Abstract

Human-wildlife conflict is increasing due to rapid natural vegetation loss and fragmentation. We investigated seasonal, temporal and spatial trends of elephant crop-raiding in the Trans Mara, Kenya during 2014-2015 and compared our results with a previous study from 1999-2000. Our results show extensive changes in crop-raiding patterns. There was a 49% increase in incidents between 1999-2000 and 2014-2015 but an 83% decline in the amount of damage per farm. Crop-raiding went from highly seasonal during 1999-2000 to year-round during 2014-2015, with crops being damaged at all growth stages. Additionally, we identified a new elephant group type involved in crop-raiding, comprising of mixed groups. Spatial patterns of crop-raiding also changed, with more incidents during 2014-2015 neighbouring the protected area, especially by bull groups. Crop-raiding intensity during 2014-15 increased with farmland area until a threshold of 0.4 km^2 within a 1 km^2 grid square, and farms within 1 km from the forest boundary, <5 km from the protected area boundary and >2 km from village centres were most at risk of crop-raiding. In the last 20 years the Mara Ecosystem has been impacted by climate change, agricultural expansion and increased cattle grazing within protected areas. Elephants seem to have responded by crop-raiding closer to refuges, more frequently and throughout the year but cause less damage overall. While this means the direct economic impact has dropped, more farmers must spend more time protecting their fields, further reducing support for conservation in communities who currently receive few benefits from living with wildlife.

Introduction

Managing competition for space and resources between people and wildlife is a critical conservation issue (Woodroffe et al. 2005). This can be a particular problem on land neighbouring protected areas, where growing human populations and the expansion of agriculture (Wittemyer et al. 2008) often lead to human-wildlife conflict (Nyhus 2016). African and Asian elephants in particular are prone to conflict because they spend much of their time living among people outside protected areas (Fernando & Pastorini 2011; Thouless et al. 2016) and because their large body size makes them more of a threat. Thus, local communities can incur substantial costs from elephants, which damage crops and property and sometimes cause human injury or loss of life (Naughton-Treves 1997). This can lead to retribution killing of elephants (Choudhury 2004; Linkie et al. 2007) and strongly undermines support for conservation efforts (Dickman 2010; Pooley et al. 2017). This means there is an urgent need to tackle this problem. In this context, understanding seasonal, temporal and spatial trends of elephant crop-raiding is critical, as it helps managers develop mitigation programmes.

Human-elephant conflict in savanna systems is often related to rainfall patterns, as the quality of natural forage declines during the dry season at the same time that crops ripen (Osborn 2004; Chiyo et al. 2005; Gubbi 2012; Goswami et al. 2015; Branco et al. 2019). Temporal patterns are generally driven by risk-avoidance behaviour, as elephants typically crop-raid at night when they are less likely to be detected by farmers (Graham et al. 2009, 2010). This risk-avoidance has also been linked to the type of elephant group involved, although this is often site-specific. For example, in some locations bull elephants are largely responsible for crop-raiding (Sukumar & Gadgil 1988; Chiyo & Cochrane 2005; Von Gerhardt et al. 2014), whereas in others female-led family groups are equally involved (Sitati et al. 2003; Graham et al. 2010; Wilson et al. 2013) or the most responsible (Smith & Kasiki 2000). Thus, crop-raiding behaviour can vary across sites, by elephant group type and over time, depending on the landscape and the behaviour of people towards elephants.

Risk-taking behaviour is also thought to predict the spatial distribution and intensity of human-elephant conflict. Once again this is context specific but there are general trends, with elephants avoiding areas where they are most likely to be detected by farmers. For example, crop-raiding tends to occur more frequently closer to forest edges and protected areas, further from roads and in areas of low human density (Sitati et al. 2003; Graham et al. 2010; Guerbois et al. 2012; Wilson et al. 2013; Goswami et al. 2015; Chen et al. 2016). However, understanding the factors that determine crop-raiding depends on analysing the data at an appropriate spatial scale. Many previous analyses used coarse-scale approaches, often to reduce spatial autocorrelation, which makes it harder to identify the spatial drivers (Songhurst & Coulson 2014).

