Food preferences determine human–elephant coexistence in African woodlands

María Montero-Botey, Alfonso San Miguel and Ramón Perea

Abstract Human–elephant coexistence remains a major conservation and livelihood challenge across elephant *Loxodonta africana* range in Africa. This study investigates the extent of elephant crop damage on 66 farms in the Selous–Niassa corridor (Tanzania), to search for potential management solutions to this problem. We found that the relative abundance of highly preferred crops (area covered by preferred crops divided by the total area of each farm) was by far the most important factor determining crop damage by elephants. Eighteen crop types were ranked according to their preference by elephants. Sweet potatoes, bananas, peanuts, onions, pumpkins and maize were the most preferred crops, with maize the most common crop among those highly preferred. On average elephants damaged 25.7% of the cultivated farmland they entered. A beta regression model suggests that a reduction in the cultivation of preferred crops from 75 to 25% of the farmland area decreases elephant crop damage by 64%. Water availability (distance to the nearest waterhole) and the presence of private investors (mostly hunting tourism companies) were of lower importance in determining elephant crop damage. Thus, damage by elephants increased with shorter distances to waterholes and decreased in areas with private investors. However, further studies are required, particularly of the perceived costs and benefits of elephants to local communities. Farm aggregation and the use of non-preferred crops that also require less water would potentially reduce elephant damage but would be a major lifestyle change for some local communities.

Keywords Crop damage, human–elephant conflict, local communities, private investment, Tanzania, water availability, Wildlife Management Areas, woodland

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María Montero-Botey, Alfonso San Miguel and Ramón Perea (Corresponding author, orcid.org/0000-0002-2206-3614) Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, Ciudad Universitaria s/n. 28040 Madrid, Spain. E-mail ramon.perea@upm.es

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Introduction

Conflict between people and wildlife has been recognized as a global conservation issue (Woodroffe et al., 2005; Fisher, 2016). African elephants *Loxodonta africana* have coexisted with people for millennia but the growth of human populations and the extension of agriculture into rangelands and forests have brought humans and elephants into direct conflict (Hoare, 1999a; Pozo et al., 2017a). Elephants frequently cause widespread damage to agriculture and water supplies, and may injure or even kill local people, who often retaliate by killing the elephants concerned (Naughton-Treves, 1998; TAWIRI, 2010; Mariki et al., 2015). As a result, human–elephant coexistence entails serious challenges for managers, local communities and elephants (Sitati et al., 2003).

Crop damage (often referred to as crop raiding) is considered the most widespread form of damage caused by elephants (Hoare, 2000). Spatial patterns of crop damage by elephants have been associated with human population density (Newmark et al., 1994), the proportion of land cultivated (Sitati et al., 2003; Pozo et al., 2017a), topography (Smith & Kasiki, 2000; Wall et al., 2006), proximity to settlements and protected areas (Hoare, 1999a), and road networks (Sitati et al., 2003), among others. Elephant movements are determined by the availability and distribution of water and food (Grainger et al., 2005; Harris et al., 2008). Elephants are particularly attracted to ripe food crops (Chiyo et al., 2005), making small farms surrounded by savannah highly vulnerable to crop damage (Graham et al., 2010). Elephants do not damage all crops equally, and some are usually more affected than others (Naughton-Treves, 1998; Walpole et al., 2004). Direct feeding represents the main source of crop damage but uprooting and trampling are also common (Gross et al., 2016). Some studies have determined elephant preferences for crops, in terms of the amount taken per unit area planted at a regional scale (Walpole et al., 2004), the frequency of crop damage events over each type of crop (Naughton-Treves, 1998), or the absolute amount taken of each crop type (Malagu et al., 2013).

