

The Elephants of Gorongosa: an Integrated Approach to Conservation and Conflict

Mitigation in the Shadow of the War

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### Authorization to Submit Thesis

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## Abstract

The recovery of Gorongosa National Park's elephant population from decimation by war is an unparalleled conservation success story. Yet, a concomitant increase in crop-raiding by elephants along the boundaries of the Park now threatens to undo restoration efforts. Our project is the first to analyze the frequency, severity and distribution of raiding events around Gorongosa, and to experimentally evaluate strategies for reducing crop damage. We combined data on movements of crop-raiding elephants with data on crop availability, patterns of precipitation, NDVI, and the nutritional quality of natural versus cultivated forages to model the drivers of spatiotemporal variation in crop-raiding behavior by elephants. In addition, after one year of tracking the movements of crop-raiding elephants with GPS collars we identified 13 key crossing points used by elephants to exit the Park and access crops. We then experimentally tested three different strategies for deterring elephants from leaving the Park to raid crops at those locations: beehive fences, chili fences, and a combination of both ("spicy beehive fences"). In addition to using GPS collar data to quantify elephant responses to the fences, we trained two teams of local community members to collect quantitative data on crop damage by elephants and to help construct and maintain the experimental fences. We also installed 24 camera traps around the fences to document elephant behavior in proximity to each fence type. Elephants strategically altered their foraging behavior in natural versus cultivated landscapes, ostensibly to increase their intake of high-quality food in both environments. Specifically, elephants actively switched from "surfing the green wave" when foraging inside the Park to selecting mature crops that were browning down outside the Park as they moved between natural and cultivated landscapes. Our mitigation experiment revealed that elephants significantly avoided areas

with beehive fences and chili fences, although all fence types increased the probability that elephants would return to the Park rather than continue on to raid crops after encountering a fence. The magnitude of this effect was greatest for the beehive fences, followed by the spicy beehive fences and fake beehives (beehive control). These results have important implications for reducing human-elephant conflict in Africa, and for helping to facilitate both the conservation of this iconic keystone species and the livelihoods of the many farmers who live in close proximity to them.

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## **Dedication**

I dedicate this work to my family who have always supported my decisions, and have always given me courage and inspiration to pursue my dreams. With all my heart to my mother Isabel, my father Fernando, my sister Giovana and to my future husband Sakkie.

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## **Chapter 1: Brown is the new green: strategic adjustment of foraging behavior by elephants in natural versus cultivated landscapes**

### *Abstract*

Over the past century natural habitats have been converted into cultivated croplands at an unprecedented rate, and crop raiding by wildlife now poses a significant threat to both wildlife conservation and human livelihoods in many parts of the world. Understanding the mechanisms that underpin movement of wildlife into agricultural landscapes is critical for developing effective mitigation strategies. The forage maturation hypothesis predicts that herbivores should match their movements with intermediate forage biomass (i.e., peak green-up), a phenomenon termed “surfing the green wave.” Crop-raiding elephants, however, often are consuming fruits and tubers, which generally mature after the peak in photosynthetic activity. Thus, although elephants have been shown to surf the green wave when foraging in natural habitats, they may adjust this strategy in cultivated landscapes by actively selecting crops that are “browning down.” This hypothesis, however, has never been tested. We combined data on movements of crop-raiding elephants with data on crop availability, patterns of precipitation, NDVI, and the nutritional quality of natural versus cultivated forages to better understand the drivers of spatiotemporal variation in crop-raiding behavior by elephants. Crop raiding increased when NDVI within the Park was low and availability of mature crops along the boundary of the Park was high. In addition, elephants actively switched between surfing the green wave and selecting forage plants that were browning down as they moved between natural and cultivated landscapes. This strategy likely increased energy intake from foraging because cultivated crops contained

significantly higher levels of digestible energy than their natural counterparts. Our study is the first to combine fine-scale GPS tracking data with detailed community based reporting of crop raiding events to quantify plasticity in the foraging behavior of elephants living in close proximity to a human-dominated landscape. Our results demonstrate that elephants adjust their behavior at fine scales to reduce the costs and increase the benefits of crop-raiding. Understanding these behavioral adjustments and the mechanisms that underpin them will aid in designing strategies for mitigating human-elephant conflict as the human population continues to grow.

## **Introduction**

Over the past century native habitats have been converted into cultivated croplands at an unprecedented rate to provide food for an exponentially growing human population (Osborn & Hill, 2005, Woodroffe, Thirgood, & Rabinowitz, 2005, Ogutu, Piepho, Dublin, Bhola, & Reid, 2009). As a result, crop raiding (i.e., when crops cultivated for the purpose of human consumption are accessed and consumed by animals) by wildlife now poses a significant threat to wildlife management and conservation, and to human livelihoods, in many parts of the world (Campbell-Smith, Simanjanrang, Leader-Williams, & Linkie, 2010). Conover (2002) estimated that economic losses from crop damage by wildlife exceed \$4.5 billion annually in the United States alone, and millions more dollars are spent by farmers and wildlife management agencies each year to prevent or mitigate those losses (Wagner, Schmidt, & Conover, 1997, Emerton, 2001). Wildlife often are strongly attracted to agricultural lands because cultivated crops typically are more palatable and have higher nutritive value (Sukumar, 1990), lower levels of toxins or secondary metabolites (Osborn &

Hill, 2005), and lower fiber content (Hoare, 1999a) than their wild counterparts. Indeed, the presence of agricultural lands can significantly alter the foraging behavior of herbivores (Navedo et al., 2013). For example, Canada geese (*Branta canadensis*) have shifted their migration patterns over the past 50 to 100 years to increase access to farmlands that provide high-quality forage (Fox & Abraham, 2017).

Understanding the mechanisms that underpin movement of wildlife into agricultural landscapes is critical for developing effective mitigation strategies. For most large herbivores forage quality plays a strong role in determining the frequency or intensity of crop-raiding behavior (Osborn, 2004, Chiyo, Cochrane, Naughton, & Basuta, 2005). For example, in the Greater Yellowstone Ecosystem, USA, abundance of high-quality forage is 200% greater in irrigated agricultural fields than in the surrounding grasslands, which has strong effects on movements of migratory elk (*Cervus canadensis*; Garrouette, Hansen, & Lawrence, 2016). Such behaviors ostensibly are rooted in the fact that herbivores prefer to forage on plants at intermediate biomass or early phenological growth stages that are more digestible and help to maximize energy intake (Bischof et al., 2012). Indeed, the forage maturation hypothesis (FMH) posits that herbivore movements at multiple scales are driven by the desire to access high-quality forage (Fryxell, 1991, Hebblewhite, Merrill, & McDermid, 2008).

Recent efforts to test predictions of the FMH have begun to shed light on herbivores' ability to track plant phenology in time and space and match their movements with intermediate forage biomass (Merkle et al., 2016, Aikens et al., 2017) – this phenomenon has been termed “surfing the green wave” (van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006, Bischof et al., 2012). A diversity of herbivores, from ungulates (Rivrud,



Heurich, Krupczynski, Müller, & Mysterud, 2016) to giant pandas (*Ailuropoda melanoleuca*; Wang et al., 2010) and birds (van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006), have been shown to utilize this strategy. In contrast, herbivores such as African elephants (*Loxodonta africana*), African buffalos (*Syncerus caffer*) and hippopotamuses (*Hippopotamus amphibious*; Kendall, 2011, Datiko & Bekele, 2013) often prefer to consume fruits and tubers when foraging in cultivated landscapes (similar to the humans that did the cultivating), and thus the FMH may be less useful for predicting spatiotemporal variation in crop-raiding behavior by those species. Fruit ripening generally occurs after the peak in photosynthetic activity (i.e., the peak in green-up) when the plant has begun to senesce and minerals and nutrients have been mobilized and translocated to the maturing fruit (or other storage organ) from vegetative parts that will soon die off (Noodén, 1988a). Thus, crop-raiding herbivores that consume mostly fruits would likely benefit more from tracking later phenological stages of plant growth than from surfing the green wave. This proposition contrasts with findings for bison (*Bison bison*; Sigaud et al., 2017) and elk (Middleton et al., 2017) that select greener areas when foraging on herbaceous plant parts (e.g., leaves and stems) in both natural habitats and agricultural lands.

Elephants (*Loxodonta africana*) are the largest extant land mammal on earth. African elephants spend 75% of the day foraging (Wyatt & Eltringham, 1974), and can consume up to 1.8% of their body weight in dry matter daily (Dierenfeld, 1994). In natural environments elephants act as a keystone species by toppling and smashing trees and shrubs that are otherwise inaccessible to smaller species for forage and refuge (Coppolillo, Gomez, Maisels, & Wallace, 2004, Pringle, 2008, Ripple et al., 2015, Coverdale et al., 2016). In agricultural landscapes, however, elephants can consume or destroy vast amounts of cultivated crops in a

single raiding event (Naughton-treves, 1998). For example, in Ghana villagers reported that a herd of six elephants could destroy half of a 3-acre farm in one raiding event (Sam, Ayesu, Agbenu, Kumordzi, & Wilson, 2003). As a consequence, many elephants are killed or injured by people every year while crop-raiding (Moss, 2001, Chiyo, Moss, Archie, Hollister-Smith, & Alberts, 2011), and human fatalities sometimes occur as well (indeed, two farmers were killed by crop-raiding elephants at our study site while our research was in progress).

Elephants are generalist foragers with diverse diets that include grasses, forbs, fruits, bark, leaves, twigs and roots (Sukumar, 2003). When foraging in agricultural landscapes, however, elephants have been shown to select mature crops over intermediate or early growth stages (Hoare, 1999a). Accordingly, crop damage by elephants tends to peak near the beginning of the dry season, when the maturation of crops coincides with declines in the quality of natural forages (Bhima, 1998, Lahm, 1996). Thus, although elephants do “surf the green wave” similar to other herbivores when foraging in natural habitats (Wall, Wittemyer, Klinkenberg, LeMay, & Douglas-Hamilton, 2013, Bohrer, Beck, & Douglas-Hamilton, 2014), they may adjust this strategy in cultivated landscapes by actively selecting crops that are “browning down.” This hypothesis, however, has never been tested.

Understanding the mechanisms that determine when and where crop raiding by elephants is most likely to occur can make mitigation efforts more effective by enabling wildlife managers to prioritize focused actions with limited resources (Sitati, Walpole, Smith, & Leader-Williams, 2003). In the increasingly human-dominated landscapes of sub-Saharan Africa such efforts will be critical for simultaneously conserving elephant populations and ensuring the welfare of the thousands of local communities that depend on

subsistence farming for their livelihoods. We studied patterns of crop-raiding by elephants in and around Gorongosa National Park, Mozambique, where the elephant population is currently recovering from decimation by a civil war that ended in 1992. The Park is surrounded by subsistence farming communities, particularly along its southern border, where the Pungue River provides an important water resource for both animals and people. The goal of our project was to identify the mechanisms that drive spatiotemporal variation in the frequency and intensity of crop raiding by elephants. We hypothesized that because elephants are generalist foragers capable of moving long distances and adjusting their behavior to variation in the foraging landscape at multiple scales, the spatiotemporal distribution of crop-raiding by elephants would be strongly related to seasonal changes in the relative abundance and distribution of high-quality forages inside versus outside of the park. Specifically we predicted (P1) that crop raiding would occur more frequently when declines in the quality of natural forage (driven by seasonal patterns of precipitation) coincided with the maturation of crops outside the Park. We also predicted (P2) that elephants would surf the green wave while foraging inside the Park, but would select mature crops that were browning down while crop raiding. Finally, we predicted (P3) that digestible energy and protein content would be significantly higher in cultivated crop plants than in natural forage species consumed by elephants within the Park.

## **Material and Methods**

### *Study Area*

We conducted our study in Gorongosa National Park (GNP), Mozambique (Fig. 1.1). Annual precipitation at GNP averages roughly 850 mm and occurs mostly during the

November – March rainy season (Tinley, 1977). Temperatures at Gorongosa range from an average minimum of 15° C during the dry season to an average maximum of 32° C during the wet season. The Park is surrounded by a 5,333-km<sup>2</sup> “buffer zone” where approximately 200,000 subsistence farmers currently reside. A large proportion of these farmers cultivate crops along the southern boundary of the Park, which is formed by the Pungue River. Prior to the civil war, which began in 1976, GNP was home to roughly 2,500 elephants. During the war, however, most of those elephants were killed to feed soldiers and to fund the purchase of arms and ammunition through the sale of ivory (Vines, 1991); by the year 2000, the elephant population numbered <200 individuals (Stalmans, 2012). Elephants are currently recovering at GNP under the auspices of the Gorongosa Restoration Project, and the most recent aerial census counted roughly 600 individuals. Following the war, however, much of the buffer zone was converted to agricultural lands (Fig. 1.2). As the elephant population has increased, so has the occurrence of human-elephant conflicts.

#### *Animal capture and location data*

To quantify spatiotemporal patterns of crop-raiding by elephants at GNP, we fit 12 male elephants with high potential for crop-raiding behavior (i.e., individuals that were captured in or in close proximity to crops) with Global Positioning System (GPS) collars (Model AWT IM-SAT, Africa Wildlife Tracking, Pretoria, South Africa). We collared six elephants in December, 2015, and six in August, 2016. We programmed GPS collars to collect and transmit a location every 30 min through the iridium satellite system for a period of two years. Each elephant was chemically immobilized via remote injection from a helicopter with a combination of thiafentanil oxalate (9 to 15 mg) and azaperone (40 to

60mg), with the dosage depending on the approximate age and size of each individual. Elephants were carefully monitored during handling and the following parameters were measured: cardiac rate (normal: 25-30 bpm), respiratory rate (normal: 4-6 breaths/minute), rectal temperature (normal: 36° to 37° C), blood oxygenation (via a portable pulse-oximeter), and invasive and non-invasive blood pressure (Cardell® Multiparametric Monitor). Thiafentanil was antagonized with Naltrexone at the end of each procedure. Elephants were recaptured and collars were removed when they reached low battery status, and by January, 2018 only two elephants still retained collars. All animal handling procedures were approved by the Animal Care and Use Committee at the University of Idaho (protocol #2015-39), and were in accordance with guidelines established by the American Society of Mammalogists (Sikes et al., 2016).

#### *Enumerator data*

To collect detailed data on crop availability and phenology, as well as on crop damage by elephants, we implemented a community-based reporting system. Based on the framework proposed by Hoare (1999b) for the IUCN African Elephant Specialist Group, we selected and trained a team of ten local community members (enumerators) to complete detailed daily reports on crop-raiding events during our study. Each enumerator was trained by qualified project personnel (i.e., researchers and staff from the conservation and agricultural departments of GNP) to collect standardized data on crop raiding events, including the location of the event, the type of crop damaged or consumed and the stage of maturation (germinating, flowering, mature). Enumerators worked in six different communities spread across 60 km of the Pungue River from August 2016 to January 2018.

We provided enumerators with bicycles to facilitate access to their assigned areas and search for evidence of crop-raiding by elephants during each morning of the study. Although enumerator data were collected primarily to test the effectiveness of mitigation trials conducted as part of a concurrent manipulative experiment, we used those data (roughly 1,600 total reports) in the present study as an index of the relative availability of crop species and stages of maturation through time. We calculated the relative availability of each crop by counting the number of times it was mentioned by the enumerators each day, and recorded the date at which each crop species was reported as being mature in each community. We qualitatively validated our index using data on planting periods and time to maturity for each crop species obtained from the agricultural technicians at GNP. The enumerator reports included >10 different types of crops, which we combined into four main groups for our analyses: maize, fruits, tubers and beans.

#### *NDVI and precipitation data*

To track green-up in our study area across space and time, we calculated values of the Normalized Difference Vegetation Index (NDVI) from the surface reflectance bands of the MODIS terra satellite (product MOD09Q1; version 006; resolution 250 m, every 8 days) from 2015 through 2017 across the study area. NDVI quantifies the “greenness” of each pixel in a landscape, and has been widely used as a proxy for vegetation phenology and net primary production (Pettoireli et al., 2011) because of its correlation with plant biomass (Dancose, Fortin & Guo, 2011). We set to ‘no data’ pixels that were classified as cloud, cloud shadow, or snow (14.5% of pixels). We smoothed each time series (i.e., each pixel) of NDVI data using a median filter with a window size of three (Merkle et al., 2016). We then

filled in ‘no data’ pixels by linearly interpolating between known NDVI values in each time series.

We collected daily precipitation data from a rain gauge located in one of the communities in the buffer zone. We then summed precipitation values every 8 days throughout the study to match the temporal resolution of our NDVI data.