Most previous elephant crop-raiding studies are also restricted to a single time period, making it difficult to determine the long-term importance of different drivers. This is a serious limitation given the rapidly changing land-use patterns and climate in most of Africa (Pozo et al. 2017). To fill this gap, we replicated a previous study from 1999-2000 on human-elephant conflict (Sitati et al. 2003) by analysing seasonal, temporal and spatial patterns of elephant crop-raiding during 2014-2015 in the Trans Mara district in Kenya, a region of high human-elephant conflict that neighbours the Masai Mara National Reserve. We did this by: i) assessing crop-raiding characteristics in terms of frequency, amount of damage and elephant group type; ii) determining temporal and seasonal trends of number of crop-raiding incidents; iii) mapping and modelling the spatial drivers of crop-raiding, repeating the previous methodology but also using new techniques to analyse the data at a finer spatial scale.

Methods

Study Area

The Trans Mara district is situated in South-West Kenya and encompasses the western portion of the Masai Mara National Reserve. The district forms part of Narok County and covers an area of 2,900 km^2. The Masai Mara National Reserve occupies 24% of this area while the remaining 76% is unprotected and was the focus of our study (Figure S1). The region's human population increased by 63% between 1999 and 2009 (Table 1) and this, together with a switch from pastoralism to farming, has led to high levels of land transformation producing more farmland, but smaller individual farms (Table 1). This means the landscape now has less and more fragmented forest cover (Table 1), consisting of farmland interspersed with a mosaic of afro-montane, semi deciduous and dry-deciduous forests and Acacia savanna woodlands (Tiller 2018). The region is also an important dispersal area for elephants and has traditionally been home to a resident population of 200-300 individuals (Sitati et al. 2003), although recent estimates are lower (Table 1). The unprotected Nyekweri forest in the Trans Mara acts as an important elephant refuge outside the park, as a portion of the Masai Mara National Reserve elephant population migrates in and out of the Trans Mara (Sitati et al. 2003). However, this leads to many crop-raiding incidents each year, so the region is recognised as a human-elephant conflict hotspot within Kenya (Litoroh et al. 2012), leading to increases in elephant deaths from poaching and conflict (Table 1). Farming practices and conflict mitigation methods have changed little in this region over the last few decades. The majority of farmers use well-established techniques to protect their farms, including fences (most commonly made from local materials such as branches) and guarding using flash lights, fire crackers and fire to deter elephants from entering their fields.

Table 1

Data collection

We collected data on elephant crop-raiding between June 2014 and November 2015 following the methods of Sitati et al. (2003). Ten enumerators were trained to use an adapted version of IUCN's training package on elephant damage (Hoare 1999b), a widely adopted, standardised human-elephant conflict monitoring system (Graham et al. 2010; Wilson et al. 2013; Songhurst & Coulson 2014). Enumerators were selected from the same 10 locations as Sitati et al. (2003), which covered the entire elephant range in the Trans Mara (Figure S1). Any crop-raiding incident that occurred within an enumerator's assigned area was visited to verify the incident and to record the location using a Garmin Etrek30 Global Positioning System (GPS). Each incident was classified as a unique event and we recorded the crop type damaged, the amount of damage, the time of the incident (to the nearest half hour), and where possible, the number of elephants involved, which was based on farmer observations during the incident and the number of elephant dung and footprints. Elephant sex and group type was assessed by the enumerators based on the size and frequency of elephant dung and footprints (Balasubramanian et al. 1995; Chiyo & Cochrane 2005).

Analysing characteristics of elephant crop-raiding

To assess crop-raiding characteristics over time we compared our results from 2014-2015 with the results from Sitati et al. (2003) during 1999-2000. In our analyses we classified elephant group as: family group; bull group; mixed group (family + bulls); or `Unknown'. We then calculated the number of crop-raiding incidents, the median percent of damage per farm, the mean amount of damage per incident and the median elephant group size involved. It should be noted that the mixed group type was not used in the 1999-2000 study because it was rarely observed and when it was, the enumerators recorded it as crop-raiding by family groups.

‘Unknown’ was used when it was not possible to assign an incident to one of the three groups types and was recorded for 37% of the incidents; data on group size and median incident duration suggest most of these incidents involve bull or family groups.

Analysing temporal and seasonal patterns of crop-raiding

We measured the monthly patterns of crop-raiding in terms of crop age, based on four categories: (1) ‘young’, crops in the seedling stage of growth; (2) ‘middle’, crops in the intermediate stage of growth; (3) ‘mature’, crops ready for consumption; (4) ‘dry’, crops ready for harvest (Sitati, 2003). We compared the seasonal patterns to mean monthly rainfall data, which were based on daily readings from weather stations across the Trans Mara. We also looked at diurnal patterns of crop-raiding but patterns were similar to the previous study (Figure S2).