The enthusiasm for private investment in, and management of, nature reserves (notably in East and Southern Africa) is an innovative and powerful force for social disruption in rural areas (Hutton et al., 2005). For example, South Africa, Botswana and Seychelles National Parks receive a large proportion of their recurrent funding from tourism (Hanks, 2003, Buckley et al., 2012; Rylance et al., 2017). Some of these tourism enterprises contribute considerably to conservation in public–communal protected areas and

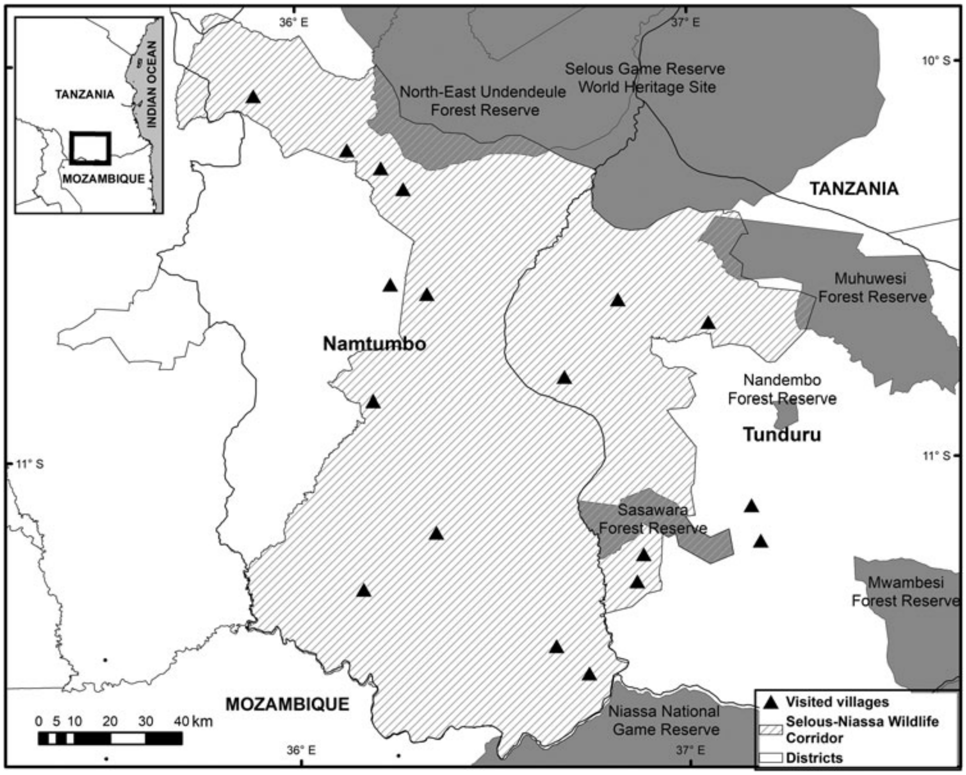

FIG. 1 Location of visited villages with crop damage by elephants in the Selous–Niassa Wildlife Corridor, Tanzania.

private reserves in Africa (Mossaz et al., 2015; Grünewald et al., 2016) through investment, for instance, in anti-poaching and fire management. In southern Tanzania, hunting by tourists is the main source of private investment in many areas. Some hunting companies provide an allowance to Game Scouts or Rangers, to motivate them to focus on anti-poaching activities or chasing away elephants. The importance of private investment in biodiversity conservation is now of particular importance (IUCN, 2016). Little is known, however, about the impact of private investment in the context of human–elephant interactions in Africa. A greater understanding is required of how private investment may affect human–elephant coexistence from the social, economic and environmental point of view, to facilitate identification of the best practices for both human well-being and elephant conservation.

In this study we evaluate the interactions between humans and elephants in the Selous–Niassa corridor in Tanzania, a priority natural corridor that includes traditional elephant routes between two of the largest remaining elephant populations in Africa (Mpanduji, 2004). Historically, in southern Tanzania, a high number of incidents, some of which have threatened human lives, have been reported and problematic animals have been killed (TAWIRI, 2010). The Selous–Niassa ecosystem therefore presents a unique opportunity to analyse the origin and extent of damage by elephants, and to seek insights into potential management and conservation solutions to reduce such damage.

