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Determinants of elephant foraging behaviour in a coupled human-natural system: Is brown the new green?

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Abstract

1. Crop raiding by wildlife poses major threats to both wildlife conservation and human well-being in agroecosystems worldwide. These threats are particularly acute in many parts of Africa, where crop raiders include globally threatened megafauna such as elephants, and where smallholder agriculture is a primary source of human livelihood. One framework for understanding herbivore feeding behaviour, the forage-maturation hypothesis, predicts that herbivores should align their movements with intermediate forage biomass (i.e., peak green-up); this phenomenon is known as "surfing the green wave." Crop-raiding elephants, however, often consume not just foliage, but also fruits and tubers (e.g., maize and potatoes), which generally mature after seasonal peaks in photosynthetic activity. Thus, although elephants have been reported to surf the green wave in natural habitats, they may utilize a different strategy in cultivated landscapes by selecting crops that are "browning down."

2. We sought to understand the factors that underpin movement of elephants into agricultural landscapes.

3. In Mozambique's Gorongosa National Park, we used movement data from GPS-collared elephants, together with precipitation records, remotely sensed estimates of landscape greenness (NDVI), DNA-based diet analysis, measurements of plant nutritional quality and survey-based metrics of crop availability to understand spatiotemporal variation in elephant crop-raiding behaviour.

4. Elephants tracked peak NDVI while foraging inside the Park. During the dry season, however, when NDVI within the Park declined and availability of mature crops was high, crop raiding increased dramatically, and elephants consistently selected crop plants that were browning down while foraging in cultivated landscapes. Crops contained significantly higher digestible energy than wild food plants, but comparable (and sometimes lower) levels of digestible protein, suggesting that this foraging strategy maximized energy rather than protein intake.

5. Our study is the first to combine GPS tracking data with high-resolution diet analysis and community-based reporting of crop availability to reveal fine-scale plasticity in foraging behaviour of elephants at the human–wildlife interface. Our results extend the forage-maturation hypothesis by showing that elephants surf

waves of plant brown-down in cultivated landscapes. These findings can aid efforts to reduce human–elephant conflict by enabling wildlife managers to prioritize mitigation actions in time and space with limited resources.

1 | INTRODUCTION

Over the past century, natural habitats have been converted into cultivated croplands at an unprecedented rate to provide food for a growing human population (Osborn & Hill, 2005; Woodroffe, Thirgood, & Rabinowitz, 2005). As a result, crop raiding (in which plants cultivated for human consumption are consumed by wild animals) now poses a significant threat to wildlife management and conservation, and to human livelihoods, in many parts of the world. Conover (2001) 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 (Emerton, 2001). Wildlife may be attracted to agricultural lands for various reasons; for example, crops may be more nutritious (Sukumar, 1990), contain lower levels of toxins or secondary metabolites (Osborn & Hill, 2005), and/or have lower fibre content (Hoare, 1999a) than wild plants. Accordingly, the presence of agricultural lands can significantly alter the foraging behaviour of herbivores (e.g., Fox & Abraham, 2017).

Understanding the mechanisms that underpin movement of wildlife into agroscapes is essential for developing effective mitigation strategies. For many large herbivores, phenological changes in plant nutrient content play a strong role in determining the timing and frequency of crop-raiding behaviour (Chiyo, Cochrane, Naughton, & Basuta, 2005; Osborn, 2004). For example, in the Greater Yellowstone Ecosystem, USA, high-quality forage can be up to 200% more abundant in irrigated agricultural fields than in the surrounding grasslands (Garroutte, Hansen, & Lawrence, 2016), and the frequency of crop raiding by elk (*Cervus canadensis*) tends to peak when this difference is greatest (Jones et al., 2014). Such patterns are thought to arise because plants cultivated for human consumption are more digestible than natural forages and because herbivores prefer to consume plants at early phenological growth stages that are more digestible and hence maximize net energy intake from foraging (Bischof et al., 2012). The forage-maturation hypothesis (FMH) posits that herbivore movements at multiple scales, from steps to migration, are driven by this preference (Fryxell, 1991; Hebblewhite, Merrill, & McDermid, 2008). Predictions of the FMH have been supported in both natural and agricultural landscapes for herbivores that feed primarily on foliage and stems, such as elk and bison (*Bison bison*; Middleton et al., 2017; Sigaud et al., 2017).

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 (Aikens et al., 2017; Merkle et al., 2016); this phenomenon has been termed "surfing the green wave" (Bischof et al., 2012; van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006). Because forage biomass and quality tend to be inversely correlated (Hebblewhite et al., 2008) and forage intake declines at low biomass, intermediate forage biomass represents an optimal balance between forage quality and availability for many herbivores (Fryxell, 1991). Indeed, a wide variety of herbivores, from ungulates (Rivrud, Heurich, Krupczynski, Müller, & Mysterud, 2016) to giant pandas (*Ailuropoda melanoleuca*; Wang et al., 2010) and birds (van der Graaf et al., 2006), have been shown to surf the green wave when foraging in natural habitats. Some large mammals, however, including elephants (*Loxodonta africana*, *Elephas maximus*), buffalos (*Syncerus caffer*), hippos (*Hippopotamus amphibius*), baboons (*Papio* spp.) and wild suids (Kendall, 2011), often consume fruits and tubers when foraging in cultivated landscapes, and thus, the FMH may be less useful for predicting spatiotemporal variation in crop-raiding behaviour by these species. Fruit ripening generally occurs after the peak in photosynthetic activity (i.e., the peak in green biomass) when plants have begun to senesce and minerals and nutrients have been mobilized and translocated to the maturing fruit (or storage organ) from vegetative parts that will soon die off. Thus, crop-raiding herbivores that consume fruits might benefit more from tracking later phenological stages of plant growth than from surfing the green wave.