### *Statistical analysis*

We used a parametric time-to-event modeling framework (Hosmer, Lemeshow, & May, 2008) to quantify the effects of environmental and agricultural variables (crop availability, NDVI inside and outside the Park, and precipitation) on the probability of an elephant crossing the southern boundary of GNP and remaining outside the Park for at least 30 minutes (i.e., a raid event). We chose 30 minutes as our threshold because the closest communities are located right on the edge of the Park; thus, as soon as an elephant crosses the Park boundary, it is immediately entering croplands. To convert elephant location data into a time-to-recurrent-event framework, we collapsed GPS locations into a daily response variable that identified whether one or more elephant GPS locations were outside the Park’s border (crop-raiding excursion). We included location data collected between 14 December, 2015 (the first day an elephant was collared) and 22 January, 2018 when the study concluded. The parametric proportional hazards model summarizes the times to an event (in this case, an elephant excursion outside the Park) as a baseline hazard (parameterized by some functional form) multiplied by the effects of a set of variables. Hazard ratios constitute the relative effect of each covariate on the event variable (Hosmer, Lemeshow, & May, 2008).

For every 8-day window during the study we calculated, for each elephant, mean NDVI of the portion of their home range that occurred inside and outside of the Park. For purposes of this analysis, “home ranges” were defined as the NDVI pixels that an elephant used at least one time during the period in which it was monitored. Prior to calculating mean values, we scaled each time series of NDVI data between 0 and 1, based on the 0.025 and 0.975 quantiles of the time series (Bischof et al., 2012). This ensured that NDVI values inside and outside the Park were directly comparable, and represented NDVI phenology rather than absolute NDVI. For each event in the time-to-event analysis, we extracted the NDVI value that was closest in time to that event.

After checking for correlation among variables, we excluded the crop type beans because it was highly correlated with maize ( $r = 0.94$ ), and maize is more prevalent than beans in the study area. Using the statistical program R (v.3.4.1), we performed an automated model selection with all possible subsets (52 total models) of the “global” survival model (Burnham & Anderson, 2002) that included NDVI inside and outside the Park, the ratio of NDVI inside versus outside the Park, distance to the Park boundary, precipitation and crop availability (fruits, maize and tuber). All variables were scaled to facilitate direct comparison of effect sizes (i.e., model coefficients; Schielzeth, 2010).

We used step selection functions (Fortin et al., 2005) to test the prediction that elephants would surf the green wave while foraging inside the Park, but would select mature crops that were browning down while crop raiding (P2). For each 30-min step we drew 10 potential target points originating from the known source point by sampling from the individual step and turning angle distributions simultaneously. These 10 points were classified as available and were compared to the used target step using conditional logistic



regression (Fortin et al., 2005). For the analysis of movement outside the Park, we removed random steps that ended up inside the Park, and then subsequently removed all strata (i.e., paired combinations of used and available steps) that included <5 random steps. We fit two models, one evaluating the influence of distance to the Park boundary, NDVI, and rate of change in NDVI on movement decisions by elephants outside the Park, and one evaluating the influence of those covariates on movement decisions inside the Park.

To test whether elephants more strongly select forages that are greening up or browning down, we calculated the rate of change in NDVI from the nearest 8-day NDVI value. Rate of change in NDVI was calculated by taking the first derivative of each time series of NDVI, and then scaling each time series of the rate of change in NDVI between 0 and 1 (Bischof et al., 2012). Positive values of the rate of change in NDVI denote periods when green-up was occurring (i.e., prior to peak NDVI), and negative values of the rate of change in NDVI denote brown down (i.e., after peak NDVI). Values of the rate of change in NDVI near zero denote periods when NDVI was either at a peak or in a valley (e.g., during the dry season). To take into account the overall productivity of an area we also extracted, for each used and available step, the absolute value of NDVI.

#### *Diet composition and forage quality*

To test the prediction that digestible energy and protein content would be significantly higher in cultivated crop plants than in natural forage species consumed by elephants within the Park (P3) we first quantified diet composition of elephants within the Park using DNA metabarcoding analysis of fecal samples. We collected 21 fresh dung samples from elephants inside GNP during the dry season (June through August) of 2016.

We collected samples after observing elephants defecating and then waiting for them to leave the area. For each sample we recorded GPS coordinates and the surrounding habitat type. Sample collection and processing followed protocols described by Kartzinel et al. (2015). Samples were collected in unused plastic bags, immediately placed on ice in a cooler, and processed the same day as follows: we homogenized samples within the collection bag and transferred pea-sized portions into tubes containing silica beads and buffer (Zymo Xpedition™ Stabilization/Lysis Solution, Zymo Research, California USA), which were then frozen (-20°C) until they could be transported to the United States and stored at -80 °C. All samples were subjected to a standard antiviral heat treatment (30 min at 72°C) before importation into the United States.

Fecal samples reflected diet over the previous 24–72 h (Steuer et al., 2011). DNA was extracted from each sample individually using the Zymo Xpedition™ Soil/Fecal DNA MiniPrep kit, per manufacturer instructions. We included one extraction control per extraction series of 25 samples. Standard PCR methods were used to amplify the P6-loop of the *trnL* intron (Taberlet et al., 2007), a widely used marker for DNA metabarcoding of vascular plants (Taberlet et al., 2012, Yoccoz et al., 2012, Kartzinel et al., 2015, Pansu et al., 2015a). We conducted three PCR replicates along with extraction and PCR controls. PCR products were purified using MinElute™ purification kits (Qiagen, Maryland USA). Sequencing libraries were prepared using a PCR-free approach and sequenced on an Illumina HiSeq 2500 (2×150 bp paired-end reads).

Sequence data were curated using OBITOOLS (Boyer et al., 2016) to (i) assemble paired end reads, (ii) assign sequences to their original samples, (iii) remove low-quality sequences and those putatively resulting from amplification/PCR errors, (iv) discard

singletons (represented only once in the dataset), and (v) assign all remaining sequences to plant taxa. To facilitate taxonomic identification of plant sequences, we built a local DNA reference database from 506 plant specimens, representing 243 species (211 genera, 63 families) and including the most abundant and widespread taxa in the study area. Taxonomic assignments were made by comparison to this local database as well as to a reference set from the European Molecular Biology Laboratory database (Ficetola et al., 2010). Plant sequences from samples with low similarity (<80% identity) to the closest reference sequence were considered putative contaminants and were discarded (Pansu et al., 2015b), as were outlying PCR replicates. Remaining sequences were designated as molecular Operational Taxonomic Units (mOTUs). For each sample, we averaged the number of reads across all retained PCR replicates and removed sequences representing <1% of averaged reads.

The Gorongosa reference database was prioritized for assignment of mOTUs, unless the score was higher with the global reference database. We extracted sequences from the local reference database that corresponded to species for which we had associated data on nutritional quality. We checked if these species shared their barcode with some of their relatives and then picked up those that matched perfectly (100% match) with the elephant diet. For species that were not present in the local database (LDB), we used their barcode from the global database (GDB).

To estimate the nutritional quality of elephant diets at GNP when feeding on natural forages, we sampled 28 plant species known to be consumed by elephants during the dry season and analyzed them for % neutral detergent fiber (NDF), % acid detergent fiber (ADF), % lignin (ADL), % ash (AIA), % crude protein (CP) and gross energy (GE; Dairy

One Forage Lab, Ithaca, New York). We then estimated digestible energy (DE) and digestible protein (DP) content of each plant species using the summative equations of Robbins et al. (1987 a,b). Similarly, we sampled all of the major crop species consumed by elephants in the buffer zone and estimated DE and DP content using the approach described above. Separate nutritional assays were conducted for different plant parts (e.g. fruit, leaves, roots, stem), and the majority of the fruits sampled were unripe, likely making our results conservative.

We combined data on diet composition with data on nutritional quality of forage plants to estimate DE and DP content of sampled (via fecal collection) elephant diets. We included a sample in this analysis only if  $\geq 70\%$  of the diet was comprised of plant species for which we had data on DE and DP ( $n = 6$ ). We calculated weighted averages of DE and DP for each sampled diet by using the proportional contribution of each plant species to the diet (determined from the metabarcoding analysis) as the weighting factor. We then estimated DE and DP of natural forage diets during the dry season as the weighted average of DE and DP estimates across individual diet samples using the proportion of the diet accounted for (based on metabarcoding analysis) in each sample as the weighting factor. Finally, to test P3 we compared mean DE and DP of the main crop species eaten by elephants in the buffer zone to mean DE and DP ( $\pm 95\%$  CI) of natural forage diets.

## **Results**

We obtained an average of 44,827 locations ( $\pm 7,679$  SD) for each of 12 male elephants that were monitored for an average of 17.4 months between 1 January, 2016 and 22 January, 2018. From those data we identified a total of 2,225 crop-raiding excursions

(crossing the Park's boundary and staying for at least 30 minutes). On average, collared elephants crossed the Park boundary to raid crops on 34% ( $\pm 12\%$  SD) of the days in which they were monitored. A 100% minimum convex polygon estimated from our location data encompassed 2,004 km<sup>2</sup>, with 72% of that area occurring inside the borders of GNP and 28% occurring in the buffer zone.

We observed marked seasonal and diel variation in patterns of crop raiding by elephants at GNP. Crop-raiding excursions increased steadily between June and September, peaked in September and October, and declined again toward baseline wet-season levels in December (Fig. 1.3). During crop-raiding excursions elephants consistently left the Park under cover of darkness between 19:00 and 21:00 hrs and returned to the Park before 05:00 hrs (Fig. 1.4). Mean duration of a raid was 8.3 hours, although a few longer excursions (up to 200 hours outside the Park) were observed. NDVI within elephants' home ranges generally peaked in late March, but on average peak NDVI occurred approximately 2 weeks later outside the Park (i.e., in the crops) than inside the Park (Fig. 1.5).

The top model for predicting the timing of crop-raiding excursions by elephants garnered 99% of the AIC weight and indicated that lower availability of fruits, maize and tubers increased the probability of elephants remaining within the Park. Higher NDVI and precipitation inside the Park also increased the probability of elephants remaining within Park boundaries (Table 1.1; Fig. 1.6). Availability of fruits outside the Park and NDVI inside the Park were the most important predictors in the model (indicated by standardized coefficients that were an order of magnitude greater than for other variables), highlighting the fundamental role of forage availability as a driver of crop raiding by elephants.

Our analyses of step selection by elephants indicated that, when outside the Park, elephants selected areas that were closer to the Park boundary. Elephants generally selected areas that had higher NDVI values whether they were foraging in natural habitats or cultivated crops (Table 1.2; Fig. 1.7). In contrast, the influence of the rate of change in NDVI on step selection was not significant when elephants were foraging in natural habitats, whereas when elephants were foraging in croplands they strongly selected areas with a negative rate of change in NDVI (Table 1.2; Fig. 1.7). This suggests that elephants switched from selecting forages that were at or near peak green-up in natural landscapes (i.e., surfing the green wave) to selecting forages that were browning down in agricultural landscapes. Additionally, step selection by elephants tended to bring them closer to the Park boundary (i.e., the coefficient for distance to the Park was negative; Table 1.2). This effect was highly significant when elephants were outside the Park and marginally significant when elephants were inside the Park. However, when individuals did venture farther from the Park boundary, their strength of selection for locations closer to the Park boundary diminished (i.e., the coefficient for the interaction term was positive; Table 1.2).

Mean DE and DP content of natural forage diets were 11.39 kJ/g and 11.5%, respectively (Fig. 1.8). Of 17 crop plants (and associated plant parts) analyzed for DE, 82% had values that exceeded the upper bound of the 95% CI for natural forage diets (Fig. 1.8). In contrast, only 15% of crop samples had values of DP that exceeded the upper bound of the 95% CI for natural forage diets (Fig. 1.8).

## Discussion

Similar to previous studies of crop-raiding behavior by elephants (e.g., Thouless, 1994, Naughton-Treves, 1998, Sitati, Walpole, Smith, & Leader-Williams, 2003), crop-raiding by the 12 collared elephants monitored during our study was mostly a nocturnal activity, likely to reduce risks of mortality or disturbance associated with humans (Cerling et al., 2006, Graham, Douglas-Hamilton, Adams, & Lee, 2009). Although GNP elephants raided crops year-round, the number of incidents dramatically increased during the dry season (between June and November). Indeed, collared elephants spent nearly 30% of their time in croplands between September and November. This peak in crop-raiding coincided with the maturation of maize and fruits outside the Park, as well as the decline in quality of natural forages inside the Park due to the lack of rain.

The presence of mature fruits outside the Park significantly increased the probability of crop-raiding (Ngama, Korte, Bindelle, Vermeulen, & Poulsen, 2016), whereas higher NDVI values (associated with increased quality and abundance of natural forages) inside the Park had the opposite effect. This highlights the fundamental role of forage availability and quality as drivers of crop raiding by elephants (Chiyo, Cochrane, Naughton, & Basuta, 2005). Under current conditions and management practices the highest-quality forage in croplands becomes available around the same time that forage quality in the Park is near its lowest point. Future efforts to mitigate human-elephant conflict (HEC) should incorporate this information into agricultural plans to avoid this scenario. For example, farmers could focus on planting crops that are less palatable to elephants (e.g., sesame, onions, chili and peanuts) during the dry season (Campos-Arceiz, Takatsuki, Ekanayaka, & Hasegawa, 2009, Ekanayaka, Campos-Arceiz, Rupasinghe, Pastorini, & Fernando, 2011).

A central tenet of the forage maturation hypothesis is that herbivores track forage at intermediate biomass by selecting patches that are at or near peak NDVI (i.e., they surf the green wave; Bischof et al., 2012). Our results were partially consistent with the FMH in that elephants did surf the green wave while foraging in natural habitats within the Park. Our study also demonstrated, however, that elephants foraging in cultivated croplands switched strategies by actively selecting mature plants that were past peak greenness. The rate of change in NDVI, which quantifies the instantaneous rate of green-up (IRG), was proposed by Bischof et al. (2012) as a means of tracking the phenological progression of plant growth from NDVI time-series. Accordingly, the coupling of IRG with animal movement data creates an avenue for identifying environmental and anthropogenic factors that facilitate or constrain the tracking of high-quality forage by herbivores (Merkle et al., 2016). Our analysis demonstrated behavioral plasticity among crop-raiding elephants; collared individuals were capable of adjusting their “surfing” strategy to target forages that were at or near peak green-up in natural landscapes but that were browning down in agricultural landscapes. Transitions in foraging strategy regularly occurred within a single 24-hr period, and likely served to optimize energy intake from foraging in both landscapes.

Our results also suggest that elephants associate crop raiding with some level of risk, and thus faced a tradeoff between obtaining high-quality forage from cultivated crops and experiencing negative interactions with humans. Elephants dealt with that apparent tradeoff in more than one way. First, they limited the majority of their crop-raiding activities to nighttime hours. Second, elephants tended to select areas that were closer to the Park’s boundary regardless of which side of that boundary they were on (although this effect was only marginally significant when elephants were inside the Park). Similar to results reported



by Sigaud et al. (2017) for bison, this pattern of behavior served to put elephants in close proximity to both the security of the Park (when crop raiding) and the high-quality forage associated with cultivated crops (when inside the Park) almost continuously. Collectively, these observations suggest that crop-raiding behavior by elephants might be modified by altering their perception of the risks associated with that behavior. For example, in the buffer zone surrounding GNP crops are regularly grown right up to the edge of the river that forms the boundary of the Park. As a result, elephants are able to access those crops easily and with minimal perceived risk because of their close proximity to the security of the Park. Our results showed that the probability of an elephant moving toward the Park boundary during a crop-raiding event decreased further from the Park, suggesting that after reaching a certain distance from the Park elephants may perceive it to be safer to remain there and wait for the following night to return to the Park.

Previous studies have indicated that an adult elephant requires 8.3 kJ/g of DE to maintain normal levels of growth, reproduction and survival (Benedict & Lee, 1938, Dierenfeld, 1994), and that because elephants only digest 40% to 50% of the dry matter they consume, they must ingest a minimum of 16.7 kJ/g to meet their physiological requirements (Dierenfeld, 1994, Rode, Chiyo, Chapman, & McDowell, 2006). Although natural forages in GNP met those proposed requirements (our analyses accounted for digestibility via the equations of Robbins et al., 1987a, b), elephants in our study likely still benefited considerably from crop raiding because of the significantly higher amount of DE present in nearly all crop species relative to natural forage diets. For example, maize fruits contained, on average, 14 kJ/g of DE, sweet potato leaves contained an average of 14.5 kJ/g, and bananas contained 13.4kJ/g, relative to an average of 11.39 kJ/g in natural forage diets.

Herbivores often prefer diets higher in DE (Berteaux et al., 1998), and this generality was clearly reflected in our results; maize, sweet potatoes, and bananas were the most frequently raided crops in the buffer zone of GNP (Fig. 1.9). In addition, our results on this front are likely conservative for multiple reasons. First, we collected samples of crops only in August of 2017, which limited our access to different phenological growth stages. At least some of the crop species we sampled likely would have contained even greater DE if mature fruits would have been sampled. Second, our natural forage samples were obtained in July and August of 2017, several months before the end of the dry season when digestibility of natural forages would have been at its lowest point. Together these limitations to our sampling suggest that the average difference in DE between cultivated crops selected by elephants and natural forage diets likely was even greater than what we reported. One important caveat is that we had no data on intake rates or handling times associated with different plant species or plant parts. The concentrated distribution of cultivated crops would likely serve to increase foraging efficiency and associated intake of DE, however, again suggesting that our results are probably conservative.