Specifically, we aimed to investigate: (1) elephant crop preferences and damage along the boundaries of the corridor, (2) the relative importance of water and food availability (preferred and non-preferred food) to crop damage by elephants, and (3) the effect of wildlife management regimes involving the presence of private investors (mostly hunting companies) on the occurrence and intensity of elephant crop damage.

Study area and species

The Selous–Niassa Wildlife Corridor includes part of the world's largest Miombo woodland ecosystem (the Selous–Niassa ecosystem), linking the Selous Game Reserve in Tanzania with the Niassa Game Reserve in Mozambique (Fig. 1). This corridor lies within the Tanzanian administrative unit of Ruvuma Region (Districts of Natumbo and Tunduru), and covers an area of c. 17,030 km². Mean annual rainfall is 1200–1300 mm in the north, decreasing towards the south to 800 mm along the Ruvuma River, with a warm and rainy season during mid November–mid May, and a mean annual temperature of c. 21 °C (Baldus & Hahn, 2009). Elevation ranges from 460 m at Ruvuma river to 1,284 m at Mtungwe Hill. Vegetation is mostly dominated by Miombo woodlands, with high spatial variation in plant composition. Savannah woodlands with baobab trees (*Adansonia* spp.) are also common along the Ruvuma River. People of the local communities are mostly subsistence farmers who focus on shifting cultivation and the production of some cash crops such as cashew nut, sesame, rice and maize. Apart from agriculture, the economy of the area also depends on forestry and mining.

The corridor is located entirely on the land owned by 30 villages. To find a balance between village development and nature conservation, a network of five contiguous Wildlife Management Areas managed by community-based organizations was created and authorized during 2003–2012 (Supplementary Table 1). These Wildlife Management Areas are communal land set aside by member villages exclusively as habitat for wildlife, with the aim of enhancing long-term conservation, supporting rural economic development and alleviating poverty through sustainable utilization of natural resources. Wildlife Management Areas allow communities to benefit directly by entering into business contracts with the private sector. However, the Wildlife Corridor is still threatened by human activities such as poaching, habitat degradation and mining. Hunting tourism is the main source of private investment in the area. An investor (a hunting company) in Mbarang'andu Wildlife Management Area provides allowances to Village Game Scouts who are responsible for chasing away elephants from farms.

Each village in the Selous–Niassa Wildlife Corridor comprises several small farms (each 0.5–3 ha) scattered through the Miombo woodland. The main crops are maize and rice but farmers also cultivate cassava, beans, peas, sesame, sunflowers, cashew nuts, sweet potatoes, sugarcane, bananas, millet, peanuts, pumpkins, tomatoes, tobacco, onions and soy. Elephant damage to crops usually occurs during the night or early in the morning. In the northern villages of the Wildlife Corridor, crops are usually damaged by large groups (10–50 individuals) of elephants, whereas in the south elephant groups are smaller (4–20 individuals). The estimated mean elephant population size in the 2014 dry season in the Wildlife Corridor was c. 1,160 ± SE 684 individuals (TAWIRI, 2015), with a higher density in the north than in the south (The African Elephant Atlas, 2017).

African elephants are large herbivores (2–6 t), active both day and night. Their food and water requirements are significant, with an individual consuming 4–6% of its body weight daily (Sukumar, 2003) in the form of grass or browse (c. 300 kg of food and 150 l of water daily). Diet is diverse, primarily grasses (including sedges), forbs, tree foliage, shrubs, bark, twigs, roots and fruits. The Niassa and Selous ecosystems were formerly important sources of poached ivory, and elephant populations decreased by > 75% during 2006–2016 in both ecosystems (Chase et al., 2016). Poaching was at its highest peak in c. 2009. Since then, elephant populations have increased slightly, particularly in the northern part of the corridor (at the border with the Selous Game Reserve), with a consequent increase in crop damage by elephants.

