al.* 2007, Metzger *et al.* 2010, Strauss *et al.* 2015). As well as direct impacts of bushmeat hunting on herbivore populations, many non-target species can be affected (Hofer *et al.* 1996, Brodie *et al.* 2009, Becker *et al.* 2013). Human hunters act as direct competition with carnivores for prey, reducing their carrying capacity and further degrading wildlife tourism (Rogan *et al.* 2017). Interventions to reduce bushmeat poaching in protected areas include effective law enforcement (e.g. ranger patrols), enabling access to alternative sources of protein and community based natural resource management (CBNRM), yet their effectiveness is rarely assessed (Loibooki *et al.* 2002, Blaikie 2006). Effective law enforcement has been found to reduce illegal activities such as bushmeat poaching in protected areas (Geldmann *et al.* 2013), and its efficiency can be improved if law enforcement agencies are aware of the true spatial and temporal patterns in bushmeat hunting (Critchlow *et al.* 2017).

Much of the literature on the ecological effects of bushmeat poaching focuses on stakeholder interviews (van Velden *et al.* 2018) and, while these provide valuable insight into the drivers and temporal patterns of bushmeat hunting, they provide little evidence for the direct impact on populations of both target and non-target species. In order to evaluate the true impacts of bushmeat poaching on animal population growth, patterns of animal abundance changes need to be compared with patterns of bushmeat hunting.

The effects of illegal bushmeat hunting on herbivore population growth in protected areas have not adequately been studied. Here, we investigate the hypothesis that population growth rates of key herbivore species are lowest in areas predicted to have high levels of bushmeat poaching within Queen Elizabeth National Park, Uganda. Here, we use a novel method for assessing the impacts of bushmeat hunting on herbivore population by applying spatially explicit population change models using realistic spatial and temporal predictions of bushmeat poaching. QENP is ideally suited for this analysis, as data on large animal abundances have been gathered from a series of comprehensive aerial surveys over a 21 year period (Wanyama 2006; Wanyama 2012; Wanyama *et al.* 2014) and ranger-collected data on a variety of illegal activities has provided spatial and temporal patterns of bushmeat hunting (Critchlow *et al.* 2015).

2.2 Methods

In order to test whether bushmeat poaching has a negative impact on herbivore population growth in protected areas, we used data from systematic aerial surveys of Queen Elizabeth National Park (QENP) in Uganda (Figure 1) to calculate spatial and temporal trends in densities of the most abundant herbivore species, Uganda kob *Kobus kob thomasi*, Cape buffalo *Syncerus caffer* and waterbuck *Kobus ellipsiprymnus*.

2.2.1 Study Area

QENP protects 1,978km² of savannah grassland and acacia woodland in Southwest Uganda. Two dry seasons and two wet seasons per year generate an average of 1475mm of rainfall, and the park is home to large populations of Uganda kob (c. N12987 +/- 6329) and buffalo (N15771 +/- 6303), with smaller populations of waterbuck, bushbuck, *Tragelaphus scriptus* and topi, *Damaliscus lunatus*. Bushmeat poaching using wire snares is relatively common in QENP, and spatial and temporal data on instances of poaching have been collected by park rangers using SMART (Spatial Monitoring and Reporting Tool) and its predecessor MIST (Management Information System) since 1999. Critchlow *et al* (2015) used these data to model the underlying spatial and temporal patterns of bushmeat poaching in QENP, removing bias in effort with occupancy models.

2.2.2 Herbivore Data

We calculated abundance changes of Uganda kob, buffalo and waterbuck from large mammal aerial surveys carried out by professional surveyors in 1995, 1999, 2000, 2004, 2006, 2010, 2014 and 2016. Surveys were carried out using systematic reconnaissance flights (SRF), as described in Norton-Griffiths (1978). Briefly, surveyors flew in a Cessna single engine aircraft, fitted with sampling rods under each wing to identify a strip approximately 150m wide on each side of the aircraft when flying at 350ft (109m) above ground level. We computed actual strip width knowing the calibration for each observer and the altitude of the aircraft. Using actual strip widths, we converted count data for each species into density per km². We divided QENP into two counting blocks (North and South sectors), divided centrally by the Maramagambo forest reserve (not surveyed). In total there were 41

transects, 2.5 km apart, divided into a total of 399 survey subunits. The spatial location of these transects and subunits remained consistent with each survey.

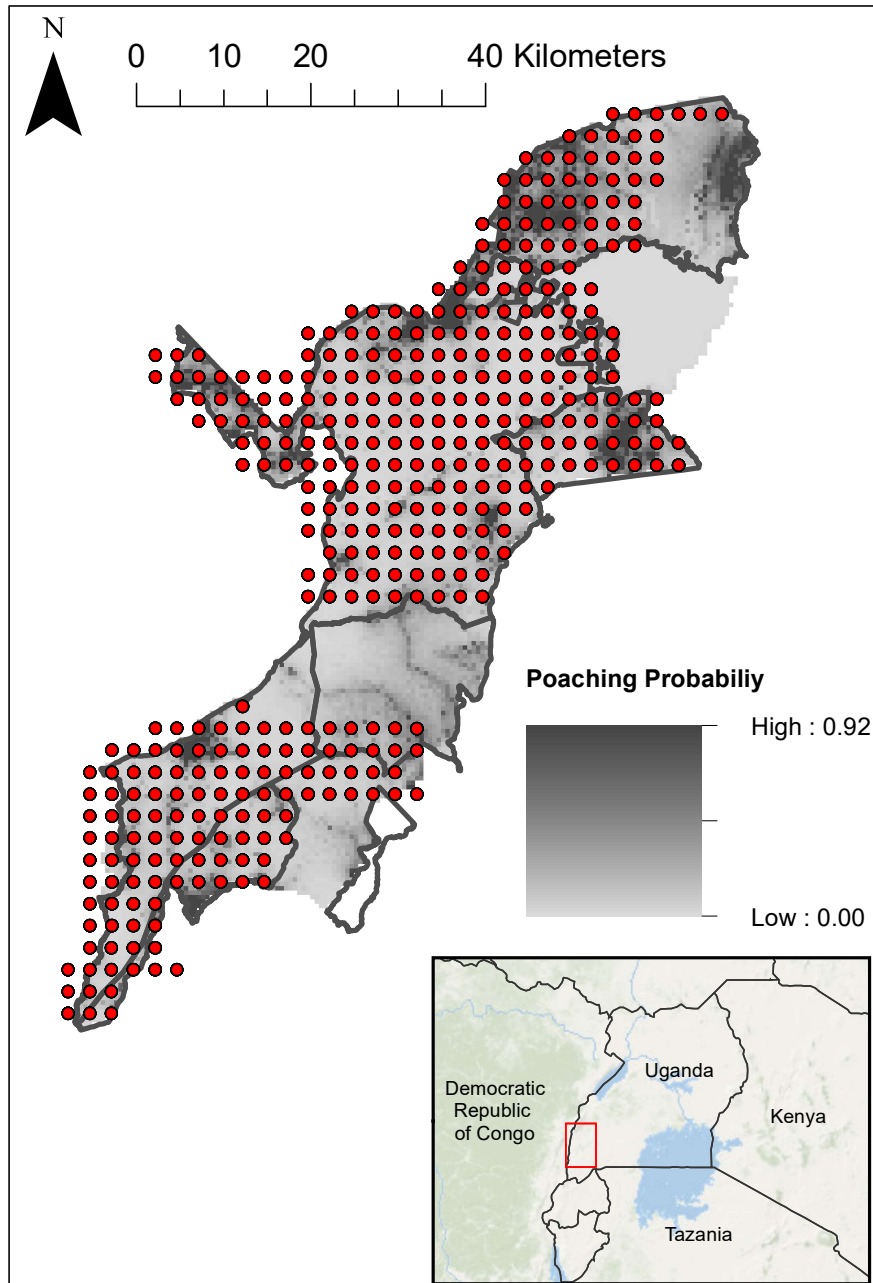


Figure 1. Cells surveyed during the large mammal aerial censuses of Queen Elizabeth National Park, 1995 – 2016. Shaded area indicates probability of bushmeat poaching from Critchlow *et al.* (2015). Inset shows detailed area within Uganda.

2.2.3 Covariates

SRF data only sample a small portion of the landscape, and offer only a snapshot of the actual distribution of animals. In order to assess whether local population changes of key herbivore species in QENP are associated with hotspots of bushmeat poaching, we modelled the population in each survey year, using distance to the park boundary, net primary productivity and occurrence of bushmeat poaching from Critchlow *et al.* (2015) as covariates.

Illegal activity data

Critchlow *et al.* (2015) presented annual maps of the incidence of illegal activities in QENP, based on a Bayesian, spatially explicit occupancy model derived from ranger-collected data. We used the annual maps of ‘animal non-commercial’ poaching (consisting of records of snares, arrests for poaching and honey gathering) in each 5km cell of QENP, for the years 1999-2014. For aerial surveys prior to 1999, we assumed the same spatial pattern as in 1999, and for aerial surveys after 2014, the 2014 model outputs were used: Critchlow *et al.* (2015) found relatively little year on year variation in the spatial pattern of poaching.

Net primary productivity (NPP) data

NPP data for QENP was gathered from MODIS (ORNL 2018) for years 2000-2016. NPP data was at 1km² resolution. For aerial surveys prior to 2000, we used NPP data from 2000.

Distance to park boundary

Spatial data on the park boundary was collected from Esri Online (2018), and for each 2.5km grid cell we computed the distance from the centre of the cell to the closest park boundary

2.2.4 Data and Analysis

To model spatial populations changes we fitted a log-linear population model with a spatial random effect using Integrated Nested Laplace Approximation (INLA) within R (R Core Team 2015). INLA provides a computationally efficient method to fit complex spatiotemporal models within a Bayesian framework (Rue *et al.* 2009). Our models accounted for spatial autocorrelation in an intrinsic conditional autoregressive model (iCAR) (Besag *et al.* 1991) and to account for the unequal time steps between aerial surveys, we incorporated a loglinear population change model from Freeman and Newson (2008), with “year” as a fixed effect. We chose this recursive model due to needing to model the change in populations from the previous survey, with spatially and temporally varying covariates. This model allowed us to model expected numbers of animals per cell, as density is much smoother than the observed counts: the location of a herd of 300 buffalo is expected to shift from cell to cell over time so mean abundance is always below this.