African elephants, the largest extant land mammal, typically spend ~75% of the day foraging (Wyatt & Eltringham, 1974) and can consume up to 1.8% of their body weight (~100 kg for an adult male) in dry matter daily (Dierenfeld, 1994). In their native environments, elephants act as a keystone species by toppling and smashing trees and shrubs that are otherwise inaccessible to smaller browsers, which increases the availability of food and refuge for various species (Coverdale et al., 2016; Pringle, 2008; Pringle et al., 2015). In agricultural landscapes, however, elephants can consume or trample vast amounts of cultivated crops in a single raiding event (Naughton-treves, 1998). For example, villagers in Ghana reported that a herd of six elephants could destroy half of a 3-acre farm in one night (Sam, Ayesu, Agbenu, Kumordzi, & Wilson, 2003). As a consequence, many elephants are killed or injured by people each

year while crop raiding (Moss, 2001), and human injuries and fatalities also are frequent (King, Fredrick, Hesron, Emmanuel, & Douglas-Hamilton, 2017).

Elephants are generalist foragers with diverse diets that include grasses, forbs, fruits, bark, leaves, twigs and roots (Sukumar, 2003). Due to the unique morphology and physiology that accompanies their enormous body size (e.g., high potential cropping rates, long retention times and low mass-specific metabolic rate; Peters, 1983; Owen-Smith, 1988), energy intake by elephants is far more likely to be constrained by their rate of forage intake than by forage quality (Wilmhurst, Fryxell, & Bergman, 2000). This constraint, in combination with the positive relationship between cropping rate and forage biomass (Gross, Shipley, Hobbs, Spalinger, & Wunder, 1993; Illius & Gordon, 1987), suggests that elephants and other megaherbivores should select forage plants at peak rather than intermediate biomass (Owen-Smith, 1988). Indeed, when foraging in agricultural landscapes, 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). This suggests that elephant foraging behaviour in cultivated landscapes may diverge from predictions of the FMH if elephants select crops that are "browning down." To date, this possibility has not been tested, and the degree to which elephants are able to increase energy intake by selecting food plants at different phenological growth stages as they move between natural and cultivated landscapes is unknown.

From 2015 to 2017, we studied patterns of crop raiding by elephants in and around Gorongosa National Park (GNP), Mozambique, where the elephant population is increasing following decimation by a 15-year civil war that ended in 1992 (Daskin, Stalmans, & Pringle, 2016; Pringle, 2017). The Park is surrounded by subsistence-farming communities, particularly along its southern border (the focal area of our study), where the Pungue River provides an important water resource for both animals and people. Our aim was to identify the mechanisms that drive spatiotemporal variation in the frequency of crop raiding by elephants. We hypothesized that because elephants are wide-ranging generalist foragers capable of adjusting their behaviour to variation in the nutritional landscape at multiple scales, crop raiding would be strongly related to seasonal changes in the distribution and quality of forages inside versus outside of the Park. We predicted (P1) that crop raiding would occur more frequently when the decline in quality of natural forages inside the Park (driven by highly seasonal precipitation patterns) coincided with the maturation of crops outside the Park. We also predicted (P2) that when elephants were foraging inside the Park, they would track the wave of green-up (i.e., would select the greenest areas available), but that they 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 plants consumed by elephants within the Park during the dry season.
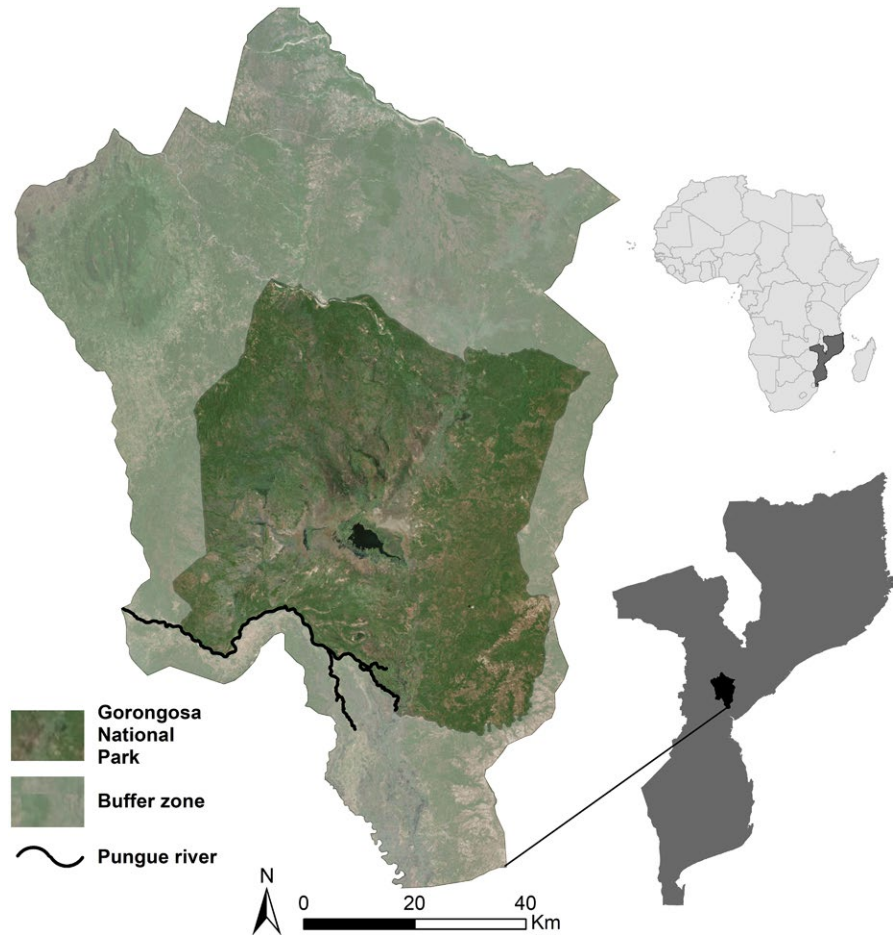
2 | MATERIALS AND METHODS