Similar to DE, mean digestible protein in natural forage diets of elephants in our study (11.5%) met physiological requirements suggested by previous authors (Dougall & Sheldrick, 1964, Dierenfeld, 1994). In contrast to DE, however, 7 of the 19 crops analyzed had DP values that fell within the 95% CI for natural forage diets, and 9 crops actually contained less DP than natural forage diets. These results suggest that protein was not likely a major driver of crop raiding by elephants in GNP.

Understanding the mechanisms that underpin spatiotemporal variation in the frequency and intensity of crop raiding by elephants is critical for the development of

effective strategies for mitigating HEC. Gorongosa National Park is currently in the midst of a twenty-year restoration project, the three main objectives of which are to restore the ecosystem, support the communities in their social-economic development, and create, in a sustainable manner, a tourist industry. Currently the conflict between crop-raiding elephants and the communities inhabiting the buffer zone around the Park is one of the main limitations to the success of the restoration project because these conflicts directly or indirectly affect all of the main goals of the restoration project. This is not an uncommon scenario in sub-Saharan Africa, and our study provides important insights into the mechanisms underpinning spatiotemporal variation in crop raiding behavior that can be used by wildlife and land managers to reduce the potential for HEC in and around protected areas.

### **Literature Cited**

- Aikens, E. O., Kauffman, M. J., Merkle, J. A., Dwinnell, S. P. H., Fralick, G. L., & Monteith, K. L. (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters*, 20, 741-750. doi: 10.1111/ele.12772.
- Benedict, F. G., & Lee, R. C. (1938). Further observations on the physiology of the elephant. *Journal of Mammalogy*, 19(2), 175-194.
- Berteaux, D., Crête, M., Huot, J., Maltais, J., & Ouellet, J. (1998). Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*, 115, 84-92.
- Bhima, R. (1998). Elephant status and conflict with humans on the western bank of Liwonde National Park, Malawi. *Pachyderm*, 24 (Jan-Jul), 74-80.

- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Moorter, B. V., & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist*, 180(4), 407-424. doi: 10.1086/667590.
- Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P., & Coissac, E. (2016). Obitools: A unix-inspired software package for DNA metabarcoding. *Molecular Ecology Resources*, 16, 176-182. doi: 10.1111/1755-0998.12428
- Bohrer, G., Beck, P. S., Douglas-Hamilton, I. (2014). Elephant movement closely tracks precipitation- driven vegetation dynamics in a Kenyan forest- savanna landscape. *Movement Ecology*, 2(2), 1-12.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. (2nd ed.) New York, Springer-Verlag.
- Campos-Arceiz, A., Takatsuki, S., Ekanayaka, S. K. K., & Hasegawa, T. (2009). The human-elephant conflict in Southeastern Sri Lanka: type of damage, seasonal patterns, and sexual differences in the raiding behavior of elephants. *Gajah*, 31, 5-14.
- Cerling, T. E., Wittemyer, G., Rasmussen, H. B., Vollrath, F., Cerling, C. E., Robinson, T. J., & Douglas-Hamilton, I. (2006). Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences*, 103(2), 371-373.
- Campbell-Smith, G., Simanjorang, H. V. P., Leader-Williams, N. & Linkie, M. (2010). Local attitudes and perceptions toward crop-raiding by orangutans (*Pongo abelii*) and other nonhuman primates in Northern Sumatra, Indonesia. *American Journal of Primatology*, 72(10), 866-876.

- Chiyo, P. I., Cochrane, E. P., Naughton, L., & Basuta, G. I. (2005). Temporal patterns of crop raiding by elephants: A response to changes in forage quality or crop availability? *African Journal of Ecology*, 43(1), 48-55.
- Chiyo, P. I., Moss, C. J., Archie, E. A., Hollister-Smith, J. A., & Alberts, S. C. (2011). Using molecular and observational techniques to estimate the number and raiding patterns of crop-raiding elephants. *Journal of Applied Ecology*, 48(3), 788-796. doi: 10.1111/j.1365-2664.2011.01967.x
- Conover, M. R. (2002). *Resolving human-wildlife conflicts: the science of wildlife damage management*. Florida, USA: Lewis Publishers.
- Coppolillo, P., Gomez, H., Maisels, F., & Wallace, R. (2004). Selection criteria for suites of landscape species as a basis for site-based conservation. *Biological Conservation*, 115(3), 419-430. doi:10.1016/S0006-3207(03)00159-9
- Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen, J. R., ... Pringle, R. M. (2016). Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology*, 97(11), 3219-3230.
- Dancose, K., Fortin, D., & Guo, X. (2011). Mechanisms of functional connectivity: The case of free-ranging bison in a forest landscape. *Ecological Applications*, 21(5), 1871–1885. doi:10.1890/10-0779.1
- Datiko, D. & Bekele, A. (2013). Conservation challenge: human-herbivore conflict in Chebera Churchura National Park, Ethiopia. *Pakistan Journal of Biological Sciences*, 16(23), 1758-1764.

- Dierenfeld, E. S. (1994). Nutrition and feeding. In: S. K. Mikota, E. L. Sargent, & G. S. Ranglack (Eds.), *Medical management of the elephant* (pp. 69-80). Michigan, USA: Indira Publishing House.
- Dougall, H. W., & Sheldrick, D. L. W. (1964). The chemical composition of a day's diet of an elephant. *East African Wildlife Journal*, 2(1), 51-59.
- Ekanayaka, S. K. K., Campos-Arceiz, A. C., Rupasinghe, M., Pastorini, J., & Fernando, P. (2011). Patterns of crop-raiding by Asian elephants in a human-dominated landscape in Southeastern Sri Lanka. *Gajah*, 34, 20-25.
- Emerton, L. (2001). The nature of benefits and the benefits of nature: Why wildlife conservation has not economically benefited communities in Africa. In: D. Hulme & M. Murphree (Eds.), *African wildlife & livelihoods: The promise & performance of community conservation* (pp 208-226). Cape Town, SA: David Philip Publishers.
- Ficetola, G., Coissac, E., Zundel, S., Riaz, T., Shehzad, W., Bessière, J., ... Pompanon, F. (2010). An in silico approach for the evaluation of DNA barcodes. *BMC genomics*, 11, 434.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence Elk movement: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86(5), 1320-1330.
- Fox, A. D., Abraham, K. F. (2017). Why geese benefit from the transition from natural vegetation to agriculture. *Ambio*, 46(s2), 188-197. doi: 10.1007/s13280-016-0879-1
- Fryxell, J. (1991). Forage quality and aggregation by large herbivores. *The American Naturalist*, 138(2), 478-498.

- Garrouette, E. L., Hansen, A. J., & Lawrence, R. L. (2016). Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. *Remote Sensing*, 8(5), 1-25. doi:10.3390/rs8050404.
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M. & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5), 445-455.
- Hebblewhite, M., Merrill, E., & McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, 78(2), 141-166.
- Hoare, R. E. (1999a). Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, 36, 689-700.
- Hoare, R. E. (1999b). Data collection and analysis protocol for human-elephant conflict situations in Africa. UICN African Elephant Specialist Group' Human-elephant conflict working group.
- Hosmer, D. W., Lemeshow, S., & May, S. (2008). *Applied survival analysis regression modeling of time-to-event data* (2nd ed.). New York: John Wiley & Sons, Inc.
- Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., ... Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences*, 112(26), 8019-8024. doi:10.1073/pnas.1503283112/-/DCSupplemental

- Kendall, C. J. (2011). The spatial and agricultural basis of crop raiding by the Vulnerable common hippopotamus *Hippopotamus amphibius* around Ruaha National Park, Tanzania. *Oryx*, 45(1), 28-34. doi:10.1017/S0030605310000359
- Lahm, S. A. (1996). A nationwide survey of crop raiding by elephants and other species in Gabon. *Pachyderm*, 21, 69-77.
- Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D.,...Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B*, 283, 20160456.
- Middleton, A. D., Kauffman, M. J., Mcwhirter, D. E., John, G., Cook, R. C., Nelson, A. A., ... Klaver, R. W. (2017). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, 94(6), 1245-1256.
- Moss, C. J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology*, 255, 145-156.
- Navedo, J. G., Arranz, D., Herrera, A. G., Salmón, P., Juanes, J. A., Masero, J. A. (2013). Agroecosystems and conservation of migratory waterbirds: Importance of coastal pastures and factors influencing their use by wintering shorebirds. *Biodiversity and Conservation*, 22, 1895–1907. doi: 10.1007/s10531-013-0516-2.
- Naughton-treves, L. (1998). Predicting patterns of crop Damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, 12(1), 156-168.
- Ngama, S., Korte, L., Bindelle, J., Vermeulen, C., & Poulsen, J. (2016). How bees deter elephants: Beehive trials with forest elephants (*Loxodonta africana cyclotis*) in Gabon. *PLOS one*, 11(5), e0155690. doi:10.1371/journal.pone.0155690



- Noodén, L. D. (1988a). Whole plant senescence. In: Noodén LD, Leopold AC (Eds.).  
Senescence and aging in plants, (pp 392–439). San Diego: Academic Press.
- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of  
Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*,  
278(1), 1-14.
- Osborn, F. V. (2004). Seasonal variation of feeding patterns and food selection by crop-  
raiding elephants in Zimbabwe. *African Journal of Ecology*, 42(4), 322-327.
- Osborn, F. V. & Hill, C. M. (2005). Techniques to reduce crop loss: human and technical  
dimensions in Africa. In: R. Woodroffe, S. Thirgood & A. Rabinowitz (Eds.), *People  
and Wildlife: Conflict or Coexistence?* (pp. 72-85). Cambridge, UK: Cambridge  
University Press.
- Pansu, J., Giguet-Covex, C., Ficetola, G. F., Gielly, L., Boyer, F., Zinger, L., ... Choler, P.  
(2015a). Reconstructing long-term human impacts on plant communities: An  
ecological approach based on lake sediment DNA. *Molecular Ecology*, 24(7), 1485-  
1498. doi: 10.1111/mec.13136
- Pansu, J., Winkworth, R. C., Hennion, F., Gielly, L., Taberlet, P., & Choler, P. (2015b).  
Long-lasting modification of soil fungal diversity associated with the introduction of  
rabbits to a remote sub-Antarctic archipelago. *Biology letters*, 11, 20150408.  
<http://dx.doi.org/10.1098/rsbl.2015.0408>
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud,  
K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen  
successes in animal ecology. *Climate Research*, 46, 15-27. doi:10.3354/cr00936

- Pringle, R. M. (2008). Elephants are agents of habitat creation for small vertebrates at the patch scale. *Ecology*, 89(1), 26-33.
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., ... Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, 1(4). 10.1126/sciadv.1400103
- Rivrud, I. M., Heurich, M., Krupczynski, P., Müller, J., & Mysterud, A. (2016). Green wave tracking by large herbivores: An experimental approach. *Ecology*, 97(12), 3547-3553.
- Robbins, C. T., Mole, S., Hagerman, A. E., & Hanley, T. A. (1987a). Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology*, 68(6), 1606-1615.
- Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C., & Mautz, W. W. (1987b). Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, 68(1), 98-107.
- Rode, K. D., Chiyo, P. I., Chapman, C. A., & McDowell, L.R. (2006). Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behavior. *Journal of Tropical Ecology*, 22, 441-449.
- Sam, M. K., Ayesu, S., Agbenu, V., Kumordzi, B. B., & Wilson, S. (2003). Reconnaissance survey of human–elephant conflict in the Dadieso area, western Ghana. *Pachyderm*, 35 (Jul-Dec), 132-136.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103-113. doi: 10.1111/j.2041-210X.2010.00012.x

- Sigaud, M., Merkle, J. A., Cherry, S. G., Fryxell, J. M., Berdahl, A., & Fortin, D. (2017). Collective decision-making promotes fitness loss in a fusion-fission society. *Ecology Letters*, 20(1), 33-40. doi: 10.1111/ele.12698.
- Sikes, R. S. & the Animal Care and Use Committee. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663-688. doi:10.1093/jmammal/gyw078
- Sitati, N. W., Walpole, M. J., Smith, R. J., & Leader-Williams, N. (2003). Predicting spatial aspects of human and elephant conflict. *Journal of Applied Ecology*, 40, 667-677.
- Stalmans, M. (2012). Monitoring the recovery of wildlife in the Parque Nacional da Gorongosa through aerial surveys. A preliminary analysis. Gorongosa National Park.
- Sukumar, R. (1990). Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, 6(1), 33-53.
- Sukumar, R. (2003). *The Living Elephants: evolutionary ecology, behavior and conservation*. Oxford, UK: Oxford University Press.
- Steuer, P., Südekum, K. H., Müller, D. W. H., Franz, R., Kaandorp, J., Clauss, M., & Hummel, J. (2011). Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, 160, 355-364. doi:10.1016/j.cbpa.2011.07.005
- Taberlet, P., Coissac, E., Pompanon, F, Gielly, L., Miquel, C., Valentini, A., ... Willerslev, E. (2007). Power and limitations of the chloroplast 979 *trnL* (UAA) intron for plant DNA barcoding. *Nucleic Acids Research*, 35(3), e14. doi:10.1093/nar/gkl938

- Taberlet, P., Prud'Homme, S. M., Campione, E., Roy, J., Miquel, C., Shehzad, W., ...  
Coissac, E. (2012). Soil sampling and isolation of extracellular DNA from large amount of starting material suitable for metabarcoding studies. *Molecular Ecology*, 21(8), 1816-1820. doi: 10.1111/j.1365-294X.2011.05317.x
- Thouless, C.R. (1994). Conflicts between humans and elephants in northern Kenya. *Oryx*, 28, 119-127. doi: 10.1017/S0030605300028428
- Tinley, K. L. (1977). Framework of the Gorongosa ecosystem. Gorongosa National Park.
- van der Graaf, S. A. J., Stahl, J., Klimkowska, A., Bakker, J. P., & Drent, R. H. (2006). Surfing on a green wave – how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea*, 94(3), 567-577.
- Vines, A. (1991). Renamo: terrorism in Mozambique. Indiana University Press.
- Wagner, K. K., Schmidt, R. H., & Conover, M. R. (1997). Compensation programs for wildlife damage in North America. *Wildlife Society Bulletin*, 25(2), 312-319.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation*, 157, 60-68.  
<http://dx.doi.org/10.1016/j.biocon.2012.07.019>
- Wang, T., Skidmore, A. K., Wang, T., Skidmore, A. K., Zeng, Z., Beck, P. S. A., ... Prins, H. H. T. (2010). Migration Patterns of Two Endangered Sympatric Species from a Remote Sensing Perspective. *Photogrammetric Engineering and Remote Sensing*, 76(12), 1343-1352. doi: 10.14358/PERS.76.12.1343

- Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005). The impact of human–wildlife conflict on natural systems. In: R. Woodroffe, S. Thirgood & A. Rabinowitz (Eds.), *People and Wildlife: Conflict or Coexistence?* (pp. 01-12). Cambridge, UK: Cambridge University Press.
- Wyatt, J. R., & Eltringham, S. K. (1974). The daily activity of the elephant in the Rwenzori National Park, Uganda. *African Journal of Ecology*, 12(4), 273-289.  
<https://doi.org/10.1111/j.1365-2028.1974.tb01037.x>
- Yoccoz, N. G., Bråthen, K. A., Gielly, L., Haile, J., Edwards, M. E., Goslar, T., ... Taberlet, P. (2012). DNA from soil mirrors plant taxonomic and growth form diversity. *Molecular Ecology*, 21(15), 3647-3655. <https://doi.org/10.1111/j.1365-294X.2012.05545.x>

Figure 1.1. Map of study area showing Gorongosa National Park, Mozambique, and the surrounding buffer zone, where approximately 200,000 people currently reside.