2.3 Results

During model selection, we used the Watanabe-Akaike criterion (WAIC) scores to identify the most important model components. WAIC scores of more than 2 indicate strongly supported parameters. In our model outputs we found strong support for the “year” effect on change in kob abundance and NPP for change in waterbuck abundance (Table 1). In these models, Δ WAIC was less than 2 for poaching probability in all species.

Table 1. WAIC scores for candidate models of herbivore population change. Bold figure indicates effects where Δ WAIC > 2, indicating strongly supported parameters.

Species	Model	WAIC	Δ WAIC	Description
Uganda kob <i>Kobus kob thomasi</i>	Full	8861.92		Full model with all covariates and year effect
	No.dist	8860.39	-1.53	Model with no distance to park boundary
	No.NPP	8862.91	0.99	Model with no NPP
	No.poach	8858.91	-4.01	Model with no bushmeat poaching
	No.year	8899.78	37.86	Model with no year effect
Buffalo <i>Syncerus caffer</i>	Full	8314.30		Full model with all covariates and year effect

	No.dist	8313.74	-0.56	Model with no distance to park boundary
	No.NPP	8311.60	-2.70	Model with no NPP
	No.poach	8312.84	-1.46	Model with no bushmeat poaching
	No.year	8310.11	-4.19	Model with no year effect
Waterbuck	Full	6721.87		Full model with all covariates and year effect
<i>Kobus ellipsiprymnus</i>	No.dist	6723.35	1.48	Model with no distance to park boundary
	No.NPP	6725.87	4.00	Model with no NPP
	No.poach	6719.51	-2.36	Model with no bushmeat poaching
	No.year	6721.21	-0.66	Model with no year effect

Densities of Uganda kob, buffalo and waterbuck varied greatly across QENP, yet the spatial patterns of abundance remained largely consistent throughout the survey period (1995 – 2016). Highest densities of all three species were in the North-eastern and South-western areas of the park (Fig 2).

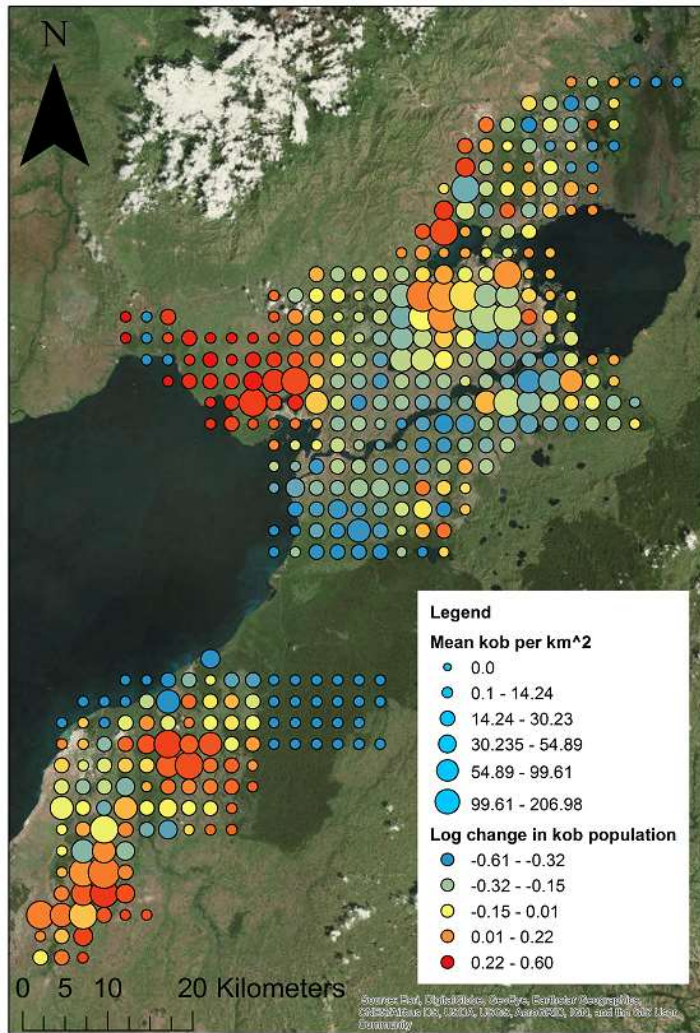


Figure 2. Model outputs of Uganda kob abundance change in Queen Elizabeth National Park. Point size indicates kob density, point colour indicates kob population growth.

Population change of all three species across the study period also varied greatly throughout QENP. In our best supported model, we found a significant negative association between abundance change of Uganda kob and occurrence probability of bushmeat hunting (Effect size = -0.099, CI = -0.0189 — -0.0106) (Fig 3.) (Table 2). This indicates that in areas that have high occurrence probability of bushmeat poaching, Uganda kob tend to show negative population growth. Similar negative

associations were found for buffalo and waterbuck, although these results were not significant (Table 2).

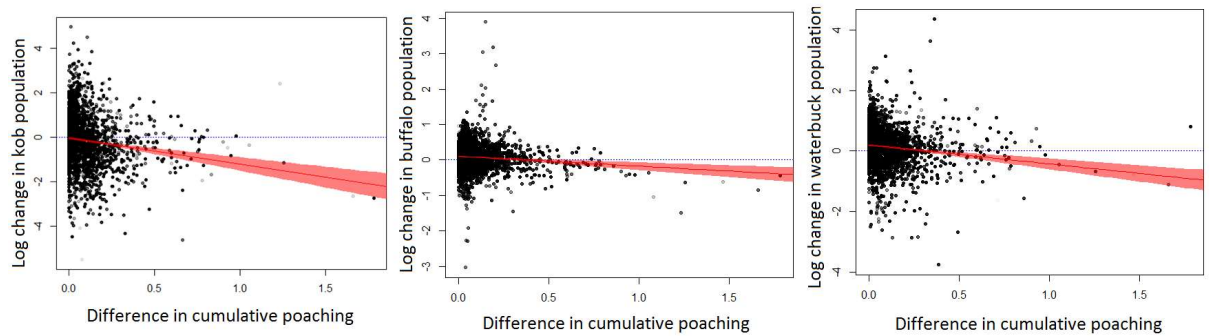


Figure 3. Relationships between herbivore population growth and cumulative bushmeat hunting. Polygons indicate 95% confidence intervals.

We also found a significant negative relationship between waterbuck population growth and distance to park boundary (effect size = -0.046, CI = -0.087 — -0.0041), indicating that waterbuck population growth decreases in central areas of the park (Table 2).

Table 2. Full model outputs of abundance change for Uganda kob, buffalo and waterbuck. Bold figures indicate effect size where confidence intervals do not overlap zero, indicating a significant result.

Species	Covariate	Effect size	Confidence Intervals	Standard deviation
Uganda kob <i>Kobus kob thomasi</i>	Bushmeat poaching	-0.099	-0.189 -0.0106	0.045
	NPP	0.071	-0.027 0.16	0.049
	Distance to boundary	-0.014	-0.027 0.0168	0.038
Buffalo <i>Syncerus caffer</i>	Bushmeat poaching	-0.047	-0.117 0.023	0.036
	NPP	-0.072	-0.156 0.009	0.041
	Distance to boundary	-0.012	-0.062 -0.009	0.025
Waterbuck <i>Kobus ellipsiprymnus</i>	Bushmeat poaching	-0.036	-0.092 0.019	0.028
	NPP	0.039	-0.023 0.019	0.032
	Distance to boundary	-0.046	-0.087 -0.0041	0.021

Model outputs showed variation in abundance change between survey years for all three species (Appendix 1, Table 3), with certain years showing positive population

growth in all species (2000, 2006, 2014), and some showing negative (2004, 2010). 2004 and 2010 showed significant negative population growth of Uganda kob.

2.4 Discussion

We set out to test whether bushmeat poaching has a negative impact on herbivore population growth in protected areas by modelling the change in herbivore abundance with regards to the occurrence probability of bushmeat poaching in QENP. In support of our hypothesis, our models indicated that bushmeat hunting reduces population growth of Uganda kob, and to a lesser extent buffalo and waterbuck. This is to be expected, as when poachers set out small wire snares and nets for bushmeat in QENP, the target species is Uganda kob (Moreto & Lemieux 2015), as they are small enough to transport, abundant and easily caught in snares and nets. In QENP, adult buffalo tend to be too large to be caught in small common wire snares (Marks 1973, Travers *et al.* 2017), and waterbuck are relatively unpalatable (Estes 1974).

A significant negative association was found between buffalo and waterbuck population growth and the distance to the park boundary. A similar, although non – significant relationship was also found for Uganda kob. This suggests that negative population growth is more common in central areas of the park. This result is unexpected, as areas bordering the park will be closest to human settlements, and provide the easiest access for hunters. QENP, however, is unique in that the majority of the park boundary (58%, not including the Southwest border with Virunga NP in DRC) is either on water (Lake George and Lake Edward), or is bordered by smaller protected areas in the greater Queen Elizabeth Protected Area (QEPA), resulting in restricted access to wildlife resources. A considerable improvement to this analysis

would be to replace “distance to park boundary” with “distance to park boundary allowing for barriers caused by water and other protected areas”, although this goes beyond the scope of this study.

The population change model adapted from Freeman and Newson (2008) uses year as a fixed effect. Certain years showed similar negative and positive population growth in all species. 2004 and 2010 in particular showed significant reduction in Uganda kob (Appendix 1, Table 3). This is in line with total numbers of species in QENP from official Uganda Wildlife Authority survey reports (Wanyama *et al.* 2014 etc). This could be caused by actual reduction in animal abundances from abiotic factors such as drought, or a rapid increase in bushmeat poaching. Alternative explanations for these temporal trends in abundance could be changes in observer effort. Wanyama *et al.* (2014) state that although the majority of surveys had been carried in the driest month, July, several surveys had been carried out in the wet season. The resulting increase in greening and canopy cover could result in reduced visibility during survey flights, and may underestimate the total animal numbers in the park (Beale *et al.* 2018). However, this seems less likely in QENP than elsewhere as dry season precipitation in QENP is still relatively high (30mm rainfall in July) and it is unlikely that season changes visibility as much as in more arid savannah ecosystems. Masih *et al.* (2014) report drought events in Uganda in 2002, 2008 and 2010, years preceding those with significant kob declines. Coupled with this, Critchlow *et al.* (2015) report a rapid rise in bushmeat poaching in QENP in the years preceding 2004 and 2010 (2001-2002 and 2009 respectively).