2.1 | Study area

In GNP (Figure 1), annual precipitation averages roughly 850 mm within the central Rift Valley where the vast majority of elephants reside, with rain falling mostly from November to March (Tinley, 1977). Temperatures 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-km² "buffer zone" where approximately 200,000 people, most of whom depend on subsistence farming, currently reside. A large number of those 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 1977, GNP was home to roughly 2,500 elephants. During the war, most of those elephants were killed to feed soldiers and to finance the purchase of arms through the sale of ivory (Vines, 1991); by the year 2000, the elephant population numbered <200 individuals (Stalmans, 2012). Elephants are currently recovering in GNP under the auspices of the Gorongosa Restoration Project, and the most recent aerial survey estimated a population of ≥650 individuals (Stalmans, Peel, & Gonçalves, 2018). Since the war, much of the current buffer zone has been converted to agricultural lands (Supporting information Appendix A; Figure A1). Consequently, as the elephant population has increased, so has the occurrence of human–elephant conflict in cultivated croplands outside the Park.

2.2 | Animal capture and location data

To quantify spatiotemporal patterns of crop raiding by elephants around GNP, we fitted 12 male elephants with high potential for crop-raiding behaviour (i.e., individuals that were captured in or in close proximity to crops) with GPS collars (Model AWT IM-SAT, Africa Wildlife Tracking, Pretoria, South Africa; weight = 14 kg). We collared six elephants in December 2015 and six in August 2016 (Supporting information Appendix B; Table B1). We programmed the collars to transmit locations every 30 min through the iridium satellite system for a period of 2 years. Each elephant was chemically immobilized via remote injection from a helicopter with a combination of thiafentanil oxalate (9–15 mg) and azaperone (40–60 mg), 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: 36–37°C), blood oxygenation (via a portable pulse oximeter) and 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 (the end of our study), 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

FIGURE 1 Map of the study area showing Gorongosa National Park, Mozambique, and the surrounding buffer zone, where approximately 200,000 people (mostly subsistence farmers) currently reside

guidelines established by the American Society of Mammalogists (Sikes & The Animal Care and Use Committee, 2016).

2.3 | 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 10 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 along 60 km of the Pungue River from August 2016 to January 2018. We paid enumerators full-time salaries and provided them 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 experiment, we also used these data (roughly 1,600

total reports) in the present study as an indicator of the availability of crop species through time. When a crop species was mentioned in daily enumerator reports ≥3 times during an 8-day period, we considered that crop to be available during that period. We used this operational definition to reduce the potential for false positives in the data (e.g., from errors in data recording) and to identify the primary periods when each crop was available to elephants. We validated our approach using data on planting periods and time to maturity for each crop species obtained from the agricultural technicians at GNP. The enumerator reports included 31 different types of crops, which we combined into four main groups for our analyses: maize, fruits, tubers and beans.

2.4 | NDVI and precipitation data

To track green-up in our study area across space and time, we calculated 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, is widely used as a proxy for vegetation phenology and above-ground net primary production (Pettorelli et al., 2005) and is highly correlated with standing plant biomass (Dancose, Fortin, & Guo, 2011). We set to "no data" pixels that were categorized as cloud, cloud shadow or snow

(14.5% of pixels) by the classification algorithm. We smoothed each time-series of NDVI data using a moving three-window median filter (Merkle et al., 2016). We then filled in the 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 outside the Park. We then summed precipitation values every 8 days throughout the study to match the temporal resolution of our NDVI data.

2.5 | Statistical analysis

To test the prediction that crop raiding would occur more frequently when declines in the quality of natural food plants inside the Park coincided with the maturation of crops outside the Park (P1), we used a parametric, recurrent time-to-event modelling framework (Hosmer, Lemeshow, & May, 2008) that quantified the effects of environmental and agricultural variables (crop availability, NDVI inside 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 min (which we defined as a raid event). We chose 30 min 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 a densely cultivated landscape (Figure A1). Our confidence in this operational definition is further bolstered by scrutiny of elephant movement patterns. With high regularity, elephants crossed the park boundary only at specific locations and times (almost invariably at night) and proceeded to areas where crops were evident in satellite imagery (formal classification of cropland vs. other human land uses would not be reliable due to traditional shifting-cultivation practices both within and between seasons). During longer forays (>1 night), elephants typically sheltered in thick cover during the day and then moved out into cultivated areas again at night.

To convert elephant location data into a time-to-recurrent-event framework, we collapsed GPS locations into a daily response variable that identified whether two-or-more consecutive elephant GPS locations were outside the Park's border. 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 time to an event (in this case, an elephant raid outside the Park) as a baseline hazard (parameterized by, in our case, a Weibull distribution) multiplied by the effects of a set of variables. Because multiple events occurred for each individual, we calculated robust standard errors using general estimating equations, which adjust *SEs* based on the assumption that events are correlated within an individual animal (Craiu, Duchesne, & Fortin, 2008). Hazard ratios quantify the relative effect of each covariate on the event variable (Hosmer et al., 2008).

For every 8-day window during the study period, we calculated, for each elephant, the mean NDVI of the portions 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 once 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 that they represented NDVI phenology (i.e., changes in relative greenness through time) 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 availability of bean crops from our analysis because they were highly correlated with availability of maize ($r = 0.94$), and maize is more prevalent than beans in the study area. We assessed relative empirical support for three variable groups (representing seven models): NDVI inside the Park, precipitation and crop availability (fruits, maize and tubers). Models were ranked using Akaike information criterion (Burnham & Anderson, 2002). All variables were scaled and centred 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 track vegetation greenness 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 (actual) target step using conditional logistic regression (Fortin et al., 2005). We fit separate movement models to data obtained inside versus outside the Park. 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. Movement data are inherently autocorrelated in time, and robust standard errors have been used to reduce the effects of such autocorrelation in step selection functions (Craiu et al., 2008; Fortin et al., 2005). The approach requires dividing observations into independent clusters, where data within a cluster are assumed to be correlated, and data among clusters are assumed to be independent (Craiu et al., 2008). Our data outside the Park fit such a framework because each "raid" event could be classified as an independent cluster (total of 2,207 clusters from 35,288 steps). Our data from inside the Park, however, do not fit the clustering framework as well because there are long sequences of steps without natural interruptions that could be classified as independent clusters. Thus, although we obtained a considerably larger sample of movements inside than outside the Park, we reduced pseudoreplication in our model of movements inside the Park by subsampling the data. We randomly selected 1 step and its associated available steps per day, per individual animal, per year in the analysis (*n* steps used to fit the model inside park = 6,114) and then specified only 12 clusters that represented each individual animal's movements. Both time-to-recurrent-event models and step selection functions were fit using the "survival" package in program R (v.3.4.1; R Core Team, 2017).