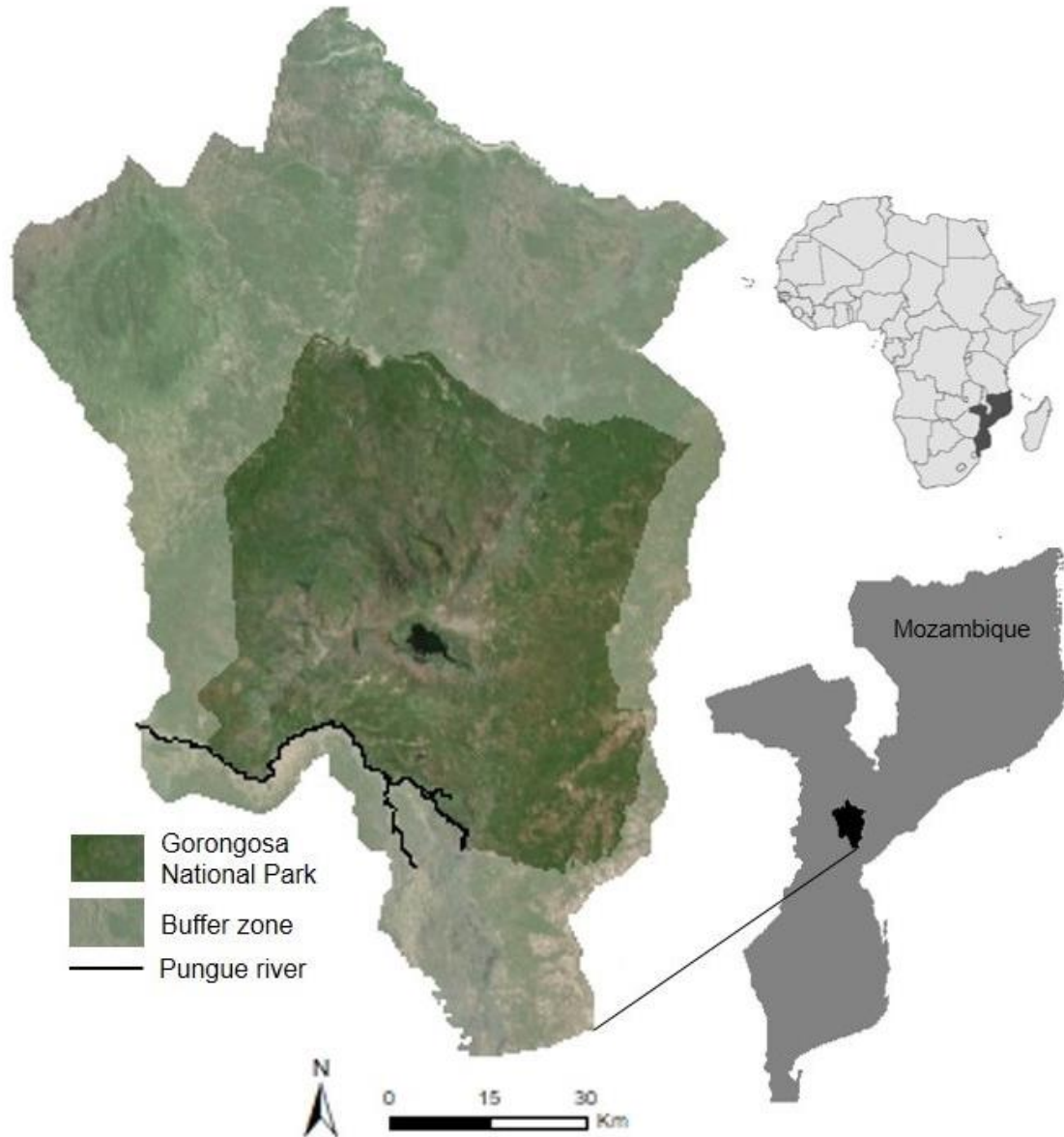


Figure 1.2. A comparison of the area immediately south of the Pungue River, which forms the southern boundary of Gorongosa National Park, Mozambique, between 1972 (prior to the start of the Mozambican Civil War) and 2010. The two aerial images highlight the immense conversion of natural habitats into agricultural fields that took place during this period.

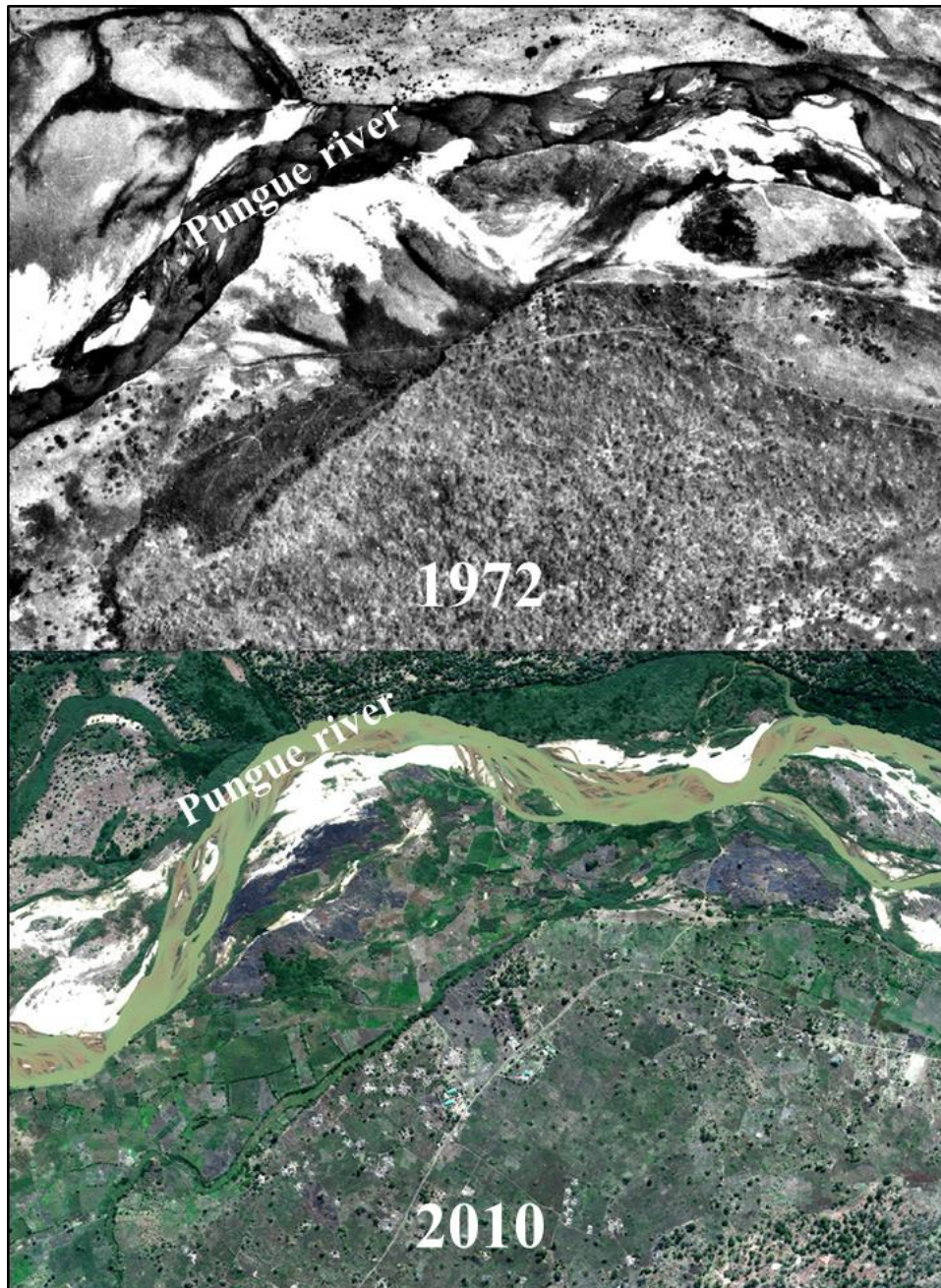


Figure 1.3. Total number of crop-raiding excursions by month for 12 GPS-collared elephants (*Loxodonta africana*) in Gorongosa National Park, Mozambique between January, 2016 and January, 2018.

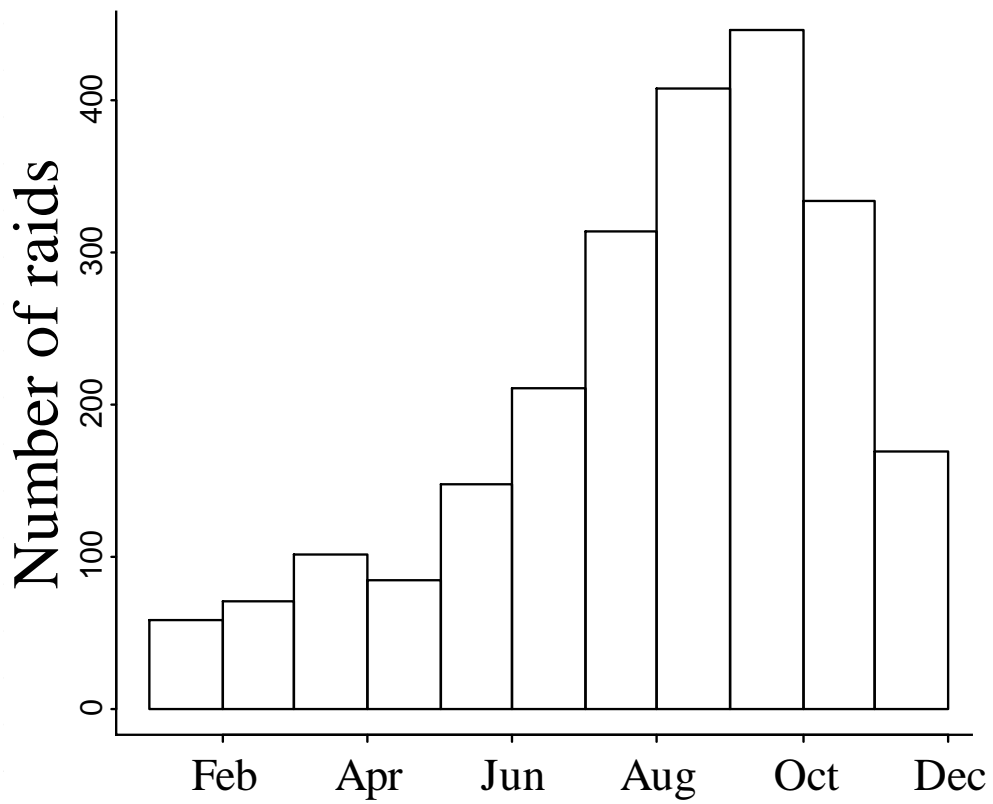




Figure 1.4. Hourly frequency of exits (crop-raiding excursions) from the Park to the buffer zone, and subsequent returns to the Park by elephants in Gorongosa National Park, Mozambique.

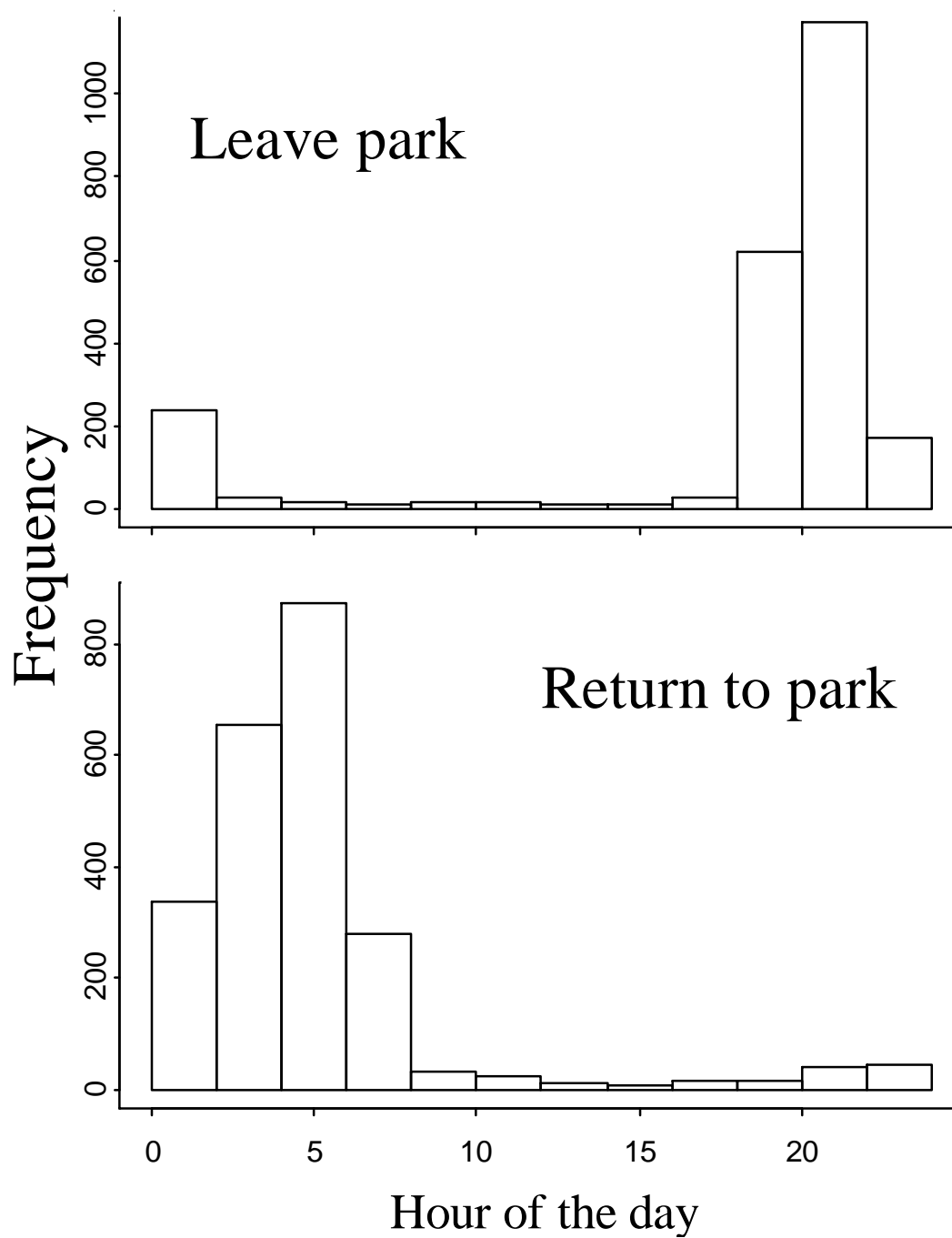


Figure 1.5. Mean NDVI of pixels that fell within elephant home ranges inside versus outside of the southern boundary of Gorongosa National Park, Mozambique.

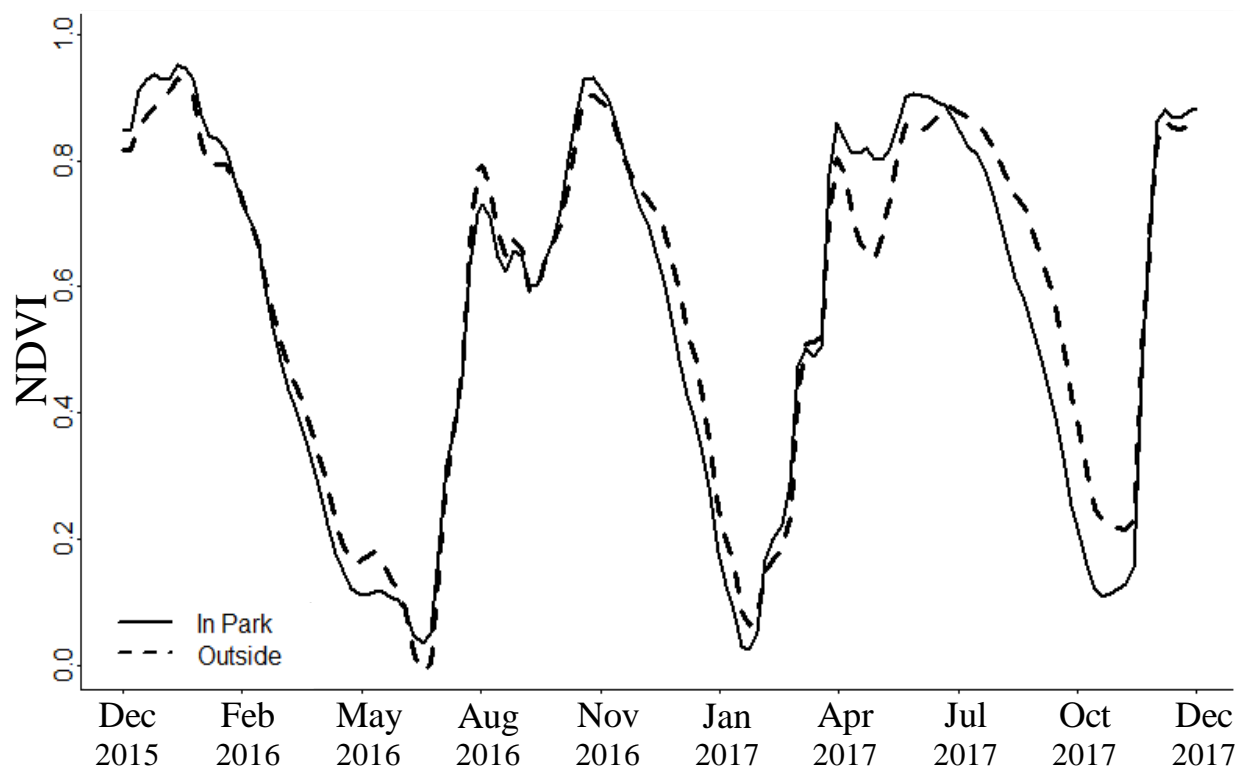


Figure 1.6. Relative probability of a crop raiding event by elephants in Gorongosa National Park, Mozambique (black line) with 95% CI (gray), and the relative values of precipitation (blue), NDVI in the Park (green), fruit availability (red), and maize availability (yellow) overlaid.