In this instance, it is difficult to ascertain if the declines in kob were caused directly by the increase in bushmeat poaching, or by the drought itself, although it is likely that drought conditions greatly increase the likelihood that individuals might resort

to illegal hunting for bushmeat, as households fail to satisfy basic needs due to failed crops or loss of livestock (Harrison *et al.* 2015). In order to expand on this analysis and investigate the real impacts of drought on these animal populations, it would be useful to include a model that uses monthly precipitation values as a covariate. In the years following 2004 and 2010, populations of all three species seemed to recover, suggesting natural resilience to environmental stressors such as drought.

In summary, our analysis suggests that population growth of key herbivore species, in particular Uganda kob, is sensitive to both spatial and temporal trends of bushmeat hunting in protected areas. Uganda kob are an important species in QENP, as they are key prey species for both leopards and lions (Balmford & Turyaho 1992; Mudumba *et al.* 2015), the removal of which may reduce valuable economic benefits in the form of wildlife tourism (Victurine 2000). Additionally, continual grazing by kob reduces the encroachment of woody cover, preserving savannah grassland which is a vital habitat to many species (Roques *et al.* 2001). These results provide support for Critchlow *et al.* (2015), which states that efficiency of law enforcement in protected areas can be greatly improved if they are aware of the true spatiotemporal patterns of illegal activities. Furthermore, this is the first time that population level impacts of bushmeat poaching have been reported in a savannah ecosystem. Previous studies have reported on the scale of bushmeat poaching. Rentsch & Packer (2005) state that 10% of the Serengeti-Mara wildebeest population is poached annually, and others postulate that declines are caused by high levels of poaching (Hofer *et al.* 1996, Metzger *et al.* 2010, Hilborn *et al.* 2006). It is important to note, however, that knowing details of offtake from poaching does not imply population change, as surplus productivity may be sufficient to counteract any population level changes (Dias 1996). The results from this chapter are novel, as they compare spatiotemporal

changes in animal abundance directly with true spatiotemporal patterns of bushmeat poaching. Using ranger-collected data, it is now possible to model where bushmeat poaching is most likely to occur in both time and space, and these results suggest that the impacts of bushmeat hunting should not be underestimated in savannah ecosystems.

Chapter 3. Spatiotemporal changes in African elephant abundance from ranger-collected data.

3.1 Introduction

Wide scale poaching, human – wildlife conflict and habitat loss are driving catastrophic declines in iconic African species such as African elephant *Loxodonta africana* and black rhino *Diceros bicornis* (Hoffmann *et al.* 2011, Ripple *et al.* 2015, Craigie *et al.* 2010), with a dramatic rise in poached elephant carcasses in recent years (Beale *et al.* 2018, Wasser *et al.* 2015). African elephants are of great ecological and economical importance, as both ecosystem engineers and drivers of global tourism respectively (Laws 1970, Fritz 2017, Moorhouse *et al.* 2017). Despite declines, African elephants are distributed across a vast range (2.3 – 3.4 million km²) (IUCN 2013), although many populations are severely fragmented (Schübler *et al.* 2017, Lobora *et al.* 2017). Understanding the spatial and temporal trends in abundance of these populations is vital to assign conservation priorities, such as assigning land as protected and allocating law enforcement resources, such as ranger patrols.

In order to understand these trends, continual monitoring of existing elephant populations is vital. Numbers of elephants poached in an area can increase rapidly due to changes in socio-economic status and market prices for ivory (Schlossberg *et al.* 2018). Numbers of elephants detected during aerial surveys of the Ruaha-Rungwa ecosystem in Southern Tanzania fell from 30,500 – 38,800 to 11,100 – 20,600 in just 6 years (Beale 2018). It is important, therefore to carry out long-term monitoring of

elephant populations at regular intervals to be able to detect these declines before populations become critically low, as severely poached elephant populations can take decades to recover (Turkalo *et al*, 2017)

Systematic reconnaissance flights (SRF) are commonly used throughout Africa to monitor populations of large mammals in and around protected areas. Using methods set out by Norton-Griffiths (1978), observers usually follow set transects in small aircraft at a constant height, and animal counts are extrapolated over the entire survey area to give an estimate of density and total population. As the transects are in set locations, the spatial distributions of animals can also be monitored. Large mammal aerial surveys using SRF are seen as the “gold standard” of animal monitoring, due to their repeatable, scientific method. Although the survey methods are robust, the data must be analysed properly, ideally calculating confidence intervals.

Large mammal aerial censuses using SRF have been carried out in Queen Elizabeth National Park in South East Uganda since 1995, and have provided valuable data on the spatiotemporal trends population trends of large mammals such as elephant, Uganda kob and buffalo. These censuses are funded by Uganda Wildlife Authority (UWA), as well as NGOs such as the Wildlife Conservation Society (WCS). Due to the large cost (\$15,000 - \$120,000 USD, pers. comms. A. Plumptre & C. Beale, 2018) and logistical difficulty of organising a full aerial census of the area, surveys are carried out infrequently (every 2-5 years). As can be seen with the Ruaha-Rungwa ecosystem, rapid population declines of African elephant can occur in these short timescales, and may go unnoticed. It would be beneficial, therefore, to be able to continuously monitor populations of African elephants, in order to pre-empt these rapid declines in numbers.

In recent years, community based monitoring (CBM) has risen in popularity (Danielsen *et al.* 2005a). CBM encompasses monitoring carried out on a local scale by local resource users, records from amateur naturalists and data from ranger patrols. Ranger-based monitoring (RBM) has taken place in Queen Elizabeth National Park, Uganda since 1995, with rangers using the smartphone software SMART (spatial monitoring and reporting tool) and its predecessor MIST (management information system). During their patrols, rangers use SMART to record the details, time and location of any illegal activities, as well as any wildlife sightings. It is problematic to use the wildlife sightings data collected using SMART for robust monitoring of animal populations within the park due to strong spatial bias. When planning patrol routes, rangers will generally go where they feel they are most likely to encounter illegal activities, and do not follow random or systematic transects required by professional monitoring methods (Critchlow *et al.* 2015; Dobson *et al.* 2018)

If this spatial bias can be removed from the wildlife sightings data recorded in SMART, then it may be possible to use it as a continuous survey, monitoring the spatial and temporal patterns of animal abundance, hence “filling the gaps” between the more expensive and logistically difficult aerial surveys.

There is a growing interest in utilising ranger-collected data to monitor populations (Danielsen *et al.* 2005b; Gray & Kalpers 2005), yet to date, ranger-collected wildlife sightings data has not been used in this way. In order to test whether ranger-collected data from MIST/SMART can be used to monitor spatial and temporal patterns in populations of African elephants we used a series of Bayesian hierarchical models adapted from Critchlow *et al.* (2015)’s study mapping the true spatiotemporal patterns of illegal activities within QENP. QENP is ideally suited for

this analysis, as rangers have recorded spatial locations of large mammals for 22 years, and due to the long running aerial censuses of the area, the accuracy of these models can be tested.

3.2 Methods

In order to test whether ranger-collected wildlife sightings data can be used to estimate spatial and temporal trends in African elephant populations we used a dataset of 150,771 position records from 11,294 ranger patrols from QENP from 1999 to 2017. During this time, rangers recorded 7,389 sightings of elephant. During patrols, rangers use the SMART smartphone application (Pimm *et al.* 2015) (and previously handheld GPS) to record the location of any wildlife sightings or illegal activities or at 30 minute intervals since the last record. These data were aggregated annually to a 500m grid of presence or pseudo-absence.

3.2.1 Estimating Ranger Effort

When rangers carry out surveillance patrols, they often follow a route where they feel they are most likely to encounter illegal activities, and only encounter wildlife passively. To account for this bias, we estimated patrol effort using methods detailed in Critchlow *et al.* (2015). Patrol effort was estimated between known points based on random bridges (Papworth *et al.* 2012). R packages `adehabitatLT` and `adehabitatHR` (Calenge 2006) were used to estimate probable routes between fixed points as a utilization distribution (UD) of each patrol on a 500m grid. Further information and code are available in Critchlow *et al.* (2015). Individual UD surfaces were summed by year to generate annual estimates of observer effort.

3.2.2 Covariates of elephant distribution

We predicted that the spatial and temporal distribution of elephants in QENP would be influenced by the following covariates; net primary productivity (NPP), distance to the park boundary, distance to water (rivers and lakes) and distance to roads. NPP data for QENP was gathered from MODIS (ORNL 2018) for years 2000-2016. NPP data was at 1 km² resolution. For patrol data prior to 2000, we used NPP data from 2000. Spatial data on the park boundary, rivers, lakes and roads was collected from Esri Online (2018), and for each grid cell we computed the distance from the centre of the cell to the closest park boundary, water or road. We used NPP as it is often used a proxy for the distribution of wildlife (Loarie *et al.* 2009; Duffy & Pettorelli 2012). We included rivers and lakes as areas in close proximity to water are more likely to have high animal densities (Redfern *et al.* 2003; Becker *et al.* 2013), and proximity to roads, as elephants generally avoid areas of human activity (Barnes *et al.* 1991)

3.2.3 Predicting spatial distribution of elephant from ranger-collected data

We used a Bayesian hierarchical modelling approach adapted from Critchlow *et al.* (2015) to analyse the spatial distribution of African elephant in QENP. This model allowed us to account for spatial autocorrelation, define the relationship between covariates and elephant sightings and explicitly account for temporal and spatial variation in the detection of elephant by ranger patrols (Critchlow *et al.* 2015, Beale *et al.* 2014). Statistical analysis was performed in R (R Core Team, 2016), using the R package inlabru (Bakka *et al.* 2018). The output from this model gave estimates of

the total number of elephant sightings per 500m grid cell in the entire time period of the study (1995 - 2017).

In order to validate these results, we used data from a series of large mammal aerial surveys of QENP between 1999 and 2016. As elephant are relatively low in abundance in the park, the data is heavily zero inflated, therefore we chose to build a basic population model using methods outlined in chapter 2. Covariates in this model were, NPP, distance to park boundary and distance to roads, rivers and lakes. Spatial data from both models were then compared using linear regression.