Our step selection functions evaluated the influence of distance to the Park boundary, NDVI and rate of change in NDVI on movement decisions by elephants inside and outside the Park. To test whether elephants more strongly selected forages that were greening up or browning down, we calculated the rate of change in NDVI from the nearest 8-day NDVI value to the date and time of each step. Rate of change in NDVI was calculated using a 3-value moving window and then scaling the resulting rates for a given pixel in a given year between −1 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), whereas negative values denote browning 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 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.

2.6 | 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 using DNA metabarcoding (Kartzinel et al., 2015; Pansu et al., 2019) of 21 fresh faecal samples collected inside GNP during the dry season (June–August) of 2016. We collected samples during immobilizations and also opportunistically after observing elephants defecating and then waiting for them to leave the area. Sample collection and processing followed protocols described by Pansu et al. (2019), and a detailed description of the metabarcoding protocol and analyses is provided in Supporting information Appendix C.
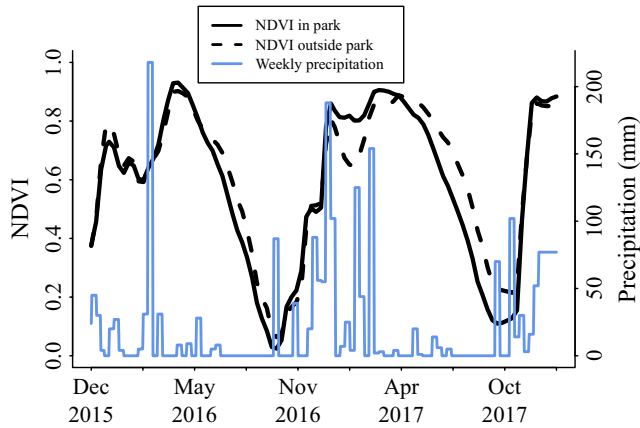
To estimate the nutritional quality of elephant diets at GNP when feeding on natural forages, we sampled 28 plant species consumed by elephants during the dry season (based on results of the diet analysis). We collected young, fully opened leaves and stems from at least three different individuals of each species. We then pooled those samples, dried them to a constant weight at 60°C, ground them in a Wiley Mill with a 1-mm screen and analysed them for % neutral detergent fibre (NDF), % acid detergent fibre (ADF), % lignin (ADL), % ash (AIA), % crude protein (CP) and gross energy (GE) (Dairy One Forage Lab, Ithaca, NY, USA). We then estimated digestible energy (DE) and digestible protein (DP) content by parameterizing the summative equations of Robbins, Mole, Hagerman, and Hanley (1987), and Robbins, Hanley, et al. (1987) with the assay results for each species. Similarly, we sampled all of the major crop species consumed by elephants outside the Park (based on enumerator reports) and estimated digestible energy and digestible protein content using the approach described for natural forages. Separate nutritional assays were conducted for different plant parts (e.g., fruit, leaves, roots and stem), and the majority of the fruits sampled were not yet ripe, likely making our results conservative (i.e., fully ripened fruits should be more digestible; hence, our analysis should underestimate the quality of crops relative to wild plants).

We combined data on diet composition with data on nutritional quality of forage plants to estimate the digestible energy and digestible protein content of elephant diets inferred from faecal samples. We included samples in this analysis only when ≥70% of the diet consisted of natural food plants for which we had data on digestible energy and digestible protein (*n* = 6). Only two of the six samples included in our analysis of natural-forage diet quality included cultivated plants, and in both instances, cultivated species comprised <2% of the diet. We calculated weighted averages of digestible energy and digestible protein for each sampled diet by using the proportional contribution of each plant species to the diet (as determined by faecal metabarcoding) as the weighting factor. We then estimated digestible energy and digestible protein of natural-forage, dry-season diets as the weighted average of digestible energy and digestible protein estimates across individual diet samples using the proportion of the diet accounted for (Supporting information Appendix C; Table C1) in each sample as the weighting factor. To test P3, we compared mean digestible energy and digestible protein of the main crop species consumed by elephants in the buffer zone to mean digestible energy and digestible protein (±95% CI) of natural-forage diets.

3 | RESULTS

We obtained an average of 44,827 locations (± 7,679 *SD*) for each of the 12 male elephants across the 17.4-month average duration of monitoring. From those data, we identified a total of 2,225 unique raiding events (mean of 172 per individual, *SD* = 77). On average, collared elephants crossed the Park boundary on 34% (± 12% *SD*) of the days in which they were monitored. A 100% minimum convex polygon estimated from our location data encompassed 2,004 km², with 72% of that area occurring inside the borders of GNP and 28% occurring outside. Seasonal home ranges for each collared elephant are shown in Supporting information Appendix B (Figure B1).