Analysing spatial patterns of crop-raiding

To investigate the spatial distribution of crop-raiding across the Trans Mara during 2014-2015, we produced GIS layers of the same eight predictor variables developed by Sitati et al. (2003): distance to rivers; distance to roads; distance to villages; distance to forest edge (unprotected area); area under forest; area under cultivation; elevation; and human population density (Supplementary materials). We then used these data in three ways to investigate which of these variables best explained the spatial conflict patterns. We restricted all the analyses to the known elephant range, which we based on data from an ongoing monitoring project of GPS collared elephant individuals (Mara Elephant Project 2017).

First, we carried out univariate analyses to investigate whether the spatial characteristics of each crop-raiding incident location differed between elephant group types, based on Kruskal-

Wallis and Mann-Whitney U tests. Second, we repeated the approach by Sitati et al. (2003) using logistic regression to determine the factors that best predict the occurrence of crop-raiding in a series of 5 x 5 km grid squares. We carried out three separate analyses based on the three group types, using ArcGIS to calculate the spatial characteristics of each grid square. There was no serious collinearity between our predictor variables (Supplementary Materials) so we rescaled them to have a mean of zero and a standard deviation of 1, as this puts the predictors on a common scale and improves the convergence of statistical models (Gelman et al. 2008). To find which factors predicted crop-raiding presence we used R (R Development Core Team 2013) and the lme4 package (Bates et al. 2016) to carry out the logistic regression, using a binomial error structure and logit link function. We used the package MuMIn (Barton 2016) to evaluate all candidate models; examine the averaged parameter estimates (Beta), standard errors and confidence intervals of the predictor variables, and; compare models using the Akaike Information Criteria (AICc), restricting the models to ΔAICc < 4 to remove implausible models.

The approach used by Sitati et al. (2003) was developed to account for zero-inflation and spatial autocorrelation in the data, but analysing crop-raiding data as a binary variable at a relatively coarse spatial resolution resulted in the potential loss of important information. Exploratory modelling found similar issues with the 2014-2015 dataset, so we adopted a new approach that let us determine which factors predicted the frequency of crop-raiding at a 1 km x 1 km resolution. This involved modelling non-zero observations only using Generalized Additive Models (GAM) that applied a smoothing term for non-linear data (Wood 2006), and incorporating distance-weighted covariates into the modelling framework using the autocov-dist function in the R package "spdep" to account for spatial autocorrelation. We carried out an analysis for each group type, dividing the elephant range into 1299 1 km x 1 km grid squares

(Figure S3 & Figure S4), and used the package mgcv to fit GAMs for family groups and mixed groups using Poisson and negative binomial error structures respectively and log link functions. We were unable to use this approach for the bull groups because there were insufficient data points for the model to run following removal of zero observations. For the final GAMs, we carried out model validation to confirm the absence of heteroscedasticity in model residuals and influential data points with high leverage (Cook's Distance > 1.0).

Results

Characteristics of elephant crop-raiding

Crop-raiding in the Trans Mara increased from 263 incidents per annum during 1999-2000 to 392 incidents per annum during 2014-2015, a rise of 49%, (Table). Despite the increase in the number of incidents, there was a decline in the area of damage per incident, as mean damage of all incidents (including where the group type was Unknown) during 1999-2000 was 1.17 ± 0.0096 ha compared to 0.20 ± 0.014 ha during 2014-2015. The percentage of each field damaged during 2014-2015 was generally low: 67% of incidents involved damage of <10% of the total cultivated area being damaged, 5% of incidents led to >50% of cultivated area being damaged, and 2% of incidents led to the entire cultivated area being damaged. Maize was the main crop eaten during both study periods, and during 2014-2015, maize was damaged in 68.8% of crop-raiding incidents. Additionally, the number of different crops eaten increased from 18 during 1999-2000 to 26 during 2014-2015.

Historically, crop-raiding was carried out by two different types of elephant group: (1) family groups and (2) bull groups, including lone bulls. However, we recorded an additional group type consisting of a family group and bulls involved in crop-raiding. These mixed groups were involved in the most incidents and caused the highest amount of damage per incident (Table 2).

Table 2

Temporal and seasonal patterns of crop-raiding

The time each group spent crop-raiding declined between 1999-2000 and 2014-2015, with the median time for family groups dropping from 3 hours to 1.5 hours and the median time for bull groups dropping from 1.5 hours to 1 hour (Table 2). The crop raiding incident duration during 2014-2015 for mixed groups was the same as for family groups.