3.2.4 Time series model of elephant distribution from ranger-collected data

In order to test the hypothesis that ranger-collected data can be used to detect declines in elephant populations, we created a time series model of elephant distribution using the same methods as above, but ranger patrol effort was calculated separately for each year. Where possible, NPP data for each specific year was also used. The predicted temporal trends from these models were then compared to the estimated trend in abundance of elephants from the QENP aerial surveys.

3.3 Results

3.3.1 Predicting spatial distribution of African elephant

We used sightings data of elephant collected by rangers in QENP to predict their spatial distribution over an 18 year period, using a Bayesian hierarchical occupancy

model. Although elephants were widely distributed across the area (Fig. 4), they were particularly common in the Northwest Kyambura region of the park, the southwest Ishasha region and along the Kazinga channel, which links Lake Edward and Lake George. Elephants were largely absent from the Maramagambo forest reserve in the southeast and most northern areas of the park.

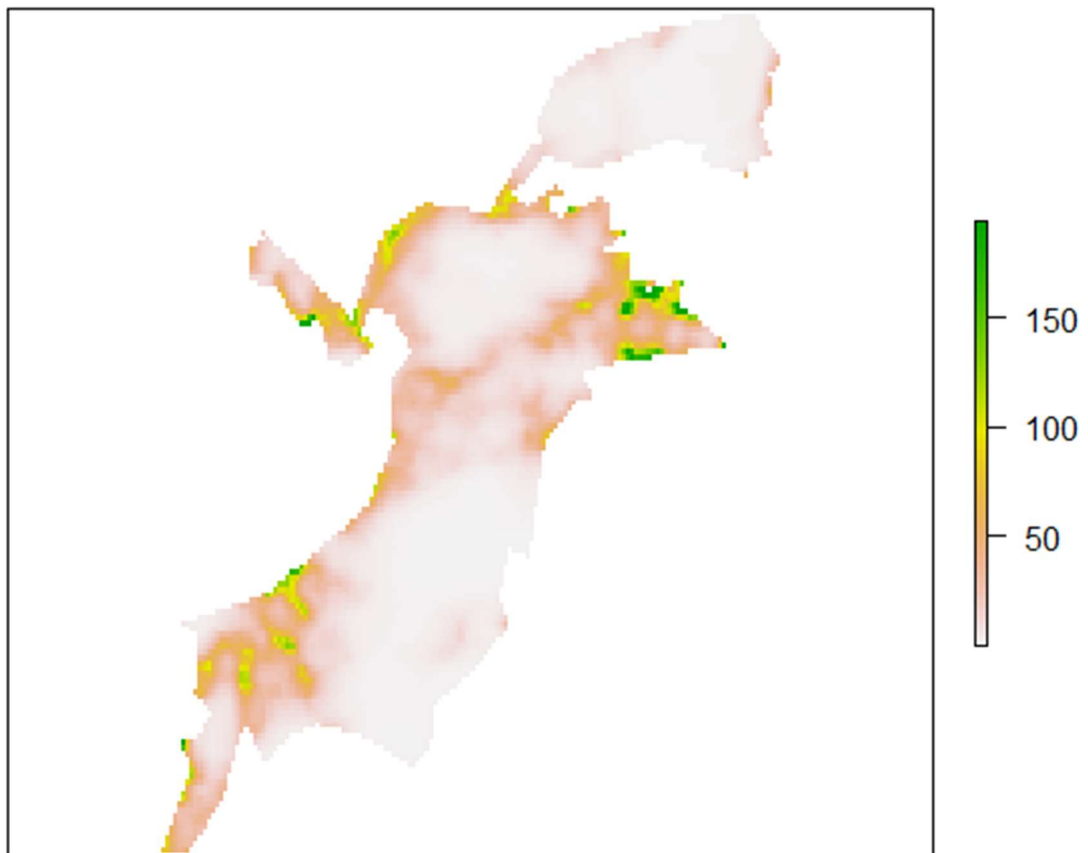


Figure 4. Mean predicted numbers of elephant sightings per year in QENP per 500m grid cell.

Comparison of the model output data with modelled data from large mammal aerial surveys showed a significant positive relationship between total number of sightings over the 18 year period and elephant density per cell over the same period ($R^2 =$

0.02, $p < 0.01$), indicating that after accounting for ranger bias, the model is able to predict the spatial distribution of elephants.

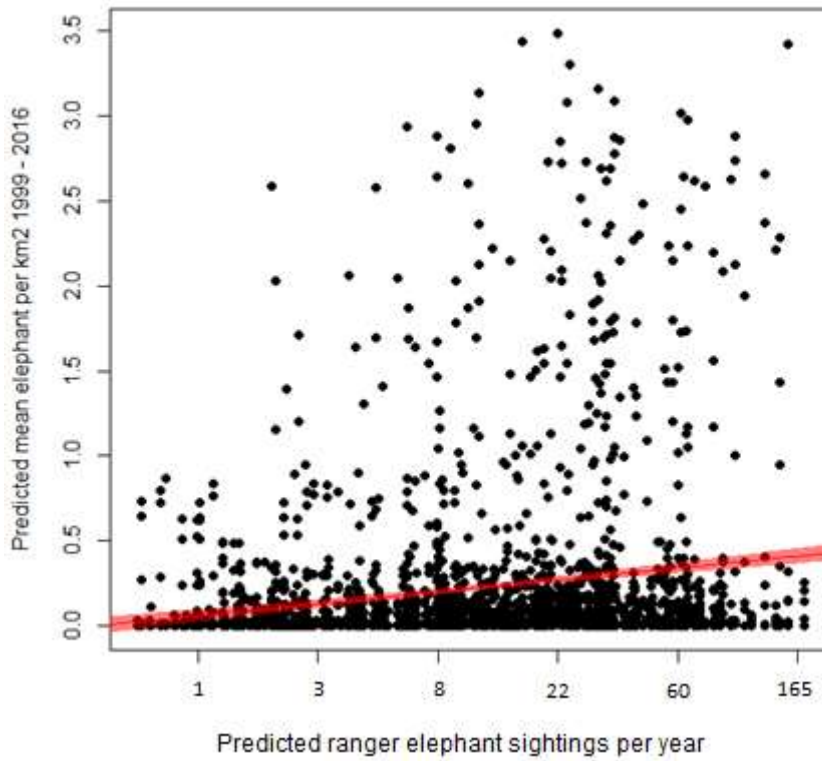


Figure 5. Relationship between predicted ranger elephant sightings per 500m cell per year and predicted elephant per km², 1999 - 2016

3.3.2 Time series model of elephant distribution

We successfully fitted models for 16 out of the 18 years for which we had data. Although there were sufficient elephant sighting and ranger patrol data, models for 2010 and 2014 failed to converge. Spatial distribution of elephant varied greatly among the 16 years (Appendix 2, Fig. 7), although most models predicted highest elephant densities in similar areas to the above spatial model (Fig. 4). Predicted elephant sightings per grid cell per year tended to increase over the 18 year period,

which coincides with a general increase in the elephant population within QENP

(Fig. 6).

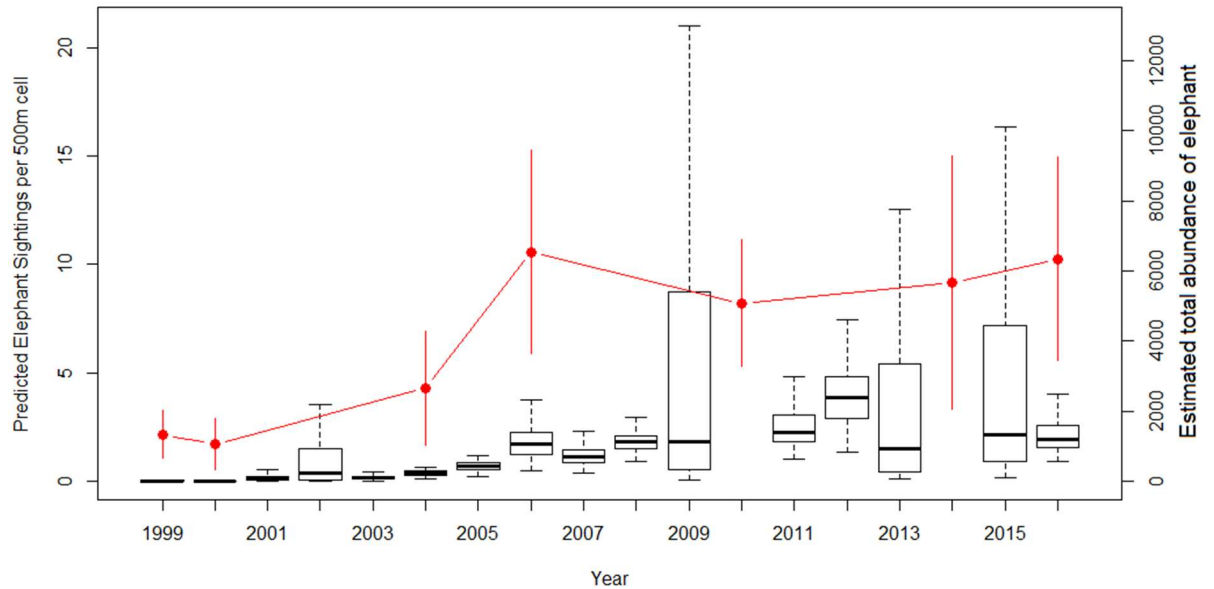


Figure 6. Annual trends in predicted elephant sightings in QENP. Red line indicates estimated total abundance of elephant from large mammal aerial surveys. Error bars indicate 95% confidence intervals.

3.4 Discussion

3.4.1 Predicting spatial distribution of African elephant

We set out to test whether ranger-collected elephant sightings data could be used to predict the spatial distribution and abundance change of African elephant in QENP. We used a Bayesian hierarchical occupancy model to predict the spatial distribution of African elephant in QENP using ranger-collected data from 1999 to 2016. In support of our hypothesis, we found a significant positive relationship between the spatial patterns of elephant encounter rates by ranger patrols and elephant density estimated from aerial surveys. Linear regression provided a very low R^2 value (0.02) for this relationship, suggesting that our model only predicts 2% of the variation in

the ranger collected data. We found that many cells that the basic population model from the aerial survey data had predicted to have very low elephant density were predicted have intermediate or high numbers of sightings by rangers. This could be due to the ranger model predicting elephants in cells where they are unlikely to be, or that modelled aerial survey data is unable to identify the true spatial distribution of elephant inside the park. Schlossberg *et al.* (2016) suggest that aerial survey observers often fail to detect all individuals present in the area, and that this could bias population estimates and confound trend estimation. This, coupled with the fact that all the aerial survey data comes from just seven surveys over 17 years makes it likely that many cells regularly containing elephant are missed. Furthermore, as the QENP aerial surveys are sample counts as opposed to total counts, only 6% of the area is actually surveyed. Over this same period, we have data from over 11,000 ranger patrols, suggesting it is more likely that rangers are able to capture the true spatial distribution of elephant in QENP.