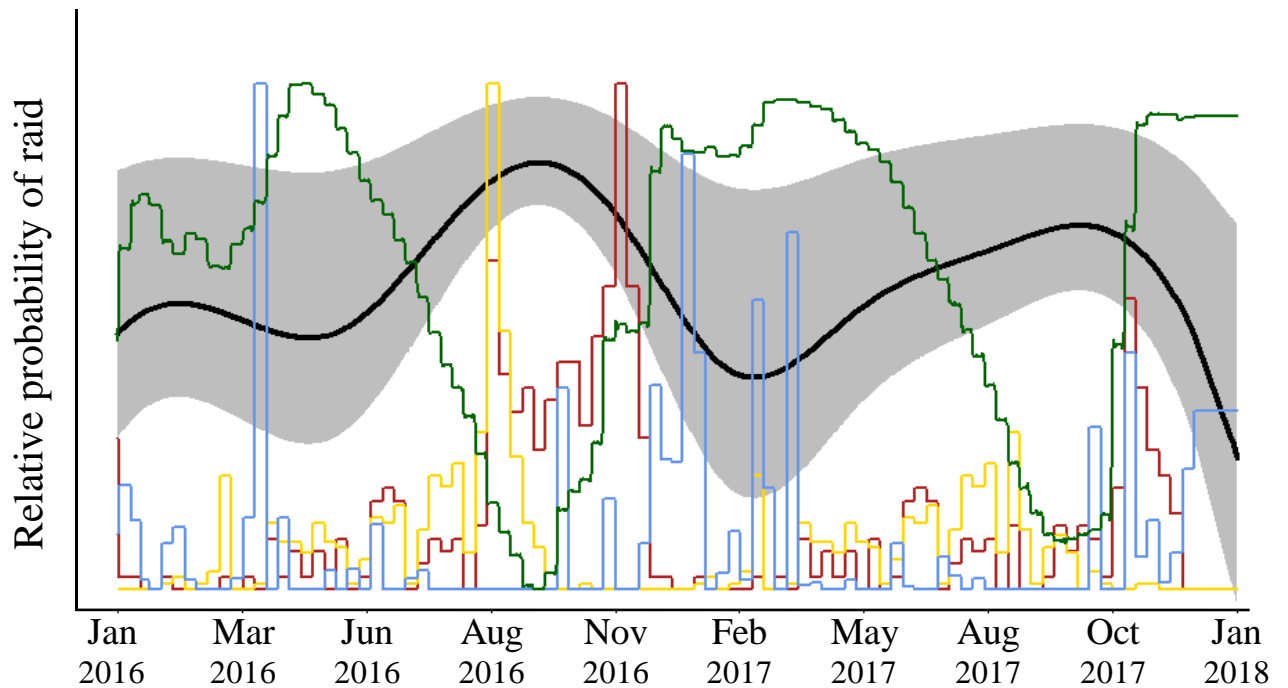


Figure 1.7. Influence of distance to the Park boundary, NDVI, and the rate of change in NDVI on step selection by elephants in natural habitats (top panels) versus cultivated croplands (bottom panels) in and around Gorongosa National Park, Mozambique. Black lines depict the model-predicted influence of each variable on step selection with other variables held constant at their means, and dashed lines depict 95% CIs.

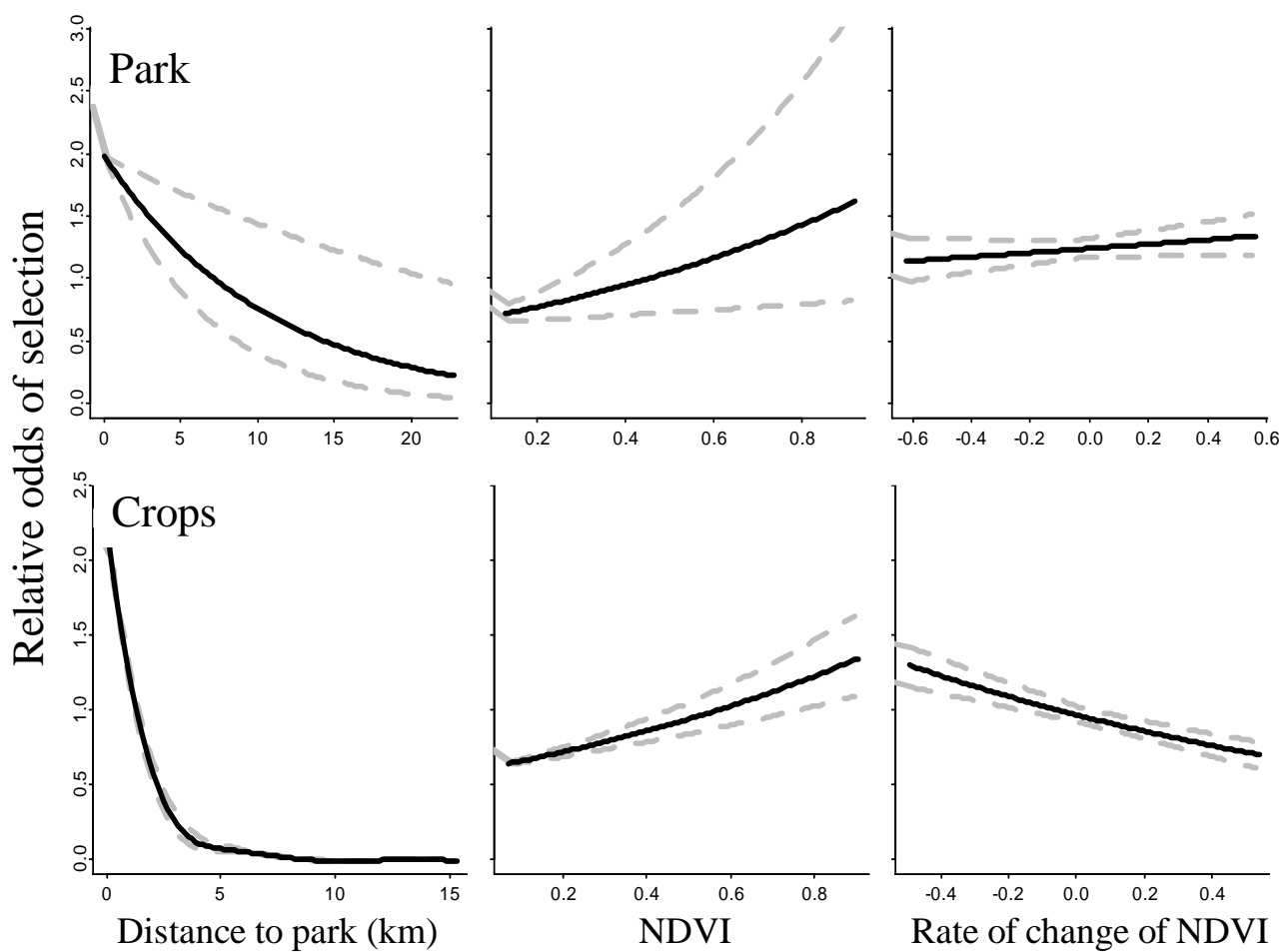


Figure 1.8. Mean ( $\pm 95\%$  CI) digestible energy (DE; kJ/g) and digestible protein (DP; %) content of elephant diets ( $n = 6$ ) when consuming natural forages within Gorongosa National Park, Mozambique, compared with the same parameters (DE and DP) for primary crop species consumed by elephants during raiding events. Most crop species were partitioned into fruits (F), leaves (L), roots (R), and stems (S) for nutritional analysis.

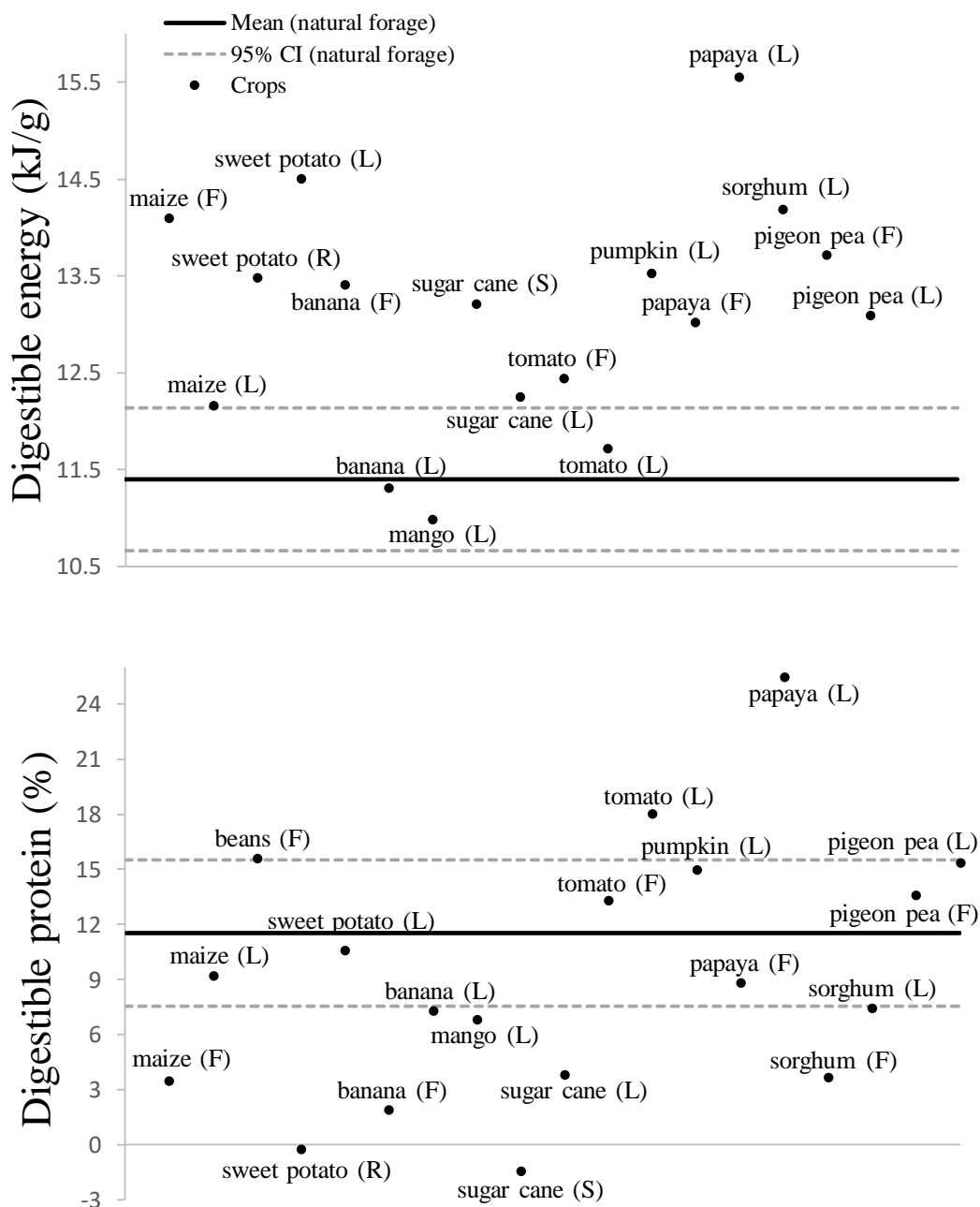


Figure 1.9. Percentage of crops raided by elephants in Gorongosa National Park according to enumerators' reports from August 2016 to December 2017.

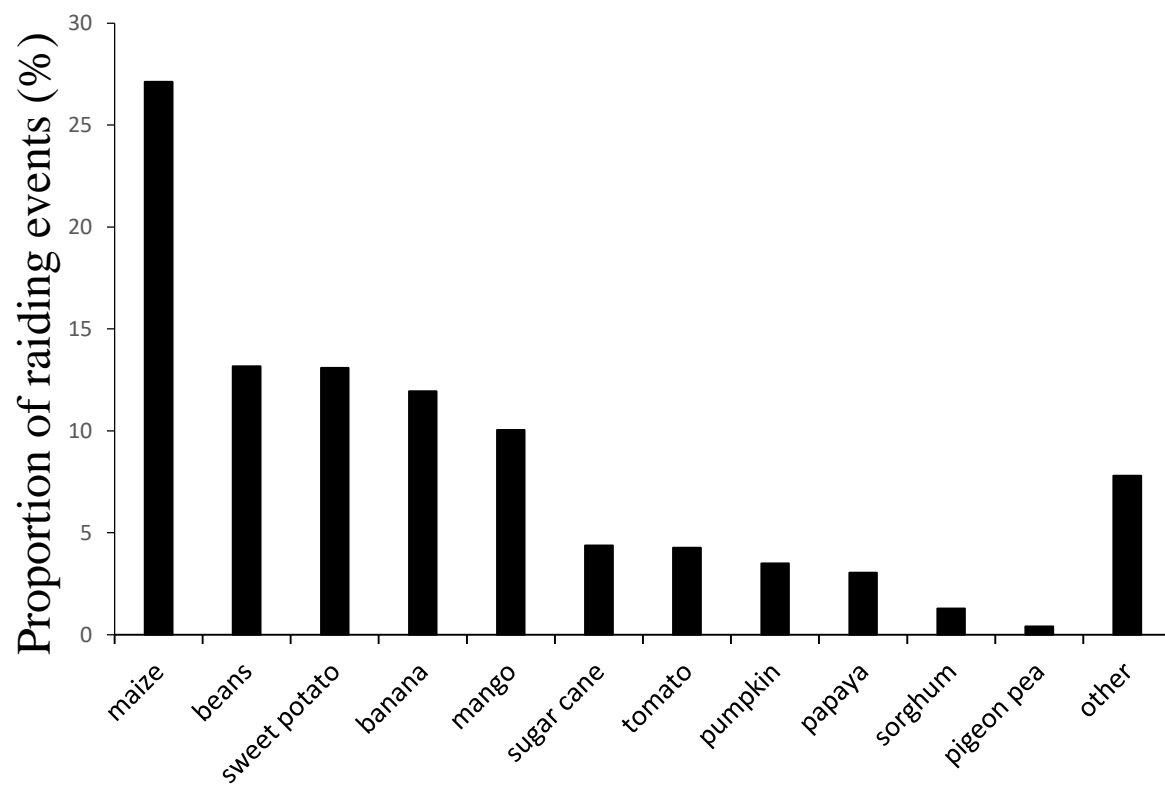


Table 1.1. Standardized model coefficients (and associated *SEs* and *P*-values) from the top model (which garnered 99% of the AIC weight) in a time-to-event analysis of crop-raiding events in Gorongosa National Park, Mozambique. Coefficients indicate the influence of each variable on the probability of an elephant remaining within Park boundaries rather than initiating a raid. Candidate predictor variables included the relative availability of fruits, maize, and tubers outside the Park, NDVI inside the Park (NDVI<sub>Park</sub>), and precipitation.

Variable	Coefficient	SE	<i>P</i>
Fruit	-0.178	0.020	<0.01
Maize	-0.026	0.015	0.088
Tuber	-0.056	0.006	<0.01
NDVI <sub>Park</sub>	0.176	0.311	<0.01
Precipitation	0.054	0.012	<0.01

Table 1.2. Standardized coefficients (and associated *SEs* and *P*-values) from models of step selection by elephants moving within the boundaries of Gorongosa National Park, Mozambique, and elephants moving within croplands surrounding the Park. Candidate predictor variables included distance to the Park boundary (km), NDVI, the rate of change in NDVI, and distance to Park: source, which was an interaction term that quantified whether strength of selection for areas closer to the Park boundary changed as a function of current distance from the boundary.

Habitat type	Variable	Coefficient	SE	<i>P</i>
Crop	Distance to Park	-0.698	0.03	<0.01
	NDVI	0.881	0.103	<0.01
	NDVIrate of change	-0.595	0.123	<0.01
	Distance to Park: source	0.079	0.012	<0.01
Park	Distance to Park	-0.093	0.049	0.104
	NDVI	1.226	0.281	0.010
	NDVIrate of change	0.069	0.324	0.822



## **Chapter 2: The elephants of Gorongosa: an integrated approach to conservation and conflict mitigation in the shadow of war**

### *Abstract*

Populations of African elephants (*Loxodonta africana*) are under considerable threat from poaching, habitat loss, and conflicts with humans. Farming strategies adopted by some local communities in many parts of Africa are progressively converting natural habitats into croplands, thereby producing increasingly fragmented landscapes for elephants to navigate. One result of such fragmentation has been a steady increase in the occurrence of human-elephant conflict (HEC), namely crop raiding by elephants. Many elephants are killed every year while raiding crops, and human fatalities sometimes occur as well, highlighting the importance of developing effective strategies for reducing the occurrence of crop raiding. Although there are many methods available for deterring elephants from crop raiding, but few studies have tested their efficacy in the wild using a rigorous experimental design. We used a combination of community-based reporting systems, elephants GPS collars, and camera traps to experimentally test the effectiveness of beehive fences, chili fences, and a combination of the two (“spicy beehive fences”) for deterring elephants from crossing outside the southern border of Gorongosa National Park, Mozambique, to raid crops in the surrounding communities. We hypothesized that overall use of key crossing points by elephants would decline after fences were constructed. We also hypothesized that elephants would be more averse to the “spicy beehive” fences than to either beehive or chili fences alone, because of the higher probability of experiencing at least one form of pain (i.e., bee stings or a reaction to the spicy chili paste) upon interacting with spicy beehive fences.