We observed marked seasonal and diel variation in the pattern of crop raiding. The frequency of raiding events increased steadily between June and September (mid-to-late dry season), peaked in September and October (late dry season), and declined again towards baseline wet-season levels in December (Supporting information Appendix D; Figure D1). During raiding events, 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 (Supporting information Appendix D; Figure D2). Mean duration of a raid was 8.3 hrs, although a few longer events (up to 200 hrs 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 in the agroscape outside the Park than inside the Park (Figure 2). In addition, there was considerable spatial heterogeneity in the timing of peak green-up within Park boundaries (i.e., locations within the Park that provided the greenest forage varied considerably through time; Supporting information Appendix E;

FIGURE 2 Mean NDVI of pixels within the portions of elephant home ranges (*n* = 12) that occurred inside versus outside the boundary of Gorongosa National Park, Mozambique, during 2016–2017, and the weekly values of precipitation
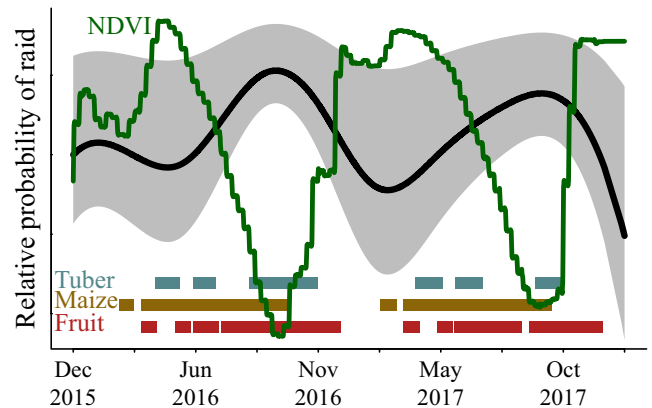
Figure E1), highlighting the potential for elephants to surf the green wave as they foraged within the Park.

The top model for predicting the timing of crop-raiding events by elephants included availability of fruits, maize and tubers, as well as NDVI inside the Park and precipitation. That model was well supported relative to other models, garnering >99% of the AIC weight (Supporting information Appendix F; Table F1), and indicated that elephants were more likely to remain within the Park when fruits and tubers were not available in the agroscape (Table 1). Higher NDVI and precipitation inside the Park also increased the probability of elephants remaining within Park boundaries (Table 1; Figure 3). 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 at least twice at large as other variables), highlighting the fundamental role of forage quality and availability as drivers of foraging behaviour and crop raiding by elephants.

Our analyses of step selection indicated that elephants generally selected areas that had high NDVI values (i.e., greener pixels) whether they were foraging inside or outside the Park (Table 2; Figure 4). We did not detect an influence of the rate of change in NDVI on movement within the park, whereas when elephants were foraging in croplands, they strongly selected areas with a negative rate of change in NDVI (Table 2; Figure 4). This suggests that when elephants were foraging in natural landscapes, they selected plants that were at or near peak greenness irrespective of whether those plants were greening up or browning down, but that they switched to selecting areas that were browning down when foraging in cultivated landscapes. Moreover, elephants often exhibited this plasticity at fine temporal scales (i.e., within a 24-hr period) as they moved between the Park and the surrounding agroscape. Elephants also chose steps that brought them closer to the Park boundary (i.e., the coefficient for distance to the Park was negative; Table 2). This effect was stronger when elephants were outside the Park than when they were inside the Park. However, when elephants did venture relatively far from the Park boundary during raiding events, the

TABLE 1 Standardized model coefficients (and associated *SE*s 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, during 2016–2017. 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 availability of fruits, maize and tubers outside the Park (dichotomously classified as available or not), NDVI inside the Park ($NDVI_{Park}$) and precipitation

Variable	Coefficient	SE	p
Fruit	−0.229	0.044	<0.01
Maize	−0.067	0.059	0.253
Tuber	−0.102	0.039	<0.01
$NDVI_{Park}$	0.207	0.034	<0.01
Precipitation	0.067	0.015	<0.01

FIGURE 3 Predicted relative probability of a crop-raiding event by elephants (*n* = 12) in Gorongosa National Park, Mozambique (black line), with 95% CI (grey), and NDVI in the Park (green), fruit availability (red), maize availability (brown) and tuber availability (blue) overlaid. Solid bars for crops indicate the presence of mature plants in the Park's buffer zone, whereas gaps indicate the absence of mature plants. Predictions were derived from a time-to-event model that quantified the relative effect of each covariate on the event variable (e.g., a raid) using GPS collar data

strength of their selection for locations closer to the Park boundary diminished (evidenced by statistical significance of the relevant interaction term; Table 2); this pattern generally was associated with raiding events that lasted >24 hr. During these longer raiding events, elephants typically remained in uncultivated patches of forest (often near the far edge of the buffer zone) during daylight hours rather than exiting and returning to the Park in the same night.

We detected 54 plant taxa (molecular operational taxonomic units, mOTUs) in the 21 elephant faecal samples analysed. Across all samples, the five most commonly consumed plant families were Fabaceae (legumes, 26.7%, with *Vachellia* [*Acacia*] spp. accounting for 11.5%), Poaceae (grasses, 20.1%, with *Phragmites mauritianus* and *Panicum* spp. each accounting for > 5%), Rhamnaceae (buckthorns, 12.9%, exclusively *Ziziphus* spp.), Malvaceae (mallows, 11.5%,

TABLE 2 Standardized coefficients (and associated robust *SE*s 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 during 2016–2017. 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	P
Crop	Distance to Park	−0.698	0.030	<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

exclusively *Grewia* spp.) and Arecaceae (palms, 7.2%). Other families represented ≤ 5% of the population diet. Four mOTUs matched cultivated plants: *Musa* sp. (banana, 4.5%), *Mangifera indica* (mango, 0.5%) and *Cajanus cajan* (pigeon pea, 0.25%); in addition, we identified *Sorghum* spp. (0.25%), which includes both native and cultivated plants in this system, along with an mOTU for which the DNA barcode is shared by a cluster of Poaceae species that includes maize (2.7% overall, 7% in samples from the collared individuals). Whereas these species occurred infrequently at the population level, they occurred at higher frequency in several individual diets (Supporting information Appendix C; Table C1).