3.4.2 Time series model of elephant distribution

We also set out to test whether ranger-collected elephant sightings data could be used to monitor trends in abundance, and be used to rapidly detect declines in populations. We successfully fitted 16 out of the 18 Bayesian hierarchical occupancy models. Visual inspection of the outputs from these models shows a large amount of spatial variation between years, which suggests that either elephant regularly change their distribution with the park, or that these models have failed to capture their true distribution. Models from 2009, 2011 and 2015 show the majority of the elephant population clustered around the outskirts of the park, which is not seen in either the overall spatial distribution model or the basic population model from the aerial survey data. These artefacts have likely arisen from the generation of the mesh,

which is used when carrying out the patrol effort calculations (Lindgren & Rue 2015; Bakka *et al.* 2018). The peripheral peak in these model outputs is obvious, therefore identifying and excluding such results should be straightforward. It is also worth noting that these methods are at the cutting edge of spatiotemporal modelling, and are in need of refining, perhaps by standardising the mesh across all years. All other models show a roughly similar distribution to the overall distribution model, with sightings more likely along the Kazinga channel and Ishasha region. All models, however, failed to pick up the high density of sightings in the Kyambura region seen in the overall model. A potential reason for this is that ranger patrol effort is calculated separately for each year, which may be adequate for analysing single years, but becomes problematic when comparing between years or calculating temporal trends. Furthermore, the degree to which elephant sightings are recorded varies between individual rangers (pers. obs.) Rangers will always record, sometimes record or never record elephant, but their patrol route will always be recorded.

The mean numbers of sightings per cell appear to follow the same trend as the estimated total abundance of elephant in QENP over the study period (Fig. 6). An increase in both elephant sightings and estimated elephant abundance occurred from 2006. This coincides with a period of civil unrest in eastern Democratic Republic of Congo (Autesserre 2007), which led to a significant migration of elephants from Virunga National Park to the adjoining QENP (Keigwin *et al.* 2018). This indicates that even though the predicted spatial distribution may not be accurate in any one year, these models may have potential in detecting increases and declines in elephant populations at short notice. As these declines are sometimes rapid (Beale *et al.* 2018), it would be greatly beneficial to use these models to monitor elephant

populations *in situ*, and be able to prioritise conservation efforts when and where they are needed.

Considering these factors, at the moment we reject the hypothesis that ranger-collected data can be used to monitor trends in abundance using these models in their current format. Despite the low explanatory power of these models, however, this analysis does demonstrate the potential for using ranger-collected data in this way. If these models can be refined, and if park rangers can be persuaded to always record elephant when they are encountered, then it may be possible to continually monitor populations with little or no additional resources.

Chapter 4. Key Findings and Conclusions

4.1 Key Findings

The preceding chapters closely examined two applications for ranger-collected data from Queen Elizabeth National Park, Uganda. For the first time, I reported population level impacts of illegal bushmeat hunting in a savannah ecosystem. In my introductory chapter, I highlighted that there are relatively few published studies investigating illegal bushmeat hunting in savannah ecosystems compared to forest ecosystems, and of those there are none studying the direct impacts on animal populations. Previous studies have alluded to the scale of bushmeat poaching in savannahs (e.g. Serengeti wildebeest (Rentsch and Packer 2015), yet understanding the extent of poaching offtake does not imply population change, as population surplus may be sufficient to counter losses from poaching (Dias 1996). I also stated that in order to understand these direct impacts, knowledge of the true spatial and temporal patterns of bushmeat poaching in the area are required. I used spatiotemporal data on the occurrence probability of bushmeat poaching in QENP from Critchlow *et al.* (2015). This data was modelled from ranger-collected data from surveillance patrols between 1995 and 2016, and by successfully removing the inherent spatial bias, the authors were able to predict the true spatial and temporal trends in bushmeat poaching. This allowed me to directly compare spatial and temporal changes in herbivore abundance to poaching risk

We modelled population change of three key herbivore species in QENP; buffalo, waterbuck and Uganda kob using spatiotemporal models of poaching probability derived from ranger-collected data as covariates. We found that that Uganda kob, the most common target for bushmeat poachers in QENP, was most affected by illegal

hunting. Furthermore, areas predicted to have high levels of poaching showed the steepest declines in kob abundance. This is a particularly significant result, as kob have both ecological and economic importance in QENP and Uganda. I also highlighted a potential link between drought conditions, an increase in poaching risk and a decrease in Uganda kob abundance. This suggests periods of environmental stress and economic hardship are likely to exacerbate declines in vulnerable species, although herbivore populations within QENP currently seem both resilient and stable. As the human population is growing rapidly in Africa, especially around protected areas, the scale of illegal bushmeat hunting is likely to increase, therefore understanding the direct impacts of illegal bushmeat hunting in protected areas will likely prove important to conservationists and policy makers alike.

In chapter 3 I used ranger-collected data on African elephant sightings in QENP to predict their spatial distribution and change in abundance over a 17 year period. Although technical advances such as smartphones are making it easier for rangers to record events such as illegal activities and wildlife sightings in the field, the analysis of this data remains problematic. As previously mentioned, the analysis of this data assumes either random or uniform effort, and depending on the particular assumptions, this may lead to systematic under- or over-estimates of animal abundance. Here, for the first time, I was able to compare ranger-collected wildlife sightings data with professionally collected survey data by removing the inherent ranger bias. I successfully predicted the spatial distribution of elephant within QENP, which I then compared to spatial data from large mammal aerial surveys across the same time period, resulting in a significant positive relationship. I then attempted to predict the spatiotemporal changes in the QENP elephant population by modelling their distribution for each year between 1999 and 2016. Although the

outputs from these models were inconclusive, the trend in sightings per year was similar to the estimated total number of elephants in the park. Potential issues with the time series model of elephant distribution in QENP could have arisen from variation in recording practices between individual rangers. These preliminary results could be used to inform conservation agencies such as UWA of the potential of ranger-collected wildlife sightings data, and how it might be used to reliably and continuously monitor animal populations within protected areas. Ultimately, it is at the discretion of agencies such as UWA to make wildlife recording mandatory, and to encourage its rangers of the numerous benefits.

While there is no substitute for robust, scientifically collected data, this thesis does offer insight into the potential uses for this kind of unstructured data to the wider conservation community. Huge amounts of data are collected annually on a vast number of species and systems globally through citizen science projects such as iNaturalist and the Global Biodiversity Information Facility (GBIF). While these projects may be expensive to develop and implement, the number of individuals recording species and their locations would not be achievable using paid researchers undertaking fieldwork. Online communities such as iSpot invite users to submit photographs of animals, plants and fungi for identification. If analysed correctly, this data could provide valuable information to those studying trends in populations or changes in distribution.

Citizen science projects have risen in popularity in recent years. In marine systems, citizen science projects such as outlined by Cerrano *et al.* (2017) suggest way in which volunteers have helped monitor the both the spread of an invasive algae and populations of several vulnerable protected species. This ad-hoc data would be have a similar structure to the ranger-collected data in QENP, and the results of this thesis

suggest that if the observer bias and observer error could be accounted for, then similar models could be created to continually monitor trends in abundance and distribution of many species across different systems.

In the introductory chapter, I highlighted the ecological and economic importance of elephants across Africa, and outlined the many threats they currently face. I went on to document how declines in elephant populations can be rapid, and how it is crucial to have monitoring programs in place to detect or even pre-empt these declines.

Professional monitoring programs, such as aerial surveys provide valuable, robust data on elephant populations, but they are costly and logistically difficult, problems which are exacerbated in developing countries. These issues often result in professional monitoring being discontinued or infrequently carried out, meaning local declines can be overlooked. If properly utilised, ranger-collected data could be used to provide continuous monitoring of vulnerable populations without requiring extra resources.

4.2 Conclusions

In summary, this thesis addresses knowledge gaps in both the direct impacts of bushmeat hunting on herbivore populations and the potential applications of ranger-collected data. Chapter 2 highlighted how ranger-collected data could be used to determine the true spatiotemporal patterns of various illegal activities in protected areas, how this in turn could be used to predict the impacts of illegal bushmeat hunting on animal populations. Chapter 3 of this thesis documented how ranger-collected wildlife sighting data could be used to predict the spatial distribution of African elephants, and highlighted the potential for detecting trends in abundance and rapid declines. Many conservation scientists are beginning to view ranger-based

monitoring and ranger-collected data as a valuable resource, due to the relatively low levels of skill and training required, as well as the low financial cost when compared with professional monitoring programs. Currently, the analysis of ranger-collected data remains problematic, due to its non-systematic nature, and building models to predict spatial or temporal changes requires high levels of training. The difficulty in analysing this data means that the possibility of detecting rapid ecological changes and implementing swift interventions may be negated. Although we are not suggesting that implementing these methods will revolutionise conservation management, it may still be an important step to improving the efficiency of both protected area law enforcement and wildlife monitoring. Through technological advances in this emerging field, software could be developed that models trends in abundance of many species using data from applications such as SMART, as well as data collected by volunteers through citizen science projects. If this software is relatively straightforward to use and its outputs easy to understand, it could be used by protected area managers or even the rangers themselves, providing rapid responses to declines in vulnerable species.