Elephants generally avoided all fence types, and after interacting with a fence (i.e., touching, smelling or attempting to manipulate with their trunk) elephants returned to the Park far more frequently than they continued a raid. Elephants were least likely to cross through beehive fences, and spicy beehive fences were the second most effective deterrent. Chili fences alone were not as effective as fences that included bees. Generally positive perceptions of the mitigation experiment among community members reaffirmed the importance of directly including local communities in efforts to mitigate HEC. Our project demonstrated that the integration of creative mitigation measures and direct involvement from local communities can simultaneously reduce the occurrence of crop raiding and improve tolerance for elephants among community members.

## **Introduction**

Humans have a long history of defending themselves and their properties against wild animals, and conflict between humans and wildlife sometimes occurs when their areas of activity overlap (Treves, Wallace, Naughton-Treves, & Morales, 2006). The number of people on earth continues to rise exponentially, and as a result, contact between people and wild animals occurs frequently throughout the world (Woodroffe, Thirgood, & Rabinowitz, 2005). Under some circumstances close proximity of humans and wildlife results in serious conflict that can lead to injuries or fatalities (of people or animals), transmission of diseases, predation on livestock, or crop-raiding (Thirgood, Woodroffe, & Rabinowitz, 2005). Thus, providing food and an acceptable quality of life to a growing human population while simultaneously preserving natural ecosystems represents a significant scientific, social and political challenge (Strassburg et al., 2014).

In many parts of Africa wildlife are viewed largely as a property of the State, and communities expect wild animals to be contained in protected areas and separated from people (Osborn & Hill, 2005). However, human settlements in close proximity to protected areas are continually expanding, often as a result of economic incentives and opportunities in and around Parks (Norton-Griffiths et al., 2008, Ogotu, Piepho, Dublin, Bhola, & Reid, 2009). Consequently, competition for land, water and food is intensifying (Sukumar, 1990, Gordon, 2009). Moreover, despite the economic benefits that often accrue from living close to protected areas, tolerance among humans for the risks associated with HWC in such areas typically remains low, and is strongly tied to the level of dependency on the resource being damaged (or at risk of being damaged) by wildlife (Treves, Wallace, Naughton-Treves, & Morales, 2006).

Availability of high-quality forage in cultivated croplands attracts wildlife (Garrouste, Hansen, & Lawrence, 2016, Middleton et al., 2017), and in Africa elephants (*Loxodonta africana*) in particular cause considerable damage to crops every year (O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000, Chiyo, Cochrane, Naughton, & Basuta, 2005). Most of the time, the benefits of obtaining higher-quality food items appear to outweigh the risks of raiding crops (Chiyo, Moss, Archie, Hollister-Smith, & Alberts, 2011, Ahlering, Millspaugh, Woods, Western, & Eggert, 2011), and it is therefore very challenging to effectively deter the largest land mammal on earth from entering croplands. Indeed, most efforts to do so fail (Graham & Ochieng, 2008). Because elephants can quickly become habituated to deterrents (Osborn & Parker, 2002), human-elephant conflict (HEC) must be managed carefully and creatively to keep from depleting limited mitigation resources (O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000). Accordingly, a shifting

combination of strategies is often necessary (Sitati, Walpole, Smith, & Leader-Williams, 2003), and where possible the choice of strategies should be informed by rigorous experimental research (Hoare, 1999).

Most strategies currently used to keep elephants from raiding crops are labor intensive and produce only temporary results. For example, the use of firecrackers, guards at the edges of fields (alone or in groups), dogs, slingshots, drums, tins and whips to make loud noises, and the throwing of burning sticks all have been reported, with varying results (Nyhus, Tilson, & Sumianto, 2000, Osborn & Parker, 2002). In addition, crop-raiding by elephants occurs mainly after sunset (Hoare, 1995, Thouless, 1994, Sitati, Walpole, Smith, & Leader-Williams, 2003), which adds another level of complexity and risk to many of the common mitigation strategies described above. Farmers are forced to actively protect fields at night, which dramatically increases the probability of a dangerous encounter with elephants or other wild animals (e.g., buffaloes, hippos and crocodiles), as well as time spent awake during the night. In many instances children are expected to help deter wildlife, and thus are kept out of school during the day so that they can help protect crops at night (Haule, Johnsen, Maganga, 2002, Kagoro-Rugunda, 2004).

Given the magnitude of the problem posed by crop raiding and its implications for both human livelihoods and elephant conservation, it is critical to develop and prioritize strategies that demand less manpower and effectively prevent elephants from accessing farms in the first place, rather than trying to scare elephants away after they have already reached a farm (Tchamba, 1996, Osborn & Parker, 2002, Sitati & Walpole, 2006). Strategies that reduce overall levels of conflict at the community scale also are preferable to individual farm-based methods (O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000), especially in areas

of high human density where diverting an elephant away from one farm may simply lead to crop raiding in another farm nearby.

Human-elephant conflict involves both elephants and humans, and effective solutions to mitigating HEC should integrate, to the greatest extent possible, the modification of elephant behavior and the alteration of human perceptions of HEC, which are shaped by a myriad of underlying and sometimes unrelated factors (Dickman, 2010). Indeed, conservation is not solely a matter of biological science but also of social science (Madden, 2004). Attitudes towards wildlife and protected areas are influenced not just by crop losses per se, but also by how much empowerment and support people receive, and the degree to which their beliefs and values are taken into consideration (Naughton-treves, 2015). Fostering communication and trust and demonstrating a genuine willingness to help address the issue can have a positive effect on the attitudes and actions of people in conflict with wildlife. Thus, working closely and directly with communities that are experiencing HEC to foster relationships and establish rapport can sometimes be an effective means of reducing conflict in the short term as longer-term mitigation strategies are tried, tested, and implemented (Madden, 2004).

Beehive fences are widely used to deter elephants from crop raiding in many countries in Africa and Asia (King, Lawrence, Douglas-Hamilton, & Vollrath, 2009). Although elephants are thick-skinned, some parts of their body (e.g., the belly, under the trunk, and behind the ears) are relatively sensitive. As a result, bee stings can cause considerable pain (Vollrath & Douglas-Hamilton, 2002), and can be used to modify elephant behavior (Karidozo & Osborn, 2005). For example, in a study in Kenya, beehive fences

reduced elephant crop-raiding by 80%, and farmers also benefited socially and financially from the sale of 228 kg of elephant-friendly honey in a 3.5-yr trial (King et al., 2017).

Chili-based deterrents also have been commonly used in different forms (spray, grease, bombs, and smoke) as a tool to reduce HEC (Hedges & Gunaryadi, 2010). A mix of chili and oil deployed in a “chili fence” design has proven to effectively repel crop-raiding elephants (Karidozo & Osborn, 2005). Elephants are known to avoid eating the fruits of the chili pepper plant, and chilies are thought to irritate their sensitive nasal tissue. For this reason, once an elephant has tested a chili fence with its trunk and experienced the associated irritation, the smell of chili and oil also becomes a psychological barrier (Wiafe & Sam, 2014).

We studied HEC in human settlements along the southern border of Gorongosa National Park, Mozambique, where the elephant population is currently recovering from decimation by a civil war that ended in 1992. The goal of our project was to integrate elephant and community-based approaches to reducing HEC by simultaneously reducing the frequency of crop-raiding by elephants and improving attitudes toward elephants among local community members. We experimentally evaluated the efficacy of three approaches to reducing elephant crop-raiding (beehive fences, chili fences, and a combination of the two, “spicy beehive” fences), and we hired and trained a large number of local community members to participate directly in the project by collecting data on crop raiding, constructing and monitoring fences, maintaining camera traps, and performing a multitude of other tasks. We used a community-based reporting system and GPS data from collared elephants to identify key conflict areas (i.e., locations frequently used by elephants to cross from the Park into agricultural fields) in which to conduct our experiment. We then collected two years of

data in a before-after control-impact (BACI) design in which use of crossing points by elephants was compared between years with (year 2) and without (year 1) fences, as well as among treatment and control fences during year 2. We hypothesized that overall use of crossing points by elephants would decline in year 2 after fences were constructed (H1). We also hypothesized that elephants would be more averse (i.e., would return to the park more frequently upon encountering the fence) to the “spicy beehive” fences than to either beehive or chili fences alone (H2).

## **Material and Methods**

### *Study Area*

We conducted our study in Gorongosa National Park (GNP), Mozambique. Annual precipitation at GNP averages roughly 850 mm and occurs mostly during the November – March rainy season (Tinley, 1977). Temperatures at Gorongosa range from an average minimum of 15° C during the dry season to an average maximum of 32° C during the wet season. The Park is surrounded by a 5,333-km<sup>2</sup> “buffer zone” where approximately 200,000 subsistence farmers currently reside. A large proportion of these farmers cultivate crops along the southern boundary of the Park, which is formed by the Pungue River (Fig. 2.1). Prior to the civil war, which began in 1976, GNP was home to roughly 2,500 elephants. During the war, however, most of those elephants were killed to feed soldiers and to fund the purchase of arms and ammunition through the sale of ivory (Vines, 1991); by the year 2000, the elephant population numbered less than 200 individuals (Stalmans, 2012). Elephants are currently recovering at GNP under the auspices of the Gorongosa Restoration Project, and the most recent aerial census counted roughly 600 individuals. Following the war, however, much of the buffer zone was converted to agricultural lands that strongly

attract elephants. Thus, as the elephant population has begun to increase, so has the occurrence of human-elephant conflicts.

#### *Animal capture and location data*

To quantify spatial and temporal patterns of crop-raiding by elephants at GNP, and to aid in evaluating the effectiveness of the mitigations trials, we fit 12 male elephants with high potential for crop-raiding behavior (i.e., individuals that were captured in or in close proximity to crops) with Global Positioning System (GPS) collars (Model AWT IM-SAT, Africa Wildlife Tracking, Pretoria, South Africa). We collared six elephants in December, 2015, and six in August, 2016. We programmed GPS collars to collect and transmit a location every thirty minutes through the iridium satellite system for a period of two years. Each elephant was chemically immobilized via remote injection from a helicopter with a combination of thiafentanil oxalate (9 to 15 mg) and azaperone (40 to 60mg), with the dosage depending on the approximate age and size of each individual. Elephants were carefully monitored during handling and the following parameters were measured: cardiac rate (normal: 25-30 bpm), respiratory rate (normal: 4-6 breaths/minute), rectal temperature (normal: 36° to 37° C), blood oxygenation (via a portable pulse-oximeter), and invasive and non-invasive blood pressure (Cardell® Multiparametric Monitor). Chemical immobilization was reversed with Naltrexone at the end of each procedure. Elephants were recaptured and all collars were removed when battery life was nearly exhausted (roughly two years of deployment), and by the end of 2017 only two elephants were still collared. All animal handling procedures were approved by the Animal Care and Use Committee at the



University of Idaho (protocol #2015-39), and were in accordance with guidelines established by the American Society of Mammalogists (Sikes et al., 2016).

### *Community-based reports*

From its inception, our project aimed to foster close working relationships with the local communities around GNP. Because HEC is a highly sensitive issue and our experiment had the potential to directly impact people's livelihoods, we spent the first year of our study (while data on crop-raiding behavior were being collected from GPS-collared animals) building strong relationships with community members at all leadership levels through a series of meetings in five different communities. These meetings were open to the public and always included men and women of different ages, local leaders, and government-level members. A translator was present to translate from Portuguese to the local language, Sena. During the meetings we explained the goals of our project and moderated debates about the best approaches for dealing with HEC (Fig. 2.2). At the conclusion of this period we incorporated suggestions and concerns from the communities directly into our study design for the mitigation experiment. For example, our initial study design involved testing the use of different elephant deterrents around individual farms, similar to previous studies (e.g., King, Lawrence, Douglas-Hamilton, & Vollrath, 2009). However, due to the high density of people around GNP, community members suggested that the mitigation trials should be focused on the primary routes used by elephants to access croplands in the first place so that a larger proportion of the communities might benefit directly from the trials. The combination of data from GPS-collared elephants and expert knowledge from community members suggested that elephants did indeed use specific crossing points along the river to

access crops, so we altered our design to capitalize on these corridors between natural and cultivated landscapes for the mitigation trials (see below).

Based on the framework suggested by Hoare (1999) for the IUCN African Elephant Specialist Group, we trained a team of twenty-four local community members to collect data on crop-raiding events, and subsequently selected ten individuals to participate directly in the study (the selection process was based on an exam and interviews following three days of training). These community members, who we termed enumerators, were given additional training by qualified project personnel to collect standardized data on crop-raiding events, including animal species involved, the location of the event (GPS point), type and area of crop damaged or consumed, and the occurrence of other types of conflict besides crop raiding (e.g., animal and human injuries or death). Enumerators worked in six different communities spread across 60 kilometers of the Pungue River from August 2016 to January 2018. Enumerators received a salary from GNP, and we provided each individual with uniforms and a bicycle to facilitate access to their assigned areas and search for evidence of crop-raiding by elephants during each morning of the study. Enumerators provided a total of 1,662 reports on crop-raiding events during the study that included the location of the event, the type of crop damaged or consumed, the stage of maturation (germinating, flowering, mature), whether other animal species were involved, and whether property other than crops was damaged.

Before the mitigation trials began in year two, we trained a second group of twenty community members to monitor and maintain fences (beehive, chili and spicy beehive) for the project. We subsequently hired six of these individuals to work as monitors following a selection process similar to the one used to identify and hire enumerators. Each monitor was

responsible for monitoring from one to four specific treatment or control fences (depending on distance to their homes and size of the fences), which they visited every morning and filled out reports on whether elephants had visited or not (based on evidence such as tracks or fresh feces), whether they crossed the fence (based on whether fences were damaged), and the approximate number of elephants that had visited the location (based on elephant tracks). The monitors also were responsible for daily maintenance of fences and camera traps, including fixing them when they were damaged and making sure the cameras were functioning properly.

#### *Mitigation experiment*

We experimentally evaluated the effectiveness of beehive fences, chili fences and a combination of both (spicy beehive fence) for deterring elephants from leaving the Park to raid crops in the communities. All fences were constructed in the buffer zone, outside the boundary of GNP (i.e., on the community side of the Pungue River). To select sites for the mitigation trials we used elephant GPS collar data in combination with information gleaned from meetings with community members and reports provided by the enumerators to identify >50 key locations where elephants commonly crossed the Pungue. To maintain a reasonable level of efficiency, we restricted our study to four communities that were most affected by crop-raiding along the southern boundary of GNP. We then visited each elephant crossing point associated with those communities to determine which ones were most appropriate for our experiment based on proximity to roads and the overall logistics of accessing and constructing fences. We eventually selected 13 suitable crossing points, and we deployed camera traps (Bushnell Trophy Cam) at each location to monitor elephant

activity for two weeks prior to constructing fences. After this period we randomly assigned treatment and control fences to each of the 13 crossings. We constructed beehive fences at three crossings, chili fences at three crossings, and spicy beehive fences at three crossings. In addition, we constructed beehive control fences (fake beehives) at two crossings and chili control fences (chili fence without chili) at two crossings. Fences varied in length from 40 to 500 m, and were designed to span the portion of each respective crossing point where elephants could easily exit the river (Figs. 2.3 and 2.4).

Our chili fences were a modified version of the design described by Karidozo & Osborn (2005), and Chang'a (2016). We used strips of cotton fabric plaited with sisal ropes and dipped in a mixture of ground bird's eye chili (*Capsicum* spp) and vegetable oil. Despite being more expensive, we used vegetable oil to decrease pollution; engine oil is more commonly used to construct chili fences, but is also an environmental pollutant (Vazquez-Duhalt, 1989). We suspended the ropes from bamboo poles at 5-m intervals along the riverbank. Maintenance involved repairing damaged sections when needed, tightening the sisal rope if it began to sag, and re-application of chili mixed with oil four times over the 3 months of the experiment.

We deployed 64 new Kenyan top-bar hives (KTBH) in the form of beehive or spicy beehive fences at six key crossing points along the Pungue. We suspended hives from poles roughly 10 m apart, and each hive was connected to its neighboring hives with ropes placed 1.5 m from the ground so that any movement of the ropes by elephants would cause the hives to swing, thus disturbing the bees. We used baling twine to connect beehive fences, whereas spicy beehive fences were connected using chili fences (prepared as described

above). Many hives were occupied even prior to deployment, and hive occupation had reached 76% by week 2 of the experiment, and 94% by week 7.

With the aid of >50 people, all of whom were local community members, we prepared crossing points for fence construction by cutting grass and constructing firebreaks to prevent the destruction of fences by fire, and to make fences more visible to elephants. We then constructed all fences over an 8-d period using 173 hard-wood poles, 149 bamboo poles, 20 fake hives (wood planks), 800 m of polypropylene baling twine, 1,200 m of sisal rope, 600 kg of chili, 64 beehives, 50 m of wire, and 200 l of vegetable oil. All fences were completed by 17 September, 2017, at the peak of the crop-raiding season.