Methods

We visited a total of 44 farms, in 13 villages, within the Corridor area and its surroundings during April–August 2016 (Fig. 1, Supplementary Table 1). To do this, we accompanied teams of Government Game Scouts (District Scouts, anti-poaching units, Selous Game Scouts) and Village Game Scouts (Supplementary Table 1) when they were chasing away elephants from the farms and we joined the work of other organizations such as WWF (Supplementary Table 2). We only visited those farms whose crops were damaged by elephants. Visits were as soon as possible after elephants were observed (from a few hours to a maximum 2 days later). We were called (mostly by the Scouts) whenever elephants were reported to be damaging crops. Time spent in each village depended on the impact of elephants and the duration of the Game Scouts' missions. In villages heavily affected by elephants we only recorded a partial ad hoc sample (15–35% of farmland based on the district damage records). In villages in which elephant damage was restricted to certain areas, we visited all the damaged farmland.

The proportion of each crop affected by elephants was estimated in the field as the ratio between the area affected (i.e. utilization) and the total area of each crop (i.e. availability). Areas were estimated during the visits and from government information, using a GPS to record areas damaged and *ArcGIS 9.3* and *10.2.2* (Esri, Redlands, USA). Distances to water points were also determined in the same way. The base river shapefile was provided by WWF, and this was combined in a new shapefile with information from Landsat orthophotos from June 2016 (Landsat-8, obtained from LandViewer; USGS, 2016). All field data were collected by MM-B.

In addition to information from the 44 farms visited (Supplementary Table 1), we also used responses to 22 human–wildlife conflict forms completed by WWF staff in November 2015 and July 2016 (Supplementary Table 2), which had the same type of information as our field datasheets but covered different crop damage events. Multiple observers were involved in the WWF data collection.

Data analysis

To analyse crop selection by elephants we used Pearson χ^2 tests. Observed values were calculated as the area damaged by elephants in each crop and the expected frequency was calculated as the proportion of each crop in each farm affected by elephants. Additionally, we estimated crop selection using the selection ratio (w_i), following Manly et al. (2002), calculated as $w_i = o_i/\pi_i$, where o_i is the proportion of the area used by elephants (i.e. proportion of each crop i with damage) and π_i is the proportion of available resources in the environment (i.e. proportion of each crop i in each farm). Positive selection (preference) occurs when $w_i > 1$ and negative selection (rejection) when $w_i < 1$. Thus, we classified each crop type according to its selection ratio as: low preference when $w_i \leq 0.75$; medium preference

TABLE 1 Estimation of selection indexes based on the occurrence of elephant *Loxodonta africana* damage to 18 crop types, ordered from high to low preference.

Crop type	Expected proportion (π_i)	Observed proportion (o_i)	Selection index (w_i)	Standardized index (B_i)[1]	Selection order	Preference group[2]
Sweet potatoes	0.02220922	0.11817851	5.32114671	0.19576674	1	High
Bananas	0.02188360	0.09264034	4.23332294	0.15574535	2	High
Peanuts	0.00207072	0.00743397	3.59003242	0.13207848	3	High
Onions	0.01181172	0.04011231	3.39597662	0.12493910	4	High
Pumpkins	0.00446930	0.01470785	3.29086305	0.12107194	5	High
Maize	0.27985307	0.39495978	1.41131125	0.05192261	6	High
Beans	0.01260981	0.01384830	1.09821667	0.04040375	7	Medium
Millet	0.02263380	0.02368537	1.04645985	0.03849960	8	Medium
Sugarcane	0.02225466	0.02244379	1.00849872	0.03710300	9	Medium
Cashew nuts	0.00383083	0.00382022	0.99723123	0.03668847	10	Medium
Cassava	0.11140652	0.10961458	0.98391526	0.03619857	11	Medium
Rice	0.31450241	0.12121233	0.38540986	0.01417936	12	Low
Peas	0.11748521	0.03371344	0.28695903	0.01055732	13	Low
Sesame	0.02951533	0.00315168	0.10678119	0.00392852	14	Low
Sunflowers	0.01915413	0.00047753	0.02493078	0.00091721	15	Low
Tomatoes	0.00223465	0.00000000	0.00000000	0.00000000	16-17-18	Low
Soy	0.00159618	0.00000000	0.00000000	0.00000000	16-17-18	Low
Tobacco	0.00047885	0.00000000	0.00000000	0.00000000	16-17-18	Low