Appendices

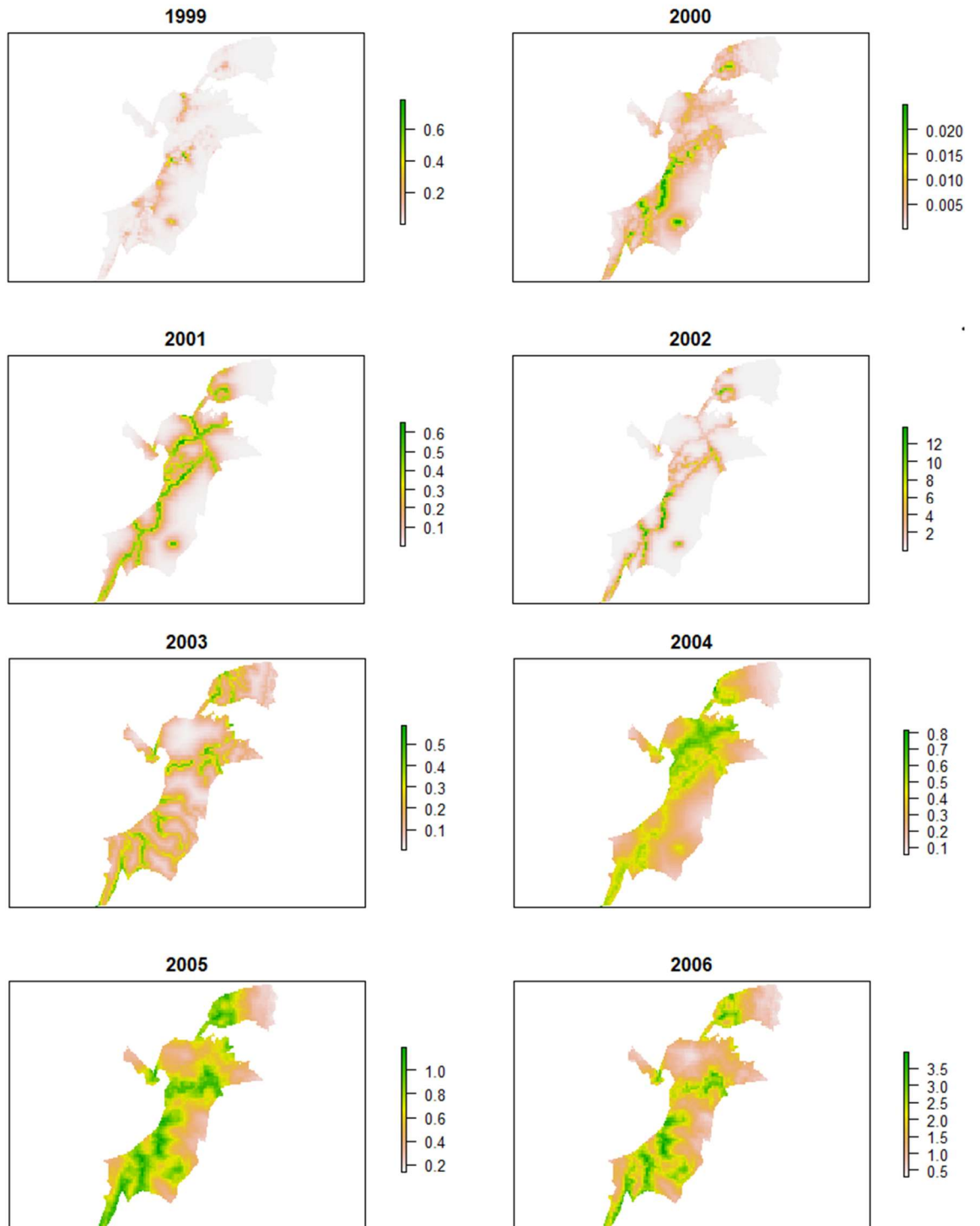
Appendix 1. Model outputs from “year” fixed effect.

Table 3. Model outputs from “year” fixed effect. Bold figures indicate effect size where confidence intervals do not overlap zero, indicating a significant result.

Species	Year	Effect size	Confidence Intervals
Uganda kob <i>Kobus kob thomasi</i>	1999	-0.0008	-0.2274 0.2252
	2000	0.1818	-0.027 0.16
	2004	-0.4122	-0.63 -0.19
	2006	0.0426	-0.18 0.26
	2010	-0.29	-0.52 -0.067
	2014	0.14	-0.071 0.35
	2016	-0.15	-0.35 0.49
	Buffalo <i>Syncerus caffer</i>	1999	0.045
2000		0.097	-0.18 0.19
2004		0.081	-0.11 0.28
2006		0.20	0.0075 0.40
2010		0.005	-0.19 0.20
2014		0.083	-0.11 0.27
2016		0.012	-0.176 0.19
Waterbuck <i>Kobus ellipsiprymnus</i>	1999	0.081	-0.065 0.23
	2000	0.15	0.006 0.29
	2004	-0.05	-0.19 0.094

	2006	0.11	-0.032 0.29
	2010	-0.44	-0.19 0.10
	2014	-0.08	-0.22 0.059
	2016	0.069	-0.068 0.20

Appendix 2. Predicted elephant sightings from time series model.



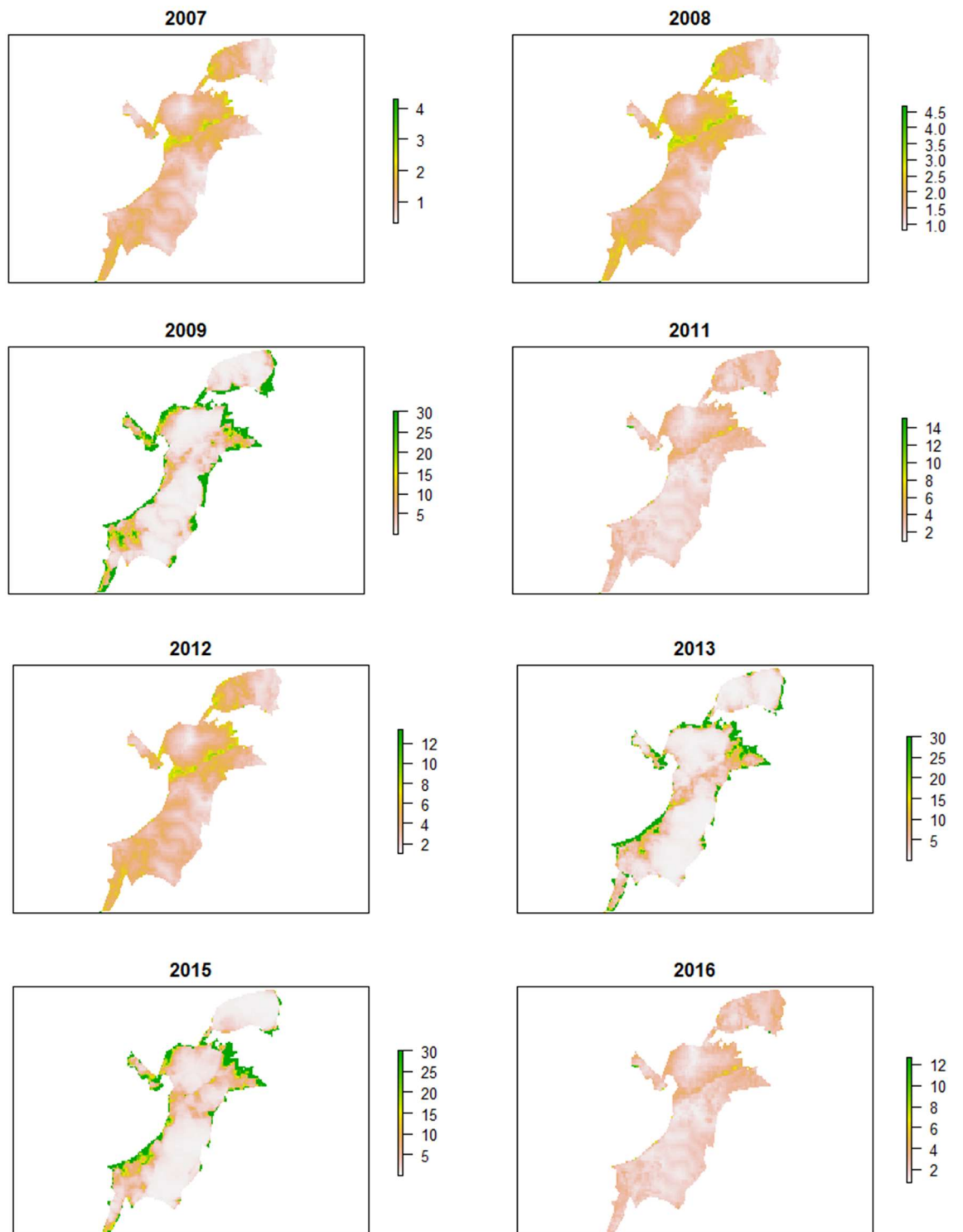


Figure 7. Predicted number of elephant sightings per year per 500m cell in QENP

References

Ahebwa, W.M., van der Duim, R. and Sandbrook, C., 2012. Tourism revenue sharing policy at Bwindi Impenetrable National Park, Uganda: a policy arrangements approach. *Journal of sustainable Tourism*, 20(3), pp.377-394.

Archabald, K. and Naughton-Treves, L., 2001. Tourism revenue-sharing around national parks in Western Uganda: early efforts to identify and reward local communities. *Environmental conservation*, 28(2), pp.135-149.

Autesserre, S., 2007. DR Congo: Explaining Peace Building Failures, 2003-2006. *Review of African Political Economy*, 34(113), pp.423-441.

Bakka, H., Rue, H., Fuglstad, G.A., Riebler, A., Bolin, D., Krainski, E., Simpson, D. and Lindgren, F., 2018. Spatial modelling with R-INLA: A review. arXiv preprint arXiv:1802.06350.

Ballantyne, R., Packer, J. and Hughes, K., 2009. Tourists' support for conservation messages and sustainable management practices in wildlife tourism experiences. *Tourism Management*, 30(5), pp.658-664.

Balmford, A. and Turyaho, M., 1992. Predation risk and lek-breeding in Uganda kob. *Animal behaviour*, 44(1), pp.117-127.

Balmford, A., Crane, P., Dobson, A., Green, R.E. and Mace, G.M., 2005. The 2010 challenge: data availability, information needs and extraterrestrial insights. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360(1454), pp.221-228.

Barnes, R.F., Barnes, K.L., Alers, M.P.T. and Blom, A., 1991. Man determines the distribution of elephants in the rain forests of northeastern Gabon. *African Journal of Ecology*, 29(1), pp.54-63.