We left fences in place for 3 months (17 September to 20 December, 2017), and continued to collect data on elephant use of each crossing point throughout that period via camera traps, daily reports from monitors, and GPS-collared elephants. We deployed 24 camera traps across the thirteen crossing points, each of which was programmed to record a sequence of 3 photos at each trigger, with a 3-s interval between photos and a delay of 30 s between triggers. In addition, during one 2-w interval, we programmed some cameras to record 30-s videos at each trigger. We combined data from camera traps, daily monitor reports, and GPS-collared elephants to produce a dataset that indicated all days during which >1 elephant approached a fence, as well as how the elephant or elephants responded to the fence (i.e., crossed the fence or returned to the Park).

### *Statistical analysis*

We evaluated the responses of elephants to treatment and control fences using two separate contingency table analyses (Zelen, 1971, De Boer & Baquete, 1998). For the first

analysis we used location data from GPS-collared elephants that were monitored before, during, and after construction of the fences ( $n = 8$ ) to calculate the number of river crossings (defined as one elephant location inside the Park immediately followed by  $>1$  location outside the Park [“exits”], or vice versa [“returns”]) that fell within a 30-m buffer around crossing points where fences were constructed in 2017 ( $n = 13$ ), as well as at crossing points that were located between fences (i.e., crossings where no fences were present). We tallied river crossings at each crossing point during 2016, when no fences were present, and 2017 after fences had been constructed (Table 2.1). For crossings that occurred at locations with fences in 2017, we used camera trap data to ensure that instances in which an elephant crossed successfully by going around a fence rather than through it (a possibility we attempted to minimize with the location of our fences) were not counted as “crossings” for purposes of the contingency table analysis. In addition, because our objective was to test the effectiveness of fences at repelling elephants, we considered elephant movements in both directions (i.e., both exits and returns) in the analysis. We used the relative proportion of river crossings that occurred at “no fence” locations during each of the two years to establish the expected value for the analysis, and used a Pearson's Chi-squared test with Yates' continuity correction (Yates, 1934) to test for differences from that expectation at each of the fence locations between 2016 (no fences present) and 2017 (fences present). Statistical significance was determined based on  $\alpha \leq 0.05$ . Some zeros were present in our contingency table, and so we also analyzed our data using Fisher's exact tests; results did not differ qualitatively between the two tests. For the second contingency table analysis, we used data from monitor reports and camera traps to calculate the number of times elephants approached each of the 13 fenced crossing locations during the two-week period prior to

fence construction and the 3-month period after fence construction during 2017. At each location we determined the proportion of the total approaches that resulted in a river crossing versus a return to the Park (Table 2.2), and these data were subsequently analyzed in a contingency table with a Chi-squared test.

## Results

Of 1,662 conflict events reported by the enumerators, 1,655 (99.5%) involved crop damage, and of those, 14 (0.84%) also involved damage to a storehouse and 6 (0.36%) involved damage to a water tank. Elephants were responsible for 86% of the reported crop-raiding events; other species that caused crop damage included Cape buffalo (11%), hippos (1.2%), birds (0.96%), monkeys (0.42%), and rats (0.42%; Fig. 2.5). During the course of our study, enumerators reported 5 wildlife-related human injuries (3 caused by crocodiles and 2 by Cape buffalo) and 6 human deaths (4 caused by crocodiles and 2 by elephants).

After using the “no fence” crossing locations to establish a baseline expectation for the number of elephant river crossings that would be expected to occur at each crossing point if no fences had been constructed in 2017 (Table 2.1), we found that crop-raiding behavior by elephants was significantly altered by our mitigation experiment. Both beehive fences ( $\chi^2 = 8.32$ ,  $df = 1$ ,  $P < 0.01$ ; Table 2.1) and chili fences ( $\chi^2 = 15.03$ ,  $df = 1$ ,  $P < 0.001$ ; Table 2.1) significantly reduced the number of river crossings that occurred at locations with those fence types in 2017. In contrast, the number of river crossings occurring at locations with spicy beehive fences, fake beehives or fake chili fences did not differ significantly ( $P > 0.05$ ) from values expected in the absence of fences (Table 2.1).

Our analysis of elephant behavior (i.e., crossed the river versus returned to the Park) at key crossing locations pre- versus post-fence construction in 2017 revealed that all fences, including both control types, significantly increased the proportion of river approaches that ended with elephants returning to the Park (Table 2.2). The magnitude of this effect was greatest for the beehive fences, followed by the spicy beehive and fake beehive (beehive control) fences (Table 2.2).

## **Discussion**

Our study evaluated the effectiveness of different fence types for altering crop-raiding behavior by elephants at a major human-wildlife interface in Mozambique. Our results demonstrated that although the total number of river crossings did not differ significantly between 2016 and 2017 (i.e., pre- versus post-treatment), the distribution of crossings along the river shifted strongly toward non-fenced locations in 2017. Although both beehive and chili-based fences were effective, fences that utilized bees were especially useful for deterring elephants from crossing into cultivated croplands. These results are similar to previous studies that tested the use of beehive fences (e.g., King, Lawrence, Douglas-Hamilton, & Vollrath, 2009) or chili fences (e.g., Chang'a et al., 2016) around individual farms. To our knowledge, however, no previous study has tested the use of elephant deterrents in the form of fences at key crossing locations between natural and cultivated landscapes. In addition, our study is among the first to utilize both a rigorous BACI design and a combination of animal- and community-based data streams (e.g., GPS locations from crop-raiding elephants, camera traps, and quantitative reports from trained community members) to experimentally test the effectiveness of multiple strategies



(including one novel strategy, the spicy beehive fence) for deterring elephants from crop raiding.

In the majority of raiding events, elephants that approached any of the fence types did not cross through the fences. Instead they either returned to the Park or moved to a different location (generally one with no fence) to cross. Surprisingly, all fence types had some deterrent effect (including control fences that lacked the putative mechanisms for deterrence), providing support for our first hypothesis that overall use of crossing points by elephants would decline after fences were constructed. Photos and video from camera traps indicated that elephants were, in general, cautious in their interactions with the fences, likely because they represented an unexpected change in the landscape they were accustomed to. This observation, although admittedly anecdotal, likely explains why even control fences had some level of impact on crop-raiding behavior. Nevertheless, prior research has demonstrated that elephants quickly habituate to harmless mitigation methods (O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000), and thus we suspect that this effect would likely attenuate in a short time.

Only one successful crossing occurred at the beehive fences after hive occupation was >60%. Hive occupation is the most critical factor determining the success of beehive fences (King, Lala, Nzumu, Mwambingu, & Douglas-Hamilton, 2017), and our beehives reached 94% hive occupation only 7 weeks after deployment. To facilitate occupation, hives should have a roof to provide shade, the entrance should be protected from direct wind, and hives must be cleaned regularly. Because some of our hives remained unoccupied for several days, daily cleaning was an important part of the maintenance performed by the monitors. In the absence of such maintenance empty hives quickly become occupied by

snakes, rodents, or insects other than bees. Water also is critical for bees, and the proximity of our beehives to the Pungue River likely helped to facilitate the high level of hive occupation observed in our study.

Elephants approaching chili fences crossed more often (64%) than they returned to the Park (36%). Thus, although this fence type did significantly reduce the number of raids relative to crossing points without fences, our chili fence design did not prove as effective as we expected. Several factors could have influenced this result. For example, chili fences demand considerably more maintenance than beehive fences to retain maximum effectiveness. It is critical to ensure that the concentration of chili powder is consistently high enough to cause irritation in the nasal tissue of elephants that touch the fence with their trunks. To meet this requirement, it is necessary to re-dip ropes in the chili-oil mixture after every rain, and roughly every 3 weeks even in the absence of rain. Bamboo poles must be stable and the chili ropes must be tight so that elephants are not able to easily step over them. Although monitors attempted to maintain fences continuously this was not always possible due to weather conditions, logistical constraints, etc., which may have contributed to the reduced effectiveness of this strategy in our study.

In our analysis of GPS location data from collared elephants, the construction of spicy beehive fences did not significantly reduce the number of raids relative to expectations at those sites, refuting our second hypothesis. Similarly, although spicy beehive fences did significantly increase the proportion of approaches that resulted in elephants returning to the Park (relative to expectations established at no-fence locations), this effect was not as strong as the effect of beehive fences alone. One explanation for this result is that the chili ropes connecting hives in the spicy beehive fences were much heavier than the simple ropes used

to connect hives in the beehive fences. As a result these ropes sagged more, making it easier for elephants to simply step over them. With the chili fences it was possible to tie the ropes very tightly to the bamboo poles. In contrast, with the spicy beehive fences it was necessary to leave the chili ropes somewhat loose to keep them from pulling the hives sideways. Improving the design of this strategy by keeping ropes at a level that prevents elephants from stepping over them would likely increase its effectiveness.

Perceptions of our project among community members generally were very positive, and this undoubtedly played a critical role in the success of our efforts. For example, camera traps in our study were affixed to bamboo poles without cable locks or other security devices in plain view, and yet no cameras were stolen or damaged (although one SD card was removed) during our 3-month experiment. Community members regularly commented on how helpful the fences were, and how much safer the fences made them feel. The general perception of the fences among community members was that even the relatively small number of fences made an important difference and contributed to their livelihoods in measurable ways. This level of buy-in from the communities was a critical component of our project, which likely would have been impossible without it. The biological and social science components of HEC are inseparable, and we strongly encourage future researchers studying HEC to fully integrate the people, perspectives, and concerns of local communities into their efforts. Ultimately the perceptions and choices of local people influence the potential for coexistence with wildlife at least as much as rigorous scientific research, and effective conservation of wildlife thus requires careful consideration of such human dimensions.

**Literature Cited**

- Ahlering, M. A., Millspaugh, J. J., Woods, R. J., Western, D., & Eggert, L. S. (2011). Elevated levels of stress hormones in crop-raiding male elephants. *Animal Conservation*, 14, 124-130. doi:10.1111/j.1469-1795.2010.00400.x
- Chang'a, A., de Souza, N., Muya, J., Keyyu, J., Mwakatobe, A., Malugu, L., ... Olson, D. (2016). Scaling-up the use of chili fences for reducing human-elephant conflict across landscapes in Tanzania. *Tropical Conservation Science*, 9(2), 921-930.
- Chiyo, P. I., Cochrane, E. P., Naughton, L., & Basuta, G. I. (2005). Temporal patterns of crop raiding by elephants: A response to changes in forage quality or crop availability? *African Journal of Ecology*, 43(1), 48-55.
- Chiyo, P. I., Moss, C. J., Archie, E. A., Hollister-Smith, J. A., & Alberts, S. C. (2011). Using molecular and observational techniques to estimate the number and raiding patterns of crop-raiding elephants. *Journal of Applied Ecology*, 48(3), 788-796. doi: 10.1111/j.1365-2664.2011.01967.x
- De Boer, M., & Baquete, D. (1998). Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique. *Environmental Conservation*, 25(3), 208-218.
- Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, 13, 458-466. doi:10.1111/j.1469-1795.2010.00368.x
- Garrouette, E. L., Hansen, A. J., & Lawrence, R. L. (2016). Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. *Remote Sensing*, 8(5), 1-25. doi: 10.3390/rs8050404.

- Gordon, I. J. (2009). What is the Future for Wild, Large Herbivores in Human-Modified Agricultural Landscapes? *Wildlife Biology*, 15(1), 1-9. <https://doi.org/10.2981/06-087>
- Graham, M. D., & Ochieng, T. (2008). Uptake and performance of farm-based measures for reducing crop raiding by elephants *Loxodonta africana* among smallholder farms in Laikipia District, Kenya. *Oryx*, 42(1), 76-82. doi: 10.1017/S0030605308000677
- Haule, K. S., Johnsen, F. H., Maganga, S. L. (2002). Striving for sustainable wildlife management: the case of Kilombero Game Controlled Area, Tanzania. *Journal of Environmental Management* 66, 31–42. doi:10.1006/jema.2002.0572
- Hedges, S., & Gunaryadi, D. (2010). Reducing human–elephant conflict: do chillies help deter elephants from entering crop fields? *Oryx*, 44(1), 139-146.  
doi:10.1017/S0030605309990093
- Hoare, R. E. (1995). Options for the control of elephants in conflict with people. *Pachyderm*, 19, 54-63.
- Hoare, R. E. (1999). Data collection and analysis protocol for human-elephant conflict situations in Africa. UICN African Elephant Specialist Group' Human-elephant conflict working group.
- Karidozo, M., & Osborn, F. V. (2005). Can bees deter elephants from raiding crops? An experiment in the communal lands of Zimbabwe. *Pachyderm*, 39, 26-32.
- Kagoro-Rugunda, G. (2004). Crop raiding around Mburo National Park, Uganda. *African Journal of Ecology* 42, 32–41.
- King, L. E., Lawrence, A., Douglas-Hamilton, I., & Vollrath, F. (2009). Beehive fence deters crop-raiding elephants. *African Journal of Ecology*, 47, 131-137.

- King, L. E., Lala, F., Nzumu, H., Mwambingu, E., & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conservation Biology*, 31(4), 743-752. doi: 10.1111/cobi.12898
- Madden, F. (2004). Creating Coexistence between Humans and Wildlife: Global Perspectives on Local Efforts to Address Human–Wildlife Conflict. *Human Dimensions of Wildlife*, 9, 247–257. doi: 10.1080/10871200490505675
- Middleton, A. D., Kauffman, M. J., Mcwhirter, D. E., John, G., Cook, R. C., Nelson, A. A., ... Klaver, R. W. (2017). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, 94(6), 1245-1256.
- Naughton-treves, L. (2015). Predicting patterns of crop Damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, 12(1), 156-168.
- Norton-Griffiths, N., Said, M. Y., Serneeels, S., Kaelo, D. S., Coughenour, M., Lamprey, R. H., Thompson, D. M. & Reid, R. S. (2008). Land use economics in the Mara area of the Serengeti ecosystem. In: Sinclair, A.R.E., Packer, C., Mduma, S.A.R. & Fryxell, J.M. (Eds.), *Serengeti III. Human impacts on ecosystem dynamics* (pp. 379–416). Chicago, IL: Chicago University Press.
- Nyhus, P. J., Tilson, R., & Sumianto (2000). Crop raiding elephants and conservation implications at Way Kambas Nat Park, Sumatra, Indonesia. *Oryx*, 34(4), 262-274.
- O'Connell-Rodwell, C. E., Rodwell, T., Rice, M., & Hart L.A. (2000). Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation*, 93, 381-391.

- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*, 278(1), 1-14.
- Osborn, F., & Parker, G. (2002). Living with Elephants II - A manual for implementing an integrated programme to reduce crop loss to elephants and to improve livelihood security, MZEP, 37 Lewisam Ave, Chisipite, Harare, Zimbabwe. 21 pages typescript.
- Osborn, F. V. & Hill, C. M. (2005). Techniques to reduce crop loss: human and technical dimensions in Africa. In: R. Woodroffe, S. Thirgood & A. Rabinowitz (Eds.), *People and Wildlife: Conflict or Coexistence?* (pp. 72-85). Cambridge, UK: Cambridge University Press.
- Sikes, R. S. & the Animal Care and Use Committee. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663-688. doi:10.1093/jmammal/gyw078
- Sitati, N. W., Walpole, M. J. (2006). Assessing farm-based measures for mitigating human-elephant conflict in Transmara District, Kenya. *Oryx*, 40(3), 279-286. doi:10.1017/S0030605306000834
- Sitati, N. W., Walpole, M. J., Smith, R. J., & Leader-Williams, N. (2003). Predicting spatial aspects of human and elephant conflict. *Journal of Applied Ecology*, 40, 667-677.
- Stalmans, M. (2012). Monitoring the recovery of wildlife in the Parque Nacional da Gorongosa through aerial surveys. A preliminary analysis. Gorongosa National Park.
- Strassburg, B. B. N., Latawiec, A. E., Barioni, L. G., Nobre, C. A., da Silva, V. P., Valentim, J. F., ... Assad, E. D. (2014). When enough should be enough: Improving

the use of current agricultural lands could meet production demands and spare natural habitats in Brazil. *Global Environmental Change* 28, 84-97.

[Http://dx.doi.org/10.1016/j.gloenvcha.2014.06.001](http://dx.doi.org/10.1016/j.gloenvcha.2014.06.001)

Sukumar, R. (1990). Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, 6(1), 33-53.

Tchamba, M. (1996). History and present status of the human/elephant conflict in the Waza-Logone region, Cameroon, West Africa. *Biological Conservation*, 75, 35–41.

Thirgood, S., Woodroffe, R., & Rabinowitz, A. (2005). The impact of human–wildlife conflict on human lives and livelihoods. In: R. Woodroffe, S. Thirgood & A. Rabinowitz (Eds.), *People and Wildlife: Conflict or Coexistence?* (pp. 13-26). Cambridge, UK: Cambridge University Press.

Thouless, C. R. (1994). Conflicts between humans and elephants in northern Kenya. *Oryx*, 28, 119-127.