Mean digestible energy and digestible protein content of natural-forage diets were 11.39 kJ/g and 11.5%, respectively (Figure 5). Of 17 crop plants (and constituent tissue types) analysed for digestible energy, 82% had values that exceeded the upper 95% confidence limit for natural-forage diets (Figure 5). In contrast, only 15% of crop samples had digestible protein values that exceeded the upper 95% confidence limit for natural-forage diets (Figure 5). Maize, sweet potatoes and bananas were the most frequently raided crops in the buffer zone of GNP (based on enumerator reports) and contained some of the highest levels of digestible energy recorded in our study (Supporting information Appendix G; Figure G1).

4 | DISCUSSION

Our results provide some of the most comprehensive evidence to date of the fundamental role of forage availability and quality as drivers of foraging behaviour by crop-raiding elephants (Chiyo et al., 2005). Consistent with our first prediction, the presence of
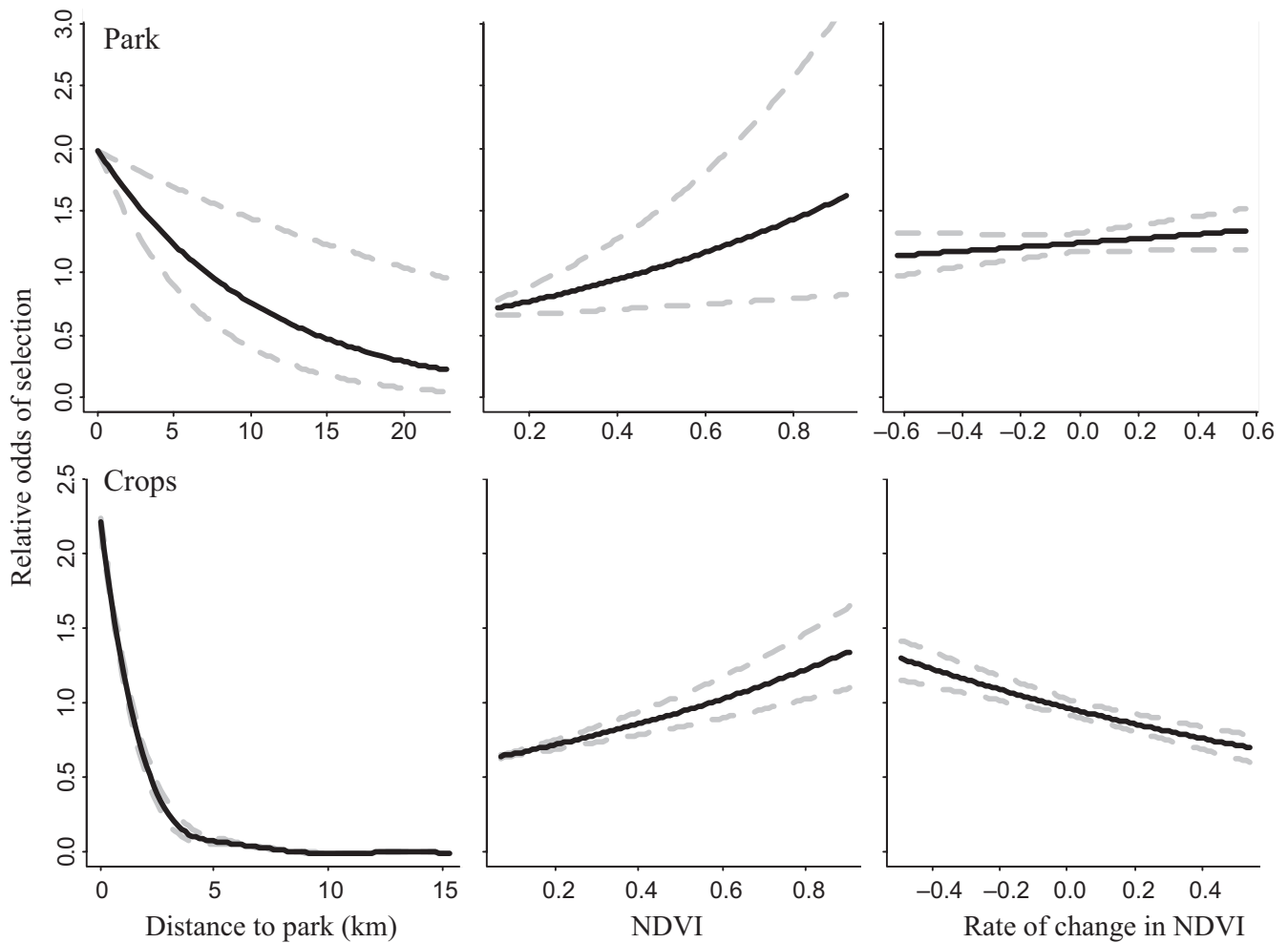
mature fruits outside GNP significantly increased the probability of crop raiding, whereas higher NDVI values inside the Park (generally associated with greater quality and abundance of natural forages; Pettorelli et al., 2005) had the opposite effect. Under current conditions and agricultural practices in and around GNP, as well as in many other parts of Africa, the highest quality forage in croplands becomes available at around the same time that forage quality in the Park is near its nadir. Future efforts to mitigate human–elephant conflict could incorporate this information into agricultural and management plans to reduce the intensity and impact of conflict.

A central tenet of the FMH is that herbivores track forage at intermediate biomass by selecting patches that are greening up and at intermediate NDVI values (Bischof et al., 2012). Our results are therefore inconsistent with the FMH as currently formulated. Elephants did not select areas of intermediate NDVI; instead, they consistently selected areas where plants were at later phenological growth stages than predicted by the FMH (i.e., at or shortly after peak NDVI) both inside and outside of the Park. This result might be explained in part by the fact that elephants are large-bodied bulk feeders (Owen-Smith, 1988) that must continually process large volumes of plant material to meet their nutritional needs (sensu Wilmhurst et al., 2000). Because these requirements are the same for elephants everywhere, we hypothesize that elephants can generally be expected to track peak forage biomass (which typically occurs simultaneously with, or even slightly later than, peak NDVI; Garroutte et al., 2016) in space and time. Moreover, in partial support of our second prediction, elephants foraging in cultivated croplands selected areas with mature plants that were past peak greenness (i.e., plants that were browning down). Together, these results suggest that the FMH should be extended to include herbivores that eat large quantities of plant parts (and frequently entire plants) that mature after the peak in green biomass.