Beale, C.M., Brewer, M.J. and Lennon, J.J., 2014. A new statistical framework for the quantification of covariate associations with species distributions. *Methods in Ecology and Evolution*, 5(5), pp.421-432.

Beale, C.M., Hauenstein, S., Mduma, S., Frederick, H., Jones, T., Bracebridge, C., Maliti, H., Kija, H. and Kohi, E.M., 2018. Spatial analysis of aerial survey data reveals correlates of elephant carcasses within a heavily poached ecosystem. *Biological Conservation*, 218, pp.258-267.

Becker M, McRobb R, Watson F, Droge E, Kanyembo B, Murdoch J, Kakumbi C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation* 158:26–36.

Bennett, E.L., 2015. Legal ivory trade in a corrupt world and its impact on African elephant populations. *Conservation Biology*, 29(1), pp.54-60.

- Besag, J., York, J and Mollie, A. 1991. Bayesian image restoration, with two applications in spatial statistics. *Annals of the Institute of Statistical Mathematics* 43:1–20.
- Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., De Semboli, B., Mbenzo, V. and S'hwa, D., 2007. Forest elephant crisis in the Congo Basin. *PLoS biology*, 5(4), p.e111.
- Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R. and Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, 306(5699), pp.1180-1183.
- Brashares, J.S. and Sam, M.K., 2005. How much is enough? Estimating the minimum sampling required for effective monitoring of African reserves. *Biodiversity & Conservation*, 14(11), pp.2709-2722.
- Brodie, J.F., Helmy, O.E., Brockelman, W.Y. and Maron, J.L., 2009. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, 19(4), pp.854-863.
- Burn, R.W., Underwood, F.M. and Blanc, J., 2011. Global trends and factors associated with the illegal killing of elephants: a hierarchical Bayesian analysis of carcass encounter data. *PLoS one*, 6(9), p.e24165.
- Calef, G.W., 1988. Maximum rate of increase in the African elephant. *African Journal of Ecology*, 26(4), pp.323-327.
- Campbell, K. and Borner, M., 1995. Population trends and distribution of Serengeti herbivores: implications for management. *Serengeti II: dynamics, management, and conservation of an ecosystem*, pp.117-145.
- Cerrano, C., Milanese, M. and Ponti, M., 2017. Diving for science-science for diving: volunteer scuba divers support science and conservation in the Mediterranean Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(2), pp.303-323.
- Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K. and Omondi, P., 2016. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, p.e2354.
- Craigie, I.D., Baillie, J.E., Balmford, A., Carbone, C., Collen, B., Green, R.E. and Hutton, J.M., 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), pp.2221-2228.
- Critchlow, R., Plumtre, A.J., Driciru, M., Rwetsiba, A., Stokes, E.J., Tumwesigye, C., Wanyama, F. and Beale, C.M., 2015. Spatiotemporal trends of illegal activities from ranger-collected data in a Ugandan national park. *Conservation biology*, 29(5), pp.1458-1470.

- Critchlow, R., Plumptre, A.J., Alidria, B., Nsubuga, M., Driciru, M., Rwetsiba, A., Wanyama, F. and Beale, C.M., 2017. Improving Law-Enforcement Effectiveness and Efficiency in Protected Areas Using Ranger-collected Monitoring Data. *Conservation Letters*, 10(5), pp.572-580.
- Danielsen, F., Jensen, A.E., Alviola, P.A., Balete, D.S., Mendoza, M., Tagtag, A., Custodio, C. and Enghoff, M., 2005a. Does monitoring matter? A quantitative assessment of management decisions from locally-based monitoring of protected areas. *Biodiversity & Conservation*, 14(11), pp.2633-2652.
- Danielsen, F., Burgess, N.D. and Balmford, A., 2005b. Monitoring matters: examining the potential of locally-based approaches. *Biodiversity & Conservation*, 14(11), pp.2507-2542.
- De Boer, W.F. and Baquete, D.S., 1998. Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique. *Environmental Conservation*, 25(3), pp.208-218.
- Dias, P.C., 1996. Sources and sinks in population biology. *Trends in Ecology & Evolution*, 11(8), pp.326-330.
- Dobson, A.D., Milner-Gulland, E.J., Beale, C.M., Ibbett, H. and Keane, A., 2018. Detecting deterrence from patrol data. *Conservation Biology*.
- Duffy, J.P. and Pettoelli, N., 2012. Exploring the relationship between NDVI and African elephant population density in protected areas. *African Journal of Ecology*, 50(4), pp.455-463.
- Estes, R.D., 1974. Social organization of the African Bovidae. The behaviour of ungulates and its relation to management, IUCN Publications.
- Fa, J.E., Peres, C.A. and Meeuwig, J., 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology*, 16(1), pp.232-237.
- Fa, J.E. and Brown, D., 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review*, 39(4), pp.231-264.
- Freeman, S.N. and Newson, S.E., 2008. On a log-linear approach to detecting ecological interactions in monitored populations. *Ibis*, 150(2), pp.250-258.
- Fritz, H., 2017. Long-term field studies of elephants: understanding the ecology and conservation of a long-lived ecosystem engineer. *Journal of Mammalogy*, 98(3), pp.603-611.
- Fusari, A. and Carpaneto, G.M., 2006. Subsistence hunting and conservation issues in the game reserve of Gile, Mozambique. *Biodiversity & Conservation*, 15(8), pp.2477-2495.

Galanti, V., Preatoni, D., Martinoli, A., Wauters, L.A. and Tosi, G., 2006. Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation. *Mammalian Biology*, 71(2), pp.99-114.

Gibson, L., Hofford, A., Dudgeon, D., Song, Y., Chen, Y., Baker, D.M. and Andersson, A., 2018. Hong Kong's delayed ivory ban endangers African elephants. *Frontiers in Ecology and the Environment*, 16(7), pp.378-380.

Ginsberg, J.R. and Milner-Gulland, E.J., 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology*, 8(1), pp.157-166.

Gobush, K.S., Mutayoba, B.M. and Wasser, S.K., 2008. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conservation Biology*, 22(6), pp.1590-1599.

Guldmond, R. and Van Aarde, R., 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *The Journal of Wildlife Management*, 72(4), pp.892-899.

Gray, M. and Kalpers, J., 2005. Ranger based monitoring in the Virunga–Bwindi region of East-Central Africa: a simple data collection tool for park management. *Biodiversity & Conservation*, 14(11), pp.2723-2741.

Hall, C., Dawson, T.P., Macdiarmid, J.I., Matthews, R.B. and Smith, P., 2017. The impact of population growth and climate change on food security in Africa: looking ahead to 2050. *International Journal of Agricultural Sustainability*, 15(2), pp.124-135.

Harrison, M., Roe, D., Baker, J., Mwedde, G., Travers, H., Plumptre, A., Rwetsiba, A. and Milner-Gulland, E.J., 2015. *Wildlife crime: a review of the evidence on drivers and impacts in Uganda*. IIED, London.

Hegerl, C., Burgess, N.D., Nielsen, M.R., Martin, E., Ciolli, M. and Rovero, F., 2017. Using camera trap data to assess the impact of bushmeat hunting on forest mammals in Tanzania. *Oryx*, 51(1), pp.87-97.

Hoare, R.E. and Du Toit, J.T., 1999. Coexistence between people and elephants in African savannas. *Conservation biology*, 13(3), pp.633-639.

Jachmann, H. and Billiow, M., 1997. Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology*, pp.233-244.

Jachmann H. 2008. Illegal wildlife use and protected area management in Ghana. *Biological Conservation* 141:1906–1918.

Keigwin, M., Wabukawo, V., Wasser, S.K. and Chapman, C.A., 2018. Impacts on transboundary elephant movements between Queen Elizabeth Conservation Area, Uganda and Parc National des Virunga, Democratic Republic of Congo. *Pachyderm*, (57), pp.118-121.

Kenney, J.S., Smith, J.L., Starfield, A.M. and McDougal, C.W., 1995. The long-term effects of tiger poaching on population viability. *Conservation Biology*, 9(5), pp.1127-1133.

Kremen, C., Merenlender, A.M. and Murphy, D.D., 1994. Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation biology*, 8(2), pp.388-397.

Kyando, M., Ikanda, D. and Røskaft, E., 2017. Hotspot elephant-poaching areas in the Eastern Selous Game Reserve, Tanzania. *African Journal of Ecology*, 55(3), pp.365-371.

Laurance WF, *et al.* 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489:290–294.

Laws, R.M., 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos*, pp.1-15.

Lindsey, P. and Bento, C., 2012. Illegal hunting and the bushmeat trade in Central Mozambique. a case-study from Coutada 9, Manica Province. *TRAFFIC East/Southern Africa*, Harare, Zimbabwe.

Lindsey PA, *et al.* 2013. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. *Biological Conservation* 160:80–96.

Leader-Williams, N., Albon, S.D. and Berry, P.S.M., 1990. Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. *Journal of Applied Ecology*, pp.1055-1087.

Lindgren, F. and Rue, H., 2015. Bayesian spatial modelling with R-INLA. *Journal of Statistical Software*, 63(19).

Loarie, S.R., van Aarde, R.J. and Pimm, S.L., 2009. Elephant seasonal vegetation preferences across dry and wet savannas. *Biological conservation*, 142(12), pp.3099-3107.

Lobora, A.L., Nahonyo, C.L., Munishi, L.K., Caro, T., Foley, C., Beale, C.M. and Eggert, L.S., 2017. Incipient signs of genetic differentiation among African elephant populations in fragmenting miombo ecosystems in south-western Tanzania. *bioRxiv*, p.210179.

Loibooki, M., Hofer, H., Campbell, K.L. and East, M.L., 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation*, 29(3), pp.391-398.