During 1999-2000 there were clear peaks in crop-raiding, one month experienced no crop-raiding, and the majority of crops damaged were mature or dry crops (Figure 1). During 2014-2015, crop-raiding occurred in every month during the 18-month monitoring period and affected crops at every growth stage. There was a decline in crop-raiding incidents in February 2015, September 2015 and October 2015 related to the period after maize harvesting. Monthly rainfall fluctuated more during 2014-2015, ranging from 5.9 mm to 230.4 mm as compared to more consistent monthly rainfall between 44.6 and 113.2mm during 1999-2000 (Figure 1). Although, the 1999-2000 data only represented 12 months of rainfall compared to 18 months from 2014-2015.

Spatial patterns of crop-raiding

Crop-raiding incidents were spatially clustered in both 1999-2000 and 2014-2015 but their locations partially changed (Figure 2). During 1999-2000, more incidents occurred in the northwest of the Trans Mara, whereas crop-raiding during 2014-2015 occurred along the edge of the protected area and close to the forest. The cluster of crop-raiding incidents in the east of the region was the same for both time periods.

Figure 1

There were differences in the distances that groups travelled from the forest to crop-raid (n = 373, x^2 = 12.393, df = 2, p = 0.002, Figure S5), with family groups raiding closest to the forest, followed by mixed groups and then bull groups (Table S1). The opposite pattern was shown for distance to protected areas, with family groups raiding furthest from the protected areas (n = 373, x^2 = 12.315, df = 2, p = 0.002, Table S1).

Of the eight potential predictor variables used in the logistic regression analysis, only area under cultivation predicted the spatial pattern of crop-raiding for family groups (β = -6.68, 95% confidence intervals = -12.01, -1.36) and mixed bull groups (β =-3.80, 95% confidence intervals = -6.68, -0.91). In both cases the probability of crop-raiding was greater in the 25 km^2 sampling units with a low percent of area under cultivation (Table S2 and S3). None of the variables we tested predicted the probability of crop-raiding by bull groups.

For the Generalised Additive Model, area under cultivation was important for predicting crop-raiding by both family and mixed groups (Table 3), with crop-raiding increasing up to a threshold of 0.4 of the grid square being farmland and then decreasing (Figure 3c & d). Distance to forest edge was also important for both group types, with more crop-raiding closer to the forest edge, until a threshold of 1.5 km after which it declined (Figure 3a & b). However, for mixed groups, this decline was followed by another increase 4 km from the forest, followed by a final decrease after 7 km, although confidence levels at these high distances were much lower

(Figure 3b). Distance to villages was another important factor for predicting crop-raiding by mixed groups, with increases in distance from village centres leading to increases in crop raiding (Figure 3f). Finally, distance to protected area also predicted crop raiding by family groups but with a fluctuating pattern, as most crop-raiding occurred closest to the protected area, although a few incidents occurred at 8 km and 15 km from the protected area (Figure 3e).

Table 3 and Figure 4

Discussion

Characteristics of elephant crop-raiding

Elephant crop-raiding in the Trans Mara has changed markedly since 1999-2000, with incidents per annum increasing by 49%. This is most likely due to the 63% increase in human population in the region and agricultural expansion, as farmland increased by 42.5% (Table 1, Tiller, 2018). Despite the increase in the number of crop-raiding incidents, the actual amount of damage per farm during 2014-2015 was much lower than during 1999-2000. The mean damage per incident was 1.17 ha during 1999-2000, compared to 0.20 ha during 2014-2015, and so the total amount of damage per annum dropped from 308 ha to 78 ha. There could be a number of reasons for this. First, the mean farm size decreased from 3.4 ha during 1999-2000 to 2.2 ha during 2014-2015, potentially reducing food availability and making it more difficult to crop-raid undetected. Second, the recorded increase in retaliatory killings (Table 1) may have made elephants more risk averse and more likely to curtail a crop-raiding incident. Third, farmers may have become more effective at guarding their fields, using the same tried and tested approaches based on guarding their fields throughout the night and using deterrents, such as fences, fire and fireworks (Sitati et al. 2005; Sitati & Walpole 2006). Fourth, recent estimates suggest the Trans Mara elephant population has declined since 1999-2000, although the Masai

Mara ecosystem has a much larger population (Thouless et al, 2017) and elephants from there continue to crop-raid in the Trans Mara (Tiller 2018).