The rate of change in NDVI, which quantifies the instantaneous rate of green-up, 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 instantaneous rate of green-up 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). Along similar lines, our results suggest that for animals foraging heavily on fruits and tubers, particularly in cultivated landscapes, researchers and practitioners should also assess the influence of negative values of instantaneous rate of green-up (i.e., the rate of brown-down), as these can be important for predicting animal movement. Our analysis demonstrated behavioural plasticity among crop-raiding elephants that likely served to optimize energy intake from foraging in both natural and cultivated landscapes.

Similar to previous studies of crop-raiding behaviour by elephants (e.g., Naughton-treves, 1998; Thouless, 1994), the 12 bulls monitored during our study raided crops mostly at night, likely to reduce the risk of disturbance, injury or mortality associated with human encounters (Graham, Douglas-Hamilton, Adams,
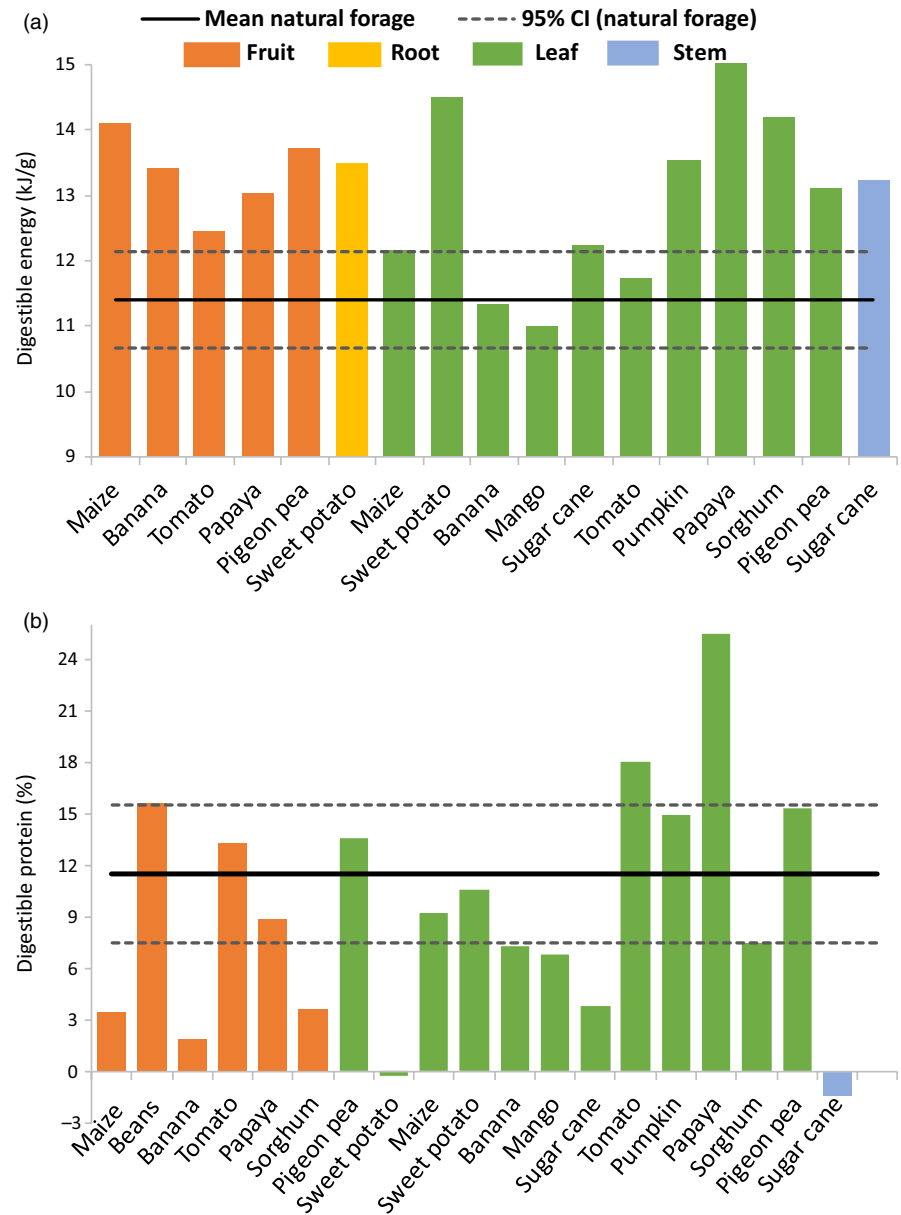
FIGURE 4 Influence of distance to the Park boundary, NDVI and the rate of change in NDVI on step selection by elephants (*n* = 12) in natural habitats (top panels) versus cultivated croplands (bottom panels) in and around Gorongosa National Park, Mozambique, during 2016–2017. Black lines depict the model-predicted influence of each variable on step selection with other variables held constant at their means, and dashed lines depict 95% CIs

& Lee, 2009). In addition, 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 contrasts with the results of some previous studies that have reported peaks in crop raiding by elephants associated with higher rainfall (e.g., Goswami, Medhi, Nichols, & Oli, 2015; Osborn, 2004; Sukumar, 2003). This discrepancy likely is at least partially related to ease of access to irrigation water in our study area. In the absence of a steady supply of water for irrigation, Hoare (1999b) reported that fewer raiding events occurred in a drought year because many crops failed to mature. In contrast, most crops in the buffer zone of GNP are grown in close proximity to the Pungue River, which provides a source of irrigation throughout the dry season. This effectively buffers communities to some degree against the risk of periodic drought and leads to a predictable phenology of crop cultivation along the Park's boundary; however, it might also increase the likelihood of catastrophic crop raiding during particularly vulnerable periods

such as dry seasons and drought years—a possibility that warrants further investigation.