- Lwanga, J.S., 2006. The influence of forest variation and possible effects of poaching on duiker abundance at Ngogo, Kibale National Park, Uganda. *African Journal of Ecology*, 44(2), pp.209-218.
- Mackenzie CA, Chapman CA, Sengupta R. 2011. Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. *Environmental Conservation* 39:38–50.
- Marealle, W.N., Fossøy, F., Holmern, T., Stokke, B.G. and Røskoft, E., 2010. Does illegal hunting skew Serengeti wildlife sex ratios?. *Wildlife Biology*, 16(4), pp.419-429.
- Martin, E., 2010. Effective law enforcement in Ghana reduces elephant poaching and illegal ivory trade. *Pachyderm*, 48, pp.24-32.
- Masih, I., Maskey, S., Mussá, F.E.F. and Trambauer, P., 2014. A review of droughts on the African continent: a geospatial and long-term perspective. *Hydrology and Earth System Sciences*, 18(9), pp.3635-3649.
- Metzger KL, Sinclair ARE, Hilborn R, Hopcraft JGC, Mduma SAR. 2010. Evaluating the protection of wildlife in parks: the case of African buffalo in Serengeti. *Biodiversity and Conservation* 19:3431–3444.
- Milner-Gulland, E.J. and Leader-Williams, N., 1992. A model of incentives for the illegal exploitation of black rhinos and elephants: poaching pays in Luangwa Valley, Zambia. *Journal of Applied Ecology*, pp.388-401.
- Milner-Gulland, E.J. and Beddington, J.R., 1993. The exploitation of elephants for the ivory trade: an historical perspective. *Proc. R. Soc. Lond. B*, 252(1333), pp.29-37.
- Moore, J.F., Mulindahabi, F., Masozera, M.K., Nichols, J.D., Hines, J.E., Turikunkiko, E. and Oli, M.K., 2018. Are ranger patrols effective in reducing poaching-related threats within protected areas?. *Journal of Applied Ecology*, 55(1), pp.99-107.
- Moorhouse, T., D'Cruze, N.C. and Macdonald, D.W., 2017. Unethical use of wildlife in tourism: what's the problem, who is responsible, and what can be done?. *Journal of Sustainable Tourism*, 25(4), pp.505-516.
- Moreto, W.D. and Lemieux, A.M., 2015. Poaching in Uganda: perspectives of law enforcement rangers. *Deviant Behavior*, 36(11), pp.853-873.
- Morrison, T.A., Estes, A.B., Mduma, S.A., Maliti, H.T., Frederick, H., Kija, H., Mwita, M., Sinclair, A.R.E. and Kohi, E.M., 2018. Informing aerial total counts with demographic models: population growth of Serengeti elephants not explained purely by demography. *Conservation Letters*, 11(3), p.e12413.
- Mudumba, T., Omoya, E.O., Mustafa Nsubuga, J.Z. and Plumptre, A.J., 2015. Home Ranges of Ishasha Lions: Size and Location in Relation to Habitat and Prey Availability. *Journal of East African Natural History*, 104(1-2), pp.227-246.

Naidoo, R., Weaver, L.C., Diggle, R.W., Matongo, G., Stuart-Hill, G. and Thouless, C., 2016. Complementary benefits of tourism and hunting to communal conservancies in Namibia. *Conservation Biology*, 30(3), pp.628-638.

Navrud, S. and Mungatana, E.D., 1994. Environmental valuation in developing countries: the recreational value of wildlife viewing. *Ecological economics*, 11(2), pp.135-151.

Nasseri, N.A., McBrayer, L.D. and Schulte, B.A., 2011. The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. *African Journal of Ecology*, 49(2), pp.133-140.

Nielsen, M.R., 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: Implications for community based wildlife management. *Biological conservation*, 128(4), pp.509-516.

Norton-Griffiths, M., 1978. Counting animals (No. 1). Serengeti Ecological Monitoring Programme, African Wildlife Leadership Foundation.

Noss, A.J., 1998. The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. *Conservation biology*, 12(2), pp.390-398.

Nuno A, Bunnefeld N, Naiman LC, Milner-Gulland EJ. 2013. A novel approach to assessing the prevalence and drivers of illegal bushmeat hunting in the serengeti. *Conservation Biology* 27:1355–1365.

ORNL DAAC. 2018. MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA. Accessed January 26, 2018

Osipova, L., Moses M., Okello, S.J., Njumbi, S., Western, D., Hayward, M., Balkenhol, N., Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant. *Journal of Applied Ecology* 55, no. 6 (2018): 2673-2684.

Penrose, D. and Call, S.M., 1995. Volunteer monitoring of benthic macroinvertebrates: regulatory biologists' perspectives. *Journal of the North American Benthological Society*, 14(1), pp.203-209.

Pimm, S.L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., Joppa, L., Kays, R. and Loarie, S., 2015. Emerging technologies to conserve biodiversity. *Trends in ecology & evolution*, 30(11), pp.685-696.

R Development Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

- Redfern, J.V., Grant, R., Biggs, H. and Getz, W.M., 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8), pp.2092-2107.
- Rentsch, D. and Packer, C., 2015. The effect of bushmeat consumption on migratory wildlife in the Serengeti ecosystem, Tanzania. *Oryx*, 49(2), pp.287-294.
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I., Levi, T., Lindsey, P.A. and Macdonald, D.W., 2015. Collapse of the world's largest herbivores. *Science Advances*, 1(4), p.e1400103.
- Rogan, M.S., Lindsey, P.A., Tambling, C.J., Golabek, K.A., Chase, M.J., Collins, K. and McNutt, J.W., 2017. Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, pp.233-242.
- Romero, G.Q., Gonçalves-Souza, T., Vieira, C. and Koricheva, J., 2015. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, 90(3), pp.877-890.
- Roques, K.G., O'connor, T.G. and Watkinson, A.R., 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38(2), pp.268-280.
- Rue, H., Martino, S. and Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the royal statistical society: Series b (statistical methodology)*, 71(2), pp.319-392.
- Rutina, L.P., Moe, S.R. and Swenson, J.E., 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildlife Biology*, 11(3), pp.207-213.
- Pringle, R.M., 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, 89(1), pp.26-33.
- Sandbrook, C.G., 2010. Putting leakage in its place: The significance of retained tourism revenue in the local context in rural Uganda. *Journal of International Development: The Journal of the Development Studies Association*, 22(1), pp.124-136.
- Schlossberg, S., Chase, M.J. and Griffin, C.R., 2018. Poaching and human encroachment reverse recovery of African savannah elephants in south-east Angola despite 14 years of peace. *PloS one*, 13(3), p.e0193469.
- Schlossberg, S., Chase, M.J. and Griffin, C.R., 2016. Testing the accuracy of aerial surveys for large mammals: An experiment with african savanna elephants (*Loxodonta africana*). *PloS one*, 11(10), p.e0164904.

Scholte, P., 2014. Population trends of antelopes in Waza National Park (Cameroon) show escalating effects of poaching and livestock intrusion. *African Journal of Ecology*, 52(3), pp.370-374.

Setsaas, T.H., Holmern, T., Mwakalebe, G., Stokke, S. and Røskaft, E., 2007. How does human exploitation affect impala populations in protected and partially protected areas?—A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation*, 136(4), pp.563-570.

Sinclair, A.R.E. and Arcese, P. eds., 1995. *Serengeti II: dynamics, management, and conservation of an ecosystem (Vol. 2)*. University of Chicago Press.

Sitati, N.W., Walpole, M.J. and Leader-Williams, N., 2005. Factors affecting susceptibility of farms to crop raiding by African elephants: using a predictive model to mitigate conflict. *Journal of applied ecology*, 42(6), pp.1175-1182.

Stiles, D., 2004. The ivory trade and elephant conservation. *Environmental Conservation*, 31(4), pp.309-321.

Strauss, M.K.L., Kilewo, M., Rentsch, D. and Packer, C., 2015. Food supply and poaching limit giraffe abundance in the Serengeti. *Population ecology*, 57(3), pp.505-516.

Thouless, C.R., 1995. Long distance movements of elephants in northern Kenya. *African journal of ecology*, 33(4), pp.321-334.

Travers, H., Mwedde, G., Archer, L., Roe, D., Plumtre, A., Baker, J., Rwetsiba, A. and Milner-Gulland, E.J., 2017. Taking action against wildlife crime in Uganda. In IIED Research Report. IIED London, UK.

Turkalo, A.K., Wrege, P.H. and Wittemyer, G., 2017. Slow intrinsic growth rate in forest elephants indicates recovery from poaching will require decades. *Journal of applied ecology*, 54(1), pp.153-159.

UNEP, CITES, IUCN, TRAFFIC. 2013. *Elephants in the dust - the African elephant crisis. A rapid response assessment*. Norway: United Nations Environment Program, GRID-Arendal.

Van Aarde, R.J. and Jackson, T.P., 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological conservation*, 134(3), pp.289-297.

Victurine, R., 2000. Building tourism excellence at the community level: Capacity building for community-based entrepreneurs in Uganda. *Journal of Travel Research*, 38(3), pp.221-229.

Wasser, S.K., Clark, W.J., Drori, O., Kisamo, E.S., Mailand, C., Mutayoba, B. and Stephens, M., 2008. Combating the illegal trade in African elephant ivory with DNA forensics. *Conservation Biology*, 22(4), pp.1065-1071.

Watson F, Becker M, McRobb R, Kanyembo B. 2013. Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. *Biological Conservation* 168:1–9.

Wanyama, F. 2006. Queen Elizabeth National Park Wildlife Census Report. Monitoring and Research Unit. Uganda Wildlife Authority.

Wanyama, F. 2012. Queen Elizabeth National Park Wildlife Census Report. Monitoring and Research Unit. Uganda Wildlife Authority.

Wanyama, F., Balole, E., Elkan, P., Mendiguetti, S., Ayebare, S., Kisame, F., Shamavu, P., Kato, R., Okiring, D., Loware, S., Wathaut, J., Tumonakiese, B., Mashagi, D., Barendse, T. and Plumptre, A.J. 2014. Technical report – Aerial surveys of the Greater Virunga Landscape. Uganda Wildlife Authority.

Wilby, A., Shachak, M. and Boeken, B., 2001. Integration of ecosystem engineering and trophic effects of herbivores. *Oikos*, 92(3), pp.436-444.

Wilfred, P. and MacColl, A.D., 2010. Income sources and their relation to wildlife poaching in Ugalla ecosystem, Western Tanzania. *African Journal of Environmental Science and Technology*, 4(12), pp.886-896.

Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O. and Brashares, J.S., 2008. Accelerated human population growth at protected area edges. *Science*, 321(5885), pp.123-126.

Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P. and Burnham, K.P., 2014. Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences*, 111(36), pp.13117-13121.

Young, T.P. and Isbell, L.A., 1991. Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology*, 87(1-2), pp.79-89

Young JA, vanManen FT, Thatcher CA. 2011. Geographic profiling to assess the risk of rare plant poaching in natural areas. *Environmental Management* 48:577–587.