[1]Ranges from 0 to 1.
[2]For definition of grouping, see text.

when $0.75 < w_i < 1.25$, and high preference when $w_i \geq 1.25$. Additionally, we calculated Manly's standardized selection ratio (B_i), for relative comparisons, which ranges from 0 to 1 (Manly et al., 2002), as: $B_i = w_i / \sum_{n=1}^{j} w_i$.

To analyse the factors influencing crop damage in each farm we used beta regression models (Cribari-Neto & Zeileis, 2010). We first built a beta regression mixed model to include the possible spatial correlation structure of data (villages) in the model using the package *glmmTMB* for *R 3.5.1* (R Core Team, 2016). Proportion of crop area damaged by elephants in each farm was the response variable. Fixed effects (predictors) were (1) Euclidean distance from the sampled farm to the nearest water supply, (2) relative abundance of highly preferred crops (area covered by preferred crops divided by the total area of each farm), and (3) the existence or not of an investor in the Wildlife Management Area of each sampled village. As village had no significant effect in the model, we built a simpler model without the random structure, using the *betareg* package (Cribari-Neto & Zeileis, 2010) in *R*. The beta regression model was fitted with a logit link function (that with the highest pseudo R^2) to obtain the predicted (fitted) values. We used model averaging to summarize all competing models. We first fitted the maximal model, containing all the predictors. We then compared all possible models by using Akaike information criterion (AIC) weights. For model comparison we used the *dredge* function in the *MuMIn* package in *R*. Finally, we obtained the importance of each predictor (from 0 to 1) using the *model.avg* function of *MuMIn*.

Results

Crops were grouped into three categories according to their selection index by elephants (Table 1), with significant differences in crop preference across the 18 crop types ($\chi^2_{17} = 3276.8$; $P < 0.0001$). Sweet potatoes, bananas, peanuts, onions and pumpkins were the most preferred crops ($w_i \geq 3$; Table 1). Maize was the most preferred crop of the crops most cultivated in the area (Table 1).

The mean per cent area damaged in each farm was 25.74 ± SE 2.94% (range 2.5–100%). In the southern part of the Corridor, where elephant populations are smaller, the mean per cent area damaged per farm was 13.06 ± SE 2.86%, whereas in the northern part it was 30.13 ± SE 3.64%. Model averaging revealed that the relative abundance of preferred food was by far the most important variable explaining crop damage on each farm (relative importance of 1), followed by the presence of investors (relative importance of 0.41; Tables 2 & 3). Distance to water supply had little importance (relative importance of 0.29; Tables 2 & 3). Thus, damage by elephants was positively associated with relative abundance of preferred food and negatively associated with distance to water supply (Fig. 2), although only relative abundance of preferred food had a significant effect on crop damage by elephants (Table 2). Farms with > 70% of their land covered by preferred crops had high elephant damage, with an area damaged > 50% (Fig. 2a). A reduction in the cultivation of preferred crops from 75 to 25% of the farmland resulted in a 64% decrease in elephant crop damage. On

TABLE 2 Summary of the beta regression model averaging (n = 8 models) for the factors affecting crop damage by elephants. Pseudo R^2 for the full model = 0.302.

Predictors	Importance[1]	Estimate ± SE	z	P
Relative abundance of preferred food	1.00	3.0633 ± 0.6527	4.693	< 0.001
Presence of investor	0.41	−0.4068 ± 0.3609	1.127	0.260
Distance to water supply	0.29	−0.0001 ± 0.0004	0.406	0.684

[1]The sum of the AIC weights across all models where the fixed effect occurs (Table 3), ranging from 0 (minimum importance) to 1 (maximum importance).

TABLE 3 Model selection (n = 8 models) for the beta regression models of crop damage by elephants. Models are ranked by AIC.