Our results suggest that elephants dealt with the risks associated with crop raiding in more than one way. In addition to raiding mostly at night, 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, and could be due to other factors such as drinking and bathing). Similar to results reported by Sigaud et al. (2017) for bison, this pattern of behaviour served to put elephants in continuously 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). 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 (Figure A1). Consequently, 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, however, that the probability of an elephant moving towards the Park boundary during a crop-raiding event decreased

FIGURE 5 Mean (a) digestible energy (DE; kJ/g) and (b) 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. Dashed lines represent 95% CIs

further from the Park, and dropped off sharply ~4 km from the Park boundary, suggesting that after reaching a certain distance from the Park elephants may perceive it to be safer to remain outside the Park until the following night before returning to the Park. Indeed, local community members rarely reported diurnal elephant movements in croplands and noted that elephants sometimes used remnant forest patches (e.g., traditional cemeteries) as shelter during the day rather than returning to the Park immediately after a night of crop raiding. Collectively, these observations suggest that crop-raiding behaviour by elephants might be modified by altering their perception of the risks associated with that behaviour. For example, the presence of community members or Park scouts actively guarding the edges of the river during the night may cause elephants to avoid those areas. Similarly, fencing areas that provide ample concealment cover, such as cemeteries, might cause elephants to feel unsafe to spend the night or travel long distances outside the Park.

Previous studies have indicated that an adult elephant requires 8.3 kJ/g of digestible energy to maintain normal levels of growth, reproduction and survival probability (Benedict & Lee, 1938; Dierenfeld, 1994). Although natural forages in GNP met those requirements, elephants in our study likely still benefited considerably from crop raiding because of the significantly higher amount of digestible energy present in nearly all crop species relative to natural-forage diets (consistent with our third prediction). For example, maize fruits contained, on average, 14 kJ/g of DE, sweet-potato leaves 14.5 kJ/g and bananas 13.4 kJ/g, relative to an average of 11.39 kJ/g in natural-forage diets. Levels of digestible energy well beyond maintenance requirements may be especially beneficial to male elephants due to the advantages conferred by larger body mass in male–male competition for access to oestrous females (Rasmussen et al., 2008).

Herbivores often prefer diets high in DE, and this generality was clearly reflected in our results; maize, sweet potatoes and bananas

contained some of the highest levels of digestible energy recorded in our study and also were the most frequently raided crops in the buffer zone of GNP according to enumerator reports (Supporting information Appendix G; Figure G1). We also note that the difference in digestible energy between natural-forage diets and cultivated crops in our study was 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 levels of digestible energy if mature fruits would have been sampled. Second, our natural-forage samples were obtained in July and August of 2017, several months prior to the end of the dry season when digestibility of natural forages would have been at its lowest point. Third, our forage samples included only leaf material, whereas wild elephants are known to eat both the leaves and less-digestible stems of food plants. Together these features of our sampling suggest that the average difference in digestible energy between cultivated crops selected by elephants and natural-forage diets is probably even greater than what we observed. One important caveat is that we had no data on intake rates or handling times associated with different plant species or plant parts. However, the concentrated distribution of cultivated crops would likely serve to increase foraging efficiency and associated intake of DE, again suggesting that our results are conservative in this regard.

Similar to DE, mean digestible protein in natural-forage diets of elephants in our study (11.5%) met minimum physiological requirements reported by previous authors (Dierenfeld, 1994; Dougall & Sheldrick, 1964). In contrast to digestible energy (and contrary to our third prediction), however, seven of the 19 crops analysed had digestible protein values that fell within the 95% CI for natural-forage diets, and nine crops actually contained lower digestible protein than natural-forage diets. These results suggest that protein was not likely a major driver of crop raiding by elephants in GNP. Future studies analysing the micronutrient composition of crop plants and natural-forage diets might yield valuable complementary insights about other nutritional correlates of elephant foraging behaviour in coupled natural-human landscapes.

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 human–elephant conflict. GNP is currently in the tenth year of a multi-decade restoration, conservation and human-development project. 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 restoration and conservation because these conflicts directly or indirectly affect all of the project's main goals—and conflict will only intensify as elephant and human populations in this region continue to grow. This is an increasingly common scenario in protected areas throughout sub-Saharan Africa, and our study provides insights that can be used to guide wildlife and land managers in designing policies for mitigating human–elephant conflict and its impacts on human livelihoods and conservation outcomes. For example, the models we developed could be used to prioritize mitigation actions (e.g., the placement of beehive or chilli-pepper fences; King, Lawrence, Douglas-Hamilton, & Vollrath, 2009; King et al., 2017; Wiafe & Sam, 2014) in time and space by forecasting hotspots of elephant crop raiding as a function of NDVI, precipitation and crop availability. Such targeted efforts are critical for effectively and efficiently managing human–wildlife conflict along the boundaries of protected areas, most of which are subject to gross funding shortfalls (Lindsey et al., 2018). Within the constraints imposed by seasonal climatic variation and livelihood requirements, our models could also be used to inform the timing of planting by subsistence-farming communities. Our results suggest that where possible, increasing synchrony between peak green-up within protected areas and crop maturation outside their boundaries could reduce the overall occurrence of crop raiding by elephants.

AUTHORS' CONTRIBUTIONS

R.A.L., P.S.B. and M.S. conceived and designed the study; P.S.B., R.A.L., A.B.P. and A.R. conducted fieldwork; P.S.B. and J.A.M. conducted movement analyses; J.P., R.M.P., A.B.P. and R.A.L. conducted diet analyses; and P.S.B. and R.A.L. wrote the manuscript; other authors made significant contributions to the draft and approved it for publication.

DATA ACCESSIBILITY

All raw data included in our analyses are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6v5v88g (Branco et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.