This reduction in total crop loss might not actually reduce human-elephant conflict, as the number of farmers affected has increased and previous studies have shown that people often perceive the amount of crop damage to be higher than the actual figure (Naughton-Treves 1997; Gillingham & Lee 1999). Such perceptions could reduce farmers' tolerance towards elephants. In addition, if this reduction in the severity of each raid is due to more mitigation effort, then farmers could be experiencing higher direct and indirect costs from guarding and investment in deterrents such as fence material (Thirgood et al. 2005; Barua et al. 2013). For example, the guarding of crops in the evening causes sleep loss and impacts on mental health, which can impact other day wage-earning activities (Barua et al., 2013). Thus, farmers living alongside elephants may feel just as impacted, creating fear and anger and perhaps helping explain the recorded increase in poaching and retributive killing (Choudhury 2004; Linkie et al. 2007).

We also found that the types of elephant group involved in crop-raiding has changed, as there was an additional group type of mixed groups comprising of family groups plus one or more bulls. Family groups have traditionally been most responsible for crop-raiding in the Trans Mara (Sitati et al. 2003) which is in contrast to studies from other parts of Africa where raiding is mostly by bull groups (Hoare 1999a; Chiyo & Cochrane 2005). Three possibilities could explain this finding : (1) family groups in the Trans Mara are less risk averse; (2) food quality is lower in the Trans Mara and so family groups have to adopt more risky behaviour to meet their nutritional requirements; (3) risks are lower, possibly because the long boundary between farmland and elephant refuges makes it easier to remain undetected. Thus, the formation of mixed groups could be because these risks have further reduced, allowing bigger groups to successfully avoid detection. Alternatively, it could be that risks have increased and so family groups prefer to crop-raid with bulls that may have more experience of encountering people. Also, it may be safer to crop-raid in larger groups (Songhurst et al. 2015), which is reflected in the larger elephant group size that we recorded during 2014-2015 compared to 1999-2000. The fact that incidents were shorter and caused less damage supports the hypothesis that this is a response to increased risks, but further research is needed to understand this change and its implications for mitigation management.

Seasonal patterns of crop-raiding

Many studies across Asia and Africa show that crop-raiding is strongly seasonal and correlated with rainfall patterns and cultivation cycles (Chiyo et al. 2005; Wilson et al. 2013; Goswami et al. 2015). Previous results in the Trans Mara were no different (Sitati 2003). However, rainfall was much more variable during our study and crop-raiding occurred throughout the year and impacted all stages of crop growth. This was not observed during 1999-2000, and contrasts with previous studies showing elephants prefer mature crops (Chiyo et al. 2005; Gubbi 2012; Chen et al. 2016). Our results suggest that crop-raiding is being driven by trade-offs between risk and food quality, with elephants possibly raiding the less mature crops because they are less likely to be guarded by farmers. Alternatively, elephants may be crop-raiding throughout the whole year because the availability and quality of grass in parts of the Masai Mara have declined in recent years due to the increasing number of livestock, human settlement and farmland (Li et al. 2020; Ogutu et al. 2011, 2016). Unfortunately, this lack of climate-related predictability has serious implications for the livelihoods and well-being of farmers, as it forces them to spend more time guarding their crops.

Spatial patterns of crop-raiding

Crop-raiding incidents in the Trans Mara were highly clustered, as is widely reported throughout Africa (Graham et al. 2010; Songhurst & Coulson 2014). However, the locations of crop-raiding partly changed, with fewer incidents in the northwest as compared to 1999-2000, and more along the edge of the protected areas and close to large forest patches. Land cover data suggest this shift is due to the spread of agricultural land since 1999-2000 (Tiller, 2018), fragmenting the forest and leaving the northwest of the region largely transformed (Table 1), leaving fewer forest patches in which elephants can seek refuge before or after crop-raiding (Graham et al. 2009; Wilson et al. 2013). We also found there were differences between elephant group types, as family groups crop-raided closest to the forest, followed by mixed groups and then bull groups. In this case, bull groups could be greater risk-takers than family groups as they travel further from the forest to crop-raid. The opposite pattern was shown for distance to protected areas, with bull groups crop-raiding closest to the protected area, although in general incidents were much further from the protected area than from forest patches. This suggests the Masai Mara National Reserve is acting as a source, rather than a staging post, for crop-raiding elephants.