Intercept	Presence of investor	Distance to water supply	Preferred food relative abundance	df	Log likelihood	AIC	ΔAIC	AIC weight
−2.1150			3.098	3	16.483	−27.0	0.00	0.425
−2.0020	−0.4046		3.036	4	17.097	−26.2	0.77	0.289
−2.0730		−0.0001	3.067	4	16.555	−25.1	1.86	0.168
−1.9530	−0.4120	−0.0002	3.000	5	17.192	−24.4	2.58	0.117
−0.7320				2	7.447	−10.9	16.07	0.000
−0.6137	−0.4898			3	8.184	−10.4	16.60	0.000
−0.6871		−0.0002		3	7.595	−9.2	17.78	0.000
−0.5602	−0.5049	−0.0003		4	8.378	−8.8	18.21	0.000

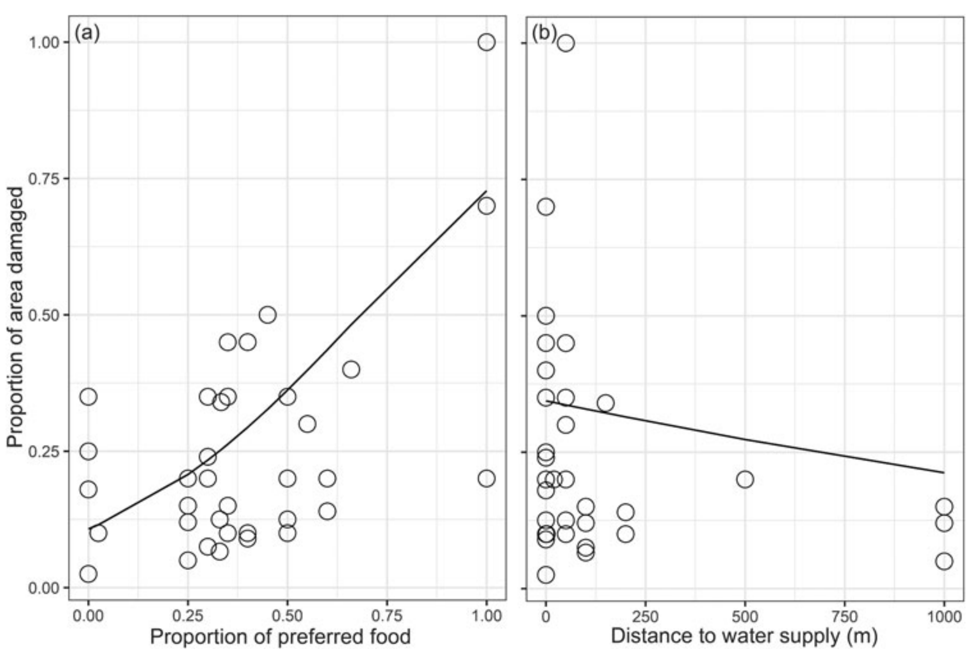

FIG. 2 Predicted proportion of elephant damage to crops in relation to (a) the proportion of preferred food (area covered by preferred crops divided by the total area of each farm), and (b) the distance to the water supply for each farm. The curves show the fitted values of the beta regression models (Table 3).

average, farms with water supply points < 250 m from the farm had > 30% of their area damaged (Fig. 2b). Area damaged by elephants was lower on farms with investors (mean per cent of area damaged 20.53 ± SE 3.32%; range 12.42–74.03%) compared to those without investors (mean per cent of area damaged 33.50 ± SE 3.06%; range 8.59–35.51%).