Tinley, K. L. (1977). Framework of the Gorongosa ecosystem. Gorongosa National Park.

Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human-wildlife conflicts: a review. *Human Dimensions of Wildlife*, 11(6), 383-396.  
doi: 10.1080/10871200600984265

Vazquez-Duhalt, R. (1989). Environmental impact of used motor oil. *Science of The Total Environment*, 79(1), 1-23.

Vines, A. (1991). *Renamo: terrorism in Mozambique*. Indiana University Press.

Vollrath, F., Douglas-Hamilton, I. (2002). African bees to control African elephants. *Naturwissenschaften*, 89, 508-511. doi:10.1007/s00114-002-0375-2



- Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005). The impact of human–wildlife conflict on natural systems. In: R. Woodroffe, S. Thirgood & A. Rabinowitz (Eds.), *People and Wildlife: Conflict or Coexistence?* (pp. 01-12). Cambridge, UK: Cambridge University Press.
- Wiafe, E. D., Sam, M. K. (2014). Evaluation of a low-tech method, pepper– grease, for combatting elephant crop-raiding activities in Kakum Conservation Area, Ghana. *Pachyderm*, 55, 38-42.
- Yates, F. (1934). Contingency Tables Involving Small Numbers and the  $\chi^2$  Test. *Supplement to the Journal of the Royal Statistical Society*, 1(2), 217-235.
- Zelen, M. (1971). The Analysis of Several  $2 \times 2$  Contingency Tables, *Biometrika*, 58(1), 129-137.

Figure 2.1. Study area in Gorongosa National Park, Mozambique. The Pungue River forms much of the southern boundary of the Park, where we conducted our experiment.

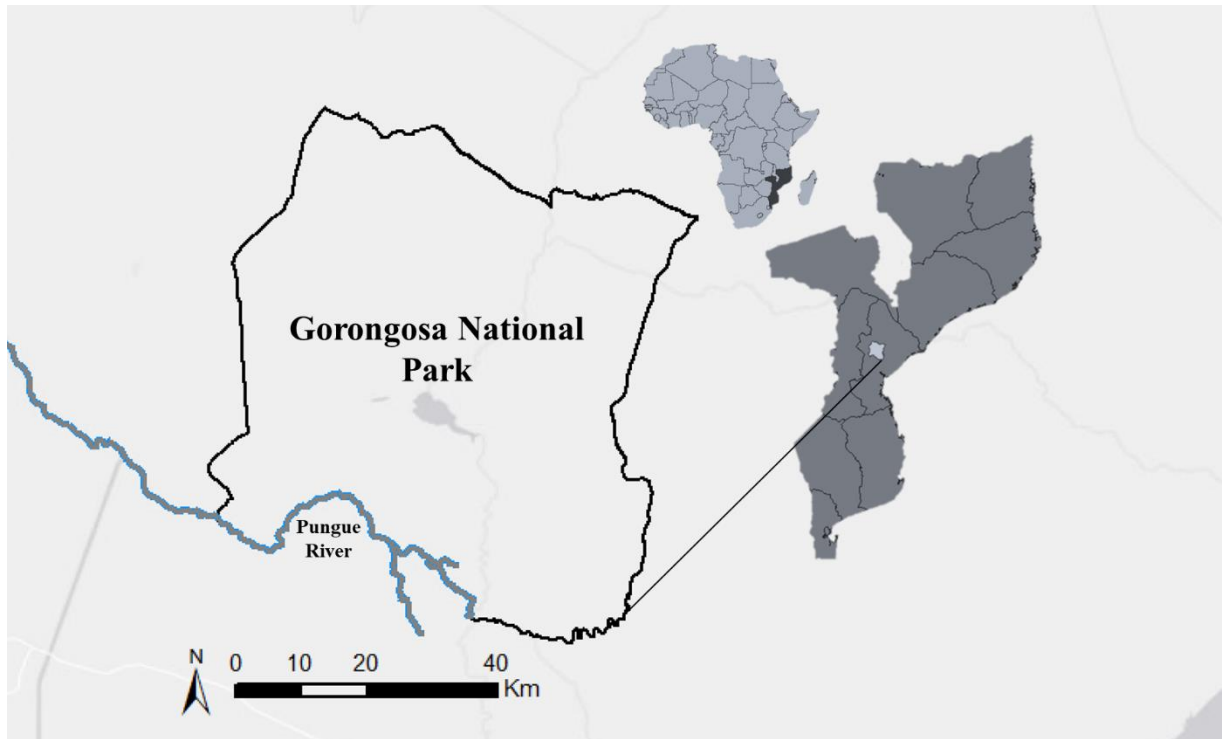


Figure 2.2. Meeting with one of the communities in the buffer zone of Gorongosa National Park to discuss the project.



Figure 2.3. Examples of elephant deterrent strategies evaluated in the buffer zone of Gorongosa National Park, Mozambique. (A) Chili fence; (B) Spicy beehive fence (beehive fences had the same design, but hives were connected by baling twine); (C) Fake chili fence (control); (D) Fake beehive fence (control).

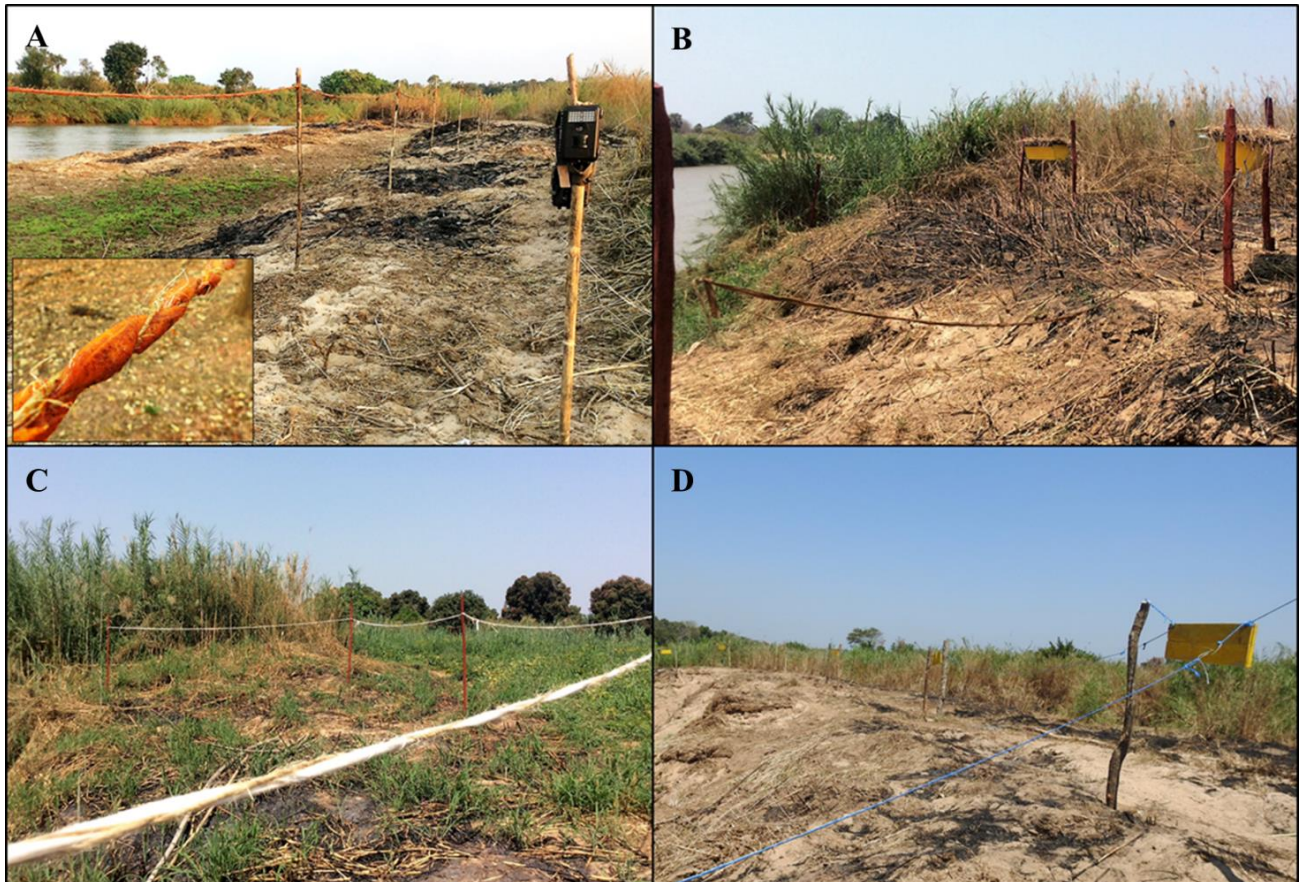




Figure 2.4. Utilization distribution derived from elephant GPS collar data showing the relative use of crossing points by collared elephants to access the communities in the buffer zone of Gorongosa National Park. Plus symbols (+) illustrate key crossing locations identified by local community members. Arrows show the 13 locations selected for our experiment.

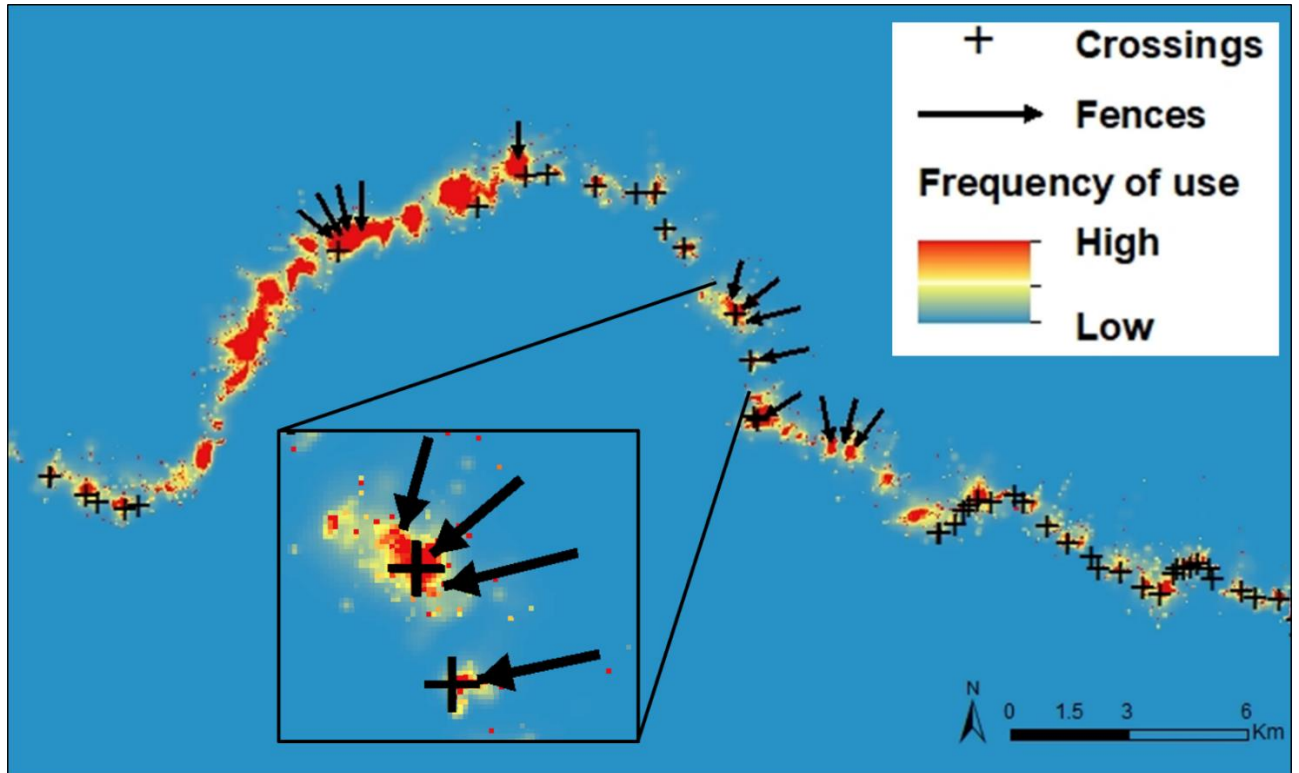


Figure 2.5. Number of crop-raiding events by different species between August 2016 and December 2017 in the buffer zone surrounding Gorongosa National Park, Mozambique.

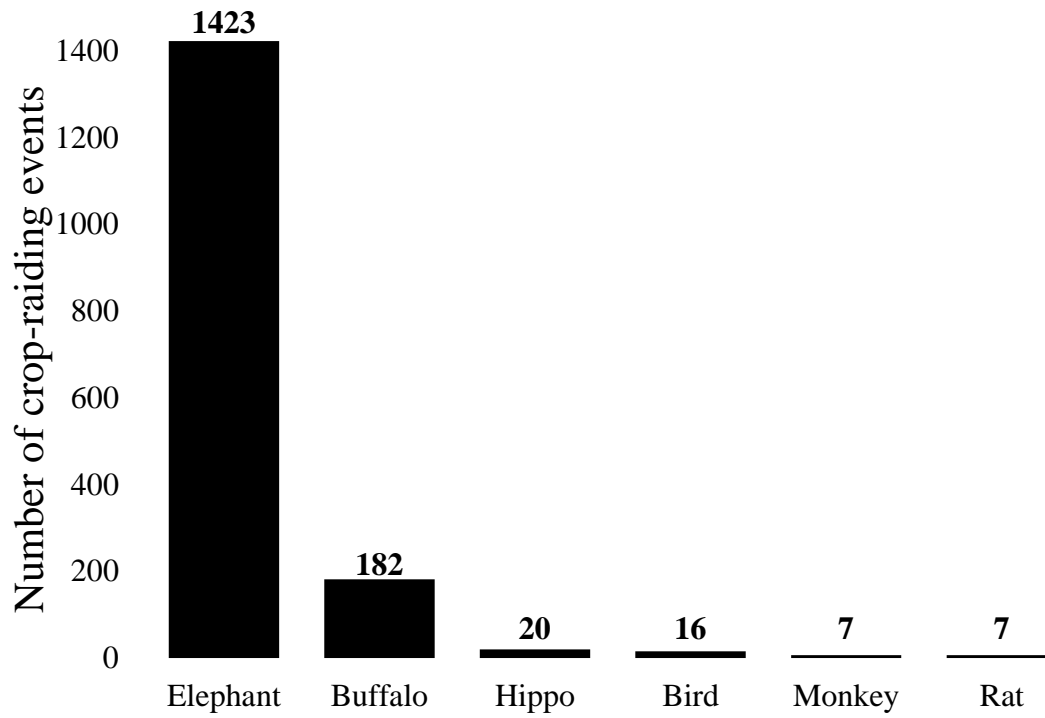


Table 2.1. Observed and expected number of river crossings by elephants in each location before (2016) and after (2017) deterrent fences were constructed, and the respective coefficients for the Chi-squared test, based on GPS collar data.

Fence type (with 30 m buffer)	Number of raids				$\chi^2$	<i>df</i>	<i>P</i>
	2016 (before the fences)		2017 (with the fences)				
	Observed	Expected	Observed	Expected			
Beehive	10	4.95	0	5	8.320	1	< 0.010
Chili	26	14.99	4	15.01	15.035	1	< 0.001
Spicy beehive	9	5.93	3	6.07	2.221	1	0.136
Beehive control	5	2.47	0	2.53	3.312	1	0.068
Chili control	6	5.41	5	5.58	0.002	1	0.959
No fence	709	-	732	-			

Table 2.2. Observed and expected number of elephant approaches in each fence type, with the number of times when they “crossed” versus “returned”, and the associated test statistics and *P*-values for the Chi-squared test, based on community reports (monitors) and camera trap data.

Fence type	Elephant approaches						$\chi^2$	<i>df</i>	<i>P</i>
	Total	Crossed		Returned					
		Observed	Expected	Observed	Expected				
Beehive	22	1	14.4	21	7.5	52.622	1	< 0.001	
Chili	80	51	60.5	29	19.5	16.778	1	< 0.001	
Spicy beehive	31	9	21.3	22	9.74	37.137	1	< 0.001	
Beehive control	12	3	9.9	9	2.1	30.545	1	< 0.001	
Chili control	16	5	12.8	11	3.2	29.356	1	< 0.001	
No fence	39	39	-	0	-				



## Appendix. IACUC Protocol.

10/6/2015

University Research Office Regulatory Compliance System


**University of Idaho  
Institutional Animal Care and Use Committee**

**Date:** Tuesday, October 6, 2015  
**To:** Ryan Long  
**From:** University of Idaho  
Institutional Animal Care and Use Committee  
**Re:** Protocol 2015-39  
The Elephants of Gorongosa: An Integrated Approach to Conservation and Conflict Mitigation in the Shadow of War

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on Tuesday, October 6, 2015.

This protocol was originally submitted for review on: Friday, September 4, 2015  
The original approval date for this protocol is: Tuesday, October 6, 2015  
This approval will remain in affect until: Thursday, October 6, 2016  
The protocol may be continued by annual updates until: Saturday, October 6, 2018

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.



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Barrie Robison, IACUC Chair