Discussion

Our results showed strong differences in elephant food selection across the 18 crop types. These differences corroborate other evidence that elephants do not damage all crops equally (Naughton-Treves, 1998; Walpole et al., 2004). Many of the highly preferred crops, such as sweet potatoes, bananas and onions, even though they are found in many villages, are not the main crops cultivated in the area. Our findings regarding food selection are in agreement with those presented by Naughton-Treves (1998) for Kibale National Park, Uganda, where banana was the most preferred crop followed by sweet potato. However, Walpole et al. (2004) reported sorghum and finger millet, followed by maize, to be the most preferred crops in the Serengeti district, with beans, sweet potatoes and cassava less preferred. In our research, all study farms were affected by elephants and crop selection was based on the relationship between actual use by elephants and crop availability at the scale of the farms. Although further studies are needed, particularly on scarce crops, our findings may be a good proxy of elephant preferences for a variety of crops.

Crop damage by elephants was strongly affected by the abundance (i.e. crop area) of preferred food and, to a lesser extent, by the distance to water supply points and the presence of private investors. Water sources have been found to be associated with spatial patterns of crop damage elsewhere (Smith & Kasiki, 2000). The relationship between the intensity of damage and the distance to water supply could be a result of the influence that water availability has on the distribution patterns of elephants, as they tend to stay close to waterholes and rivers (Thomas et al., 2008). The presence of investors in Wildlife Management Areas showed an importance of 0.41 in explaining crop damage by elephants, and we found a tendency indicating that farms with an investor could have less damage by elephants, but further studies of this are required. Hunting by tourists (the main source of private investment) seems to have limited effectiveness in reducing human–wildlife conflicts as private hunters do not usually select problem animals as trophies (Jackson & Nowell, 1996). Some studies (Treves & Karanth, 2003; Wielgus & Peebles, 2014) consider hunting an inadequate management tool for reducing human–carnivore conflicts, which could even increase the problem in the case of wounded animals or destruction of pack dynamics. On the other hand, as most hunters are willing to hunt in areas lacking high densities of viewable wildlife or tourism infrastructure, the potential for trophy hunting to generate incentives for conservation on communally owned lands and, by doing so, support human–wildlife coexistence, should not be ignored (Lindsey et al., 2006; Naidoo et al., 2016).

Given that the proportion of land on which elephants' preferred food is grown is a major factor explaining crop damage by elephants, it is important to test and implement a variety of deterrent methods to decrease the attraction of preferred food sources. The use of less preferred crops, such as sesame, tomatoes, tobacco and soy, among others (Table 1), could help reduce the intensity of crop damage. Cultivation of unpalatable crops can be used to mitigate crop damage by elephants (Chiyo et al., 2005; Parker & Osborn, 2006; Gross et al., 2016). The use of non-preferred crops that also require less water would be preferable (e.g. peas, tobacco, sesame). This would be an upheaval for local communities, however, as the main food crops are currently maize and cassava, and livelihoods are often highly dependent on the crops grown. Further studies are required to evaluate the economic and social implications of changing crop types.

Previous studies (Sitati & Walpole, 2006; Hoare, 2012) concluded that a combination of strategies may be the most effective way to minimize crop damage by elephants. It could be particularly useful to focus on methods based on early warning systems (Pozo et al., 2017b). A first step in implementing deterrent methods affordably is probably aggregation of farmland. If farms are close together, it will be less costly and easier to protect them and to establish the most effective method of deterrence. However, any shifts in crop location have associated difficulties related to the availability of water and soil fertility.

As in any negative interaction between wildlife and people, any solution must be implemented in collaboration with local communities. Several approaches could be used to increase community awareness of the potential benefits of wildlife-friendly management. One approach would be to seek investors that make the area valuable. Our results show an apparent contribution of investors to reduce crop damage by elephants. However, further studies are needed, with a larger sample size and more rigorous comparisons between areas with and without investors (i.e. controlling for potentially confounding factors), to improve understanding of the factors involved in farm and crop selection by elephants and any potential relationship with different management schemes.

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Author contributions Conception of experiments, data collection: MM-B; refining of methods: ASM; data analysis: RP; writing: all authors.

Conflicts of interest None.

Ethical standards This research had the necessary approvals and permits from appropriate institutions and statutory authorities in both the host country and the researchers' country of origin, and otherwise abided by the *Oryx* guidelines on ethical standards.

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