To look at spatial predictors of crop-raiding, we first investigated changes since 1999-2000 by repeating the analysis of Sitati et al (2003), based on 25 km^2 sampling units. Like this previous study, we found that area under cultivation was a predictor of crop-raiding, but in our case, this only applied to family and mixed groups and the relationship was opposite, with more crop-raiding in units with the least farmland cover. A possible explanation is that during 1999-2000 many of the sampling units were completely forested, so the units with the highest amount of farmland contained the most crops but were also close to forest patch refuges. In contrast, by 2014-2015 deforestation meant the sampling units with the most farmland tended to be much further from forest patches. Instead, the units that were raided tended to include forest patches and so had less farmland cover (Sitati et al. 2003; Graham et al. 2010; Wilson et al. 2013; Goswami et al. 2015). Thus, in effect both the 1999-2000 and 2014-2015 models predicted that elephant crop-raiding depended on the presence of elephants and crops, although how this correlated with the measured factors changed with time. This intuitive result provides little information to help inform mitigation, highlighting the need for new, more-detailed spatial analyses at a much finer scale.

To analyse the 2014-2015 data at a finer scale, we used Generalised Additive Models that accounted for the spatial autocorrelation in the 1 km^2 resolution dataset. We found that crop-raiding by both family and mixed groups was related to the availability of crops and distance to forest, and also that family groups raided closer to protected area, and mixed groups raided further from village centres. For both group types, crop-raiding increased with area of the planning unit under cultivation until a threshold of 40% of the 1 km^2 sample unit was farmland, after which it declined. At this point, the risk of human retaliation may have been too high because refuges were too far away (Graham et al. 2009), providing more evidence that deforestation has driven the observed change in crop-raiding spatial patterns. Our analysis also showed that farms 1 km from the forest boundary, 5 km from the protected area boundary and >2 km from village centres were most at risk of crop-raiding, although there was a multimodal pattern at larger distances which supports anecdotal evidence that elephants based inside the protected area show different crop-raiding patterns than those found outside (Figure 3d and 3e). These findings are consistent with other studies showing that more crop-raiding occurs within 6 km of the forest or protected area (Graham et al. 2010; Gubbi 2012; Guerbois et al. 2012), and in areas with lower densities of people (Graham et al. 2010; Chen et al. 2016). Therefore, targeting mitigation in these ‘hotspots’ could be effective. These results also show the advantage of using a Generalised Additive Model to analyse crop-raiding patterns, as it provides more nuanced information about the spatial patterns. However, it also requires more data, so in this case we could not analyse crop-raiding by bull groups and so could only gain insights from the univariate and logistic regression analyses.

The future co-existence of humans and elephants

This study illustrates the value of long-term conflict monitoring using standardised measures (Hoare, 1999a), showing that patterns of crop raiding changed significantly in the Trans Mara between 2001 and 2015. Some of these changes were expected, as spatial patterns often depend on the presence of forest refuges, so human population growth and deforestation has inevitably led to more incidents taking place closer to the protected area. More surprising was the emergence of year-round crop-raiding patterns and a new type of crop-raiding group, based on family and bull groups merging. This was likely to have been driven by changing rainfall patterns, and possibly by cattle number increases, including in the protected area, reducing the availability of a key grazing resource (Li et al. 2020; Ogutu et al. 2016).

All these factors have led to a larger number of less severe incidents. But while the total amount of damage has dropped it is likely that more people are impacted and for longer periods during the year, further reducing support for conservation in communities who currently receive few benefits from living with wildlife (Walpole & Thouless 2005), and perhaps explaining why illegal killing of elephants in the Trans Mara has increased (CITES Secretariat, 2015). Climate change, habitat loss and low protected area management effectiveness are issues throughout Africa, and so our study suggests that human-wildlife conflict patterns are likely to change throughout the continent. Thus, there is a pressing need to work with affected farmers to monitor and understand such changes, helping inform mitigation strategies and build tolerance.

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Table 1. Changes in the Trans Mara between the two study periods for human population (KNBS, 1999 and 2009), farmland area (Tiller, 2018), farm size and forest cover (Sitati, 2003 and Tiller, 2018), elephant population size (Sitati, 2003 and Thouless et al, 2016) and illegal elephant deaths (CITES, 2015)

Types of changes in the Trans Mara	**1999-2000**	**2014-2015**
Number of people	168,721 (1999 census)	274,500 (2009 census)
Area of farmland (km^2)	945.7	1347.8
Mean farm size (ha)	3.4	2.2
Forest cover (km^2)	348.1	231.3
Median forest patch size (Hectare)	5.4	1.4
Elephant population	200-300	100
Elephant deaths from poaching or conflict	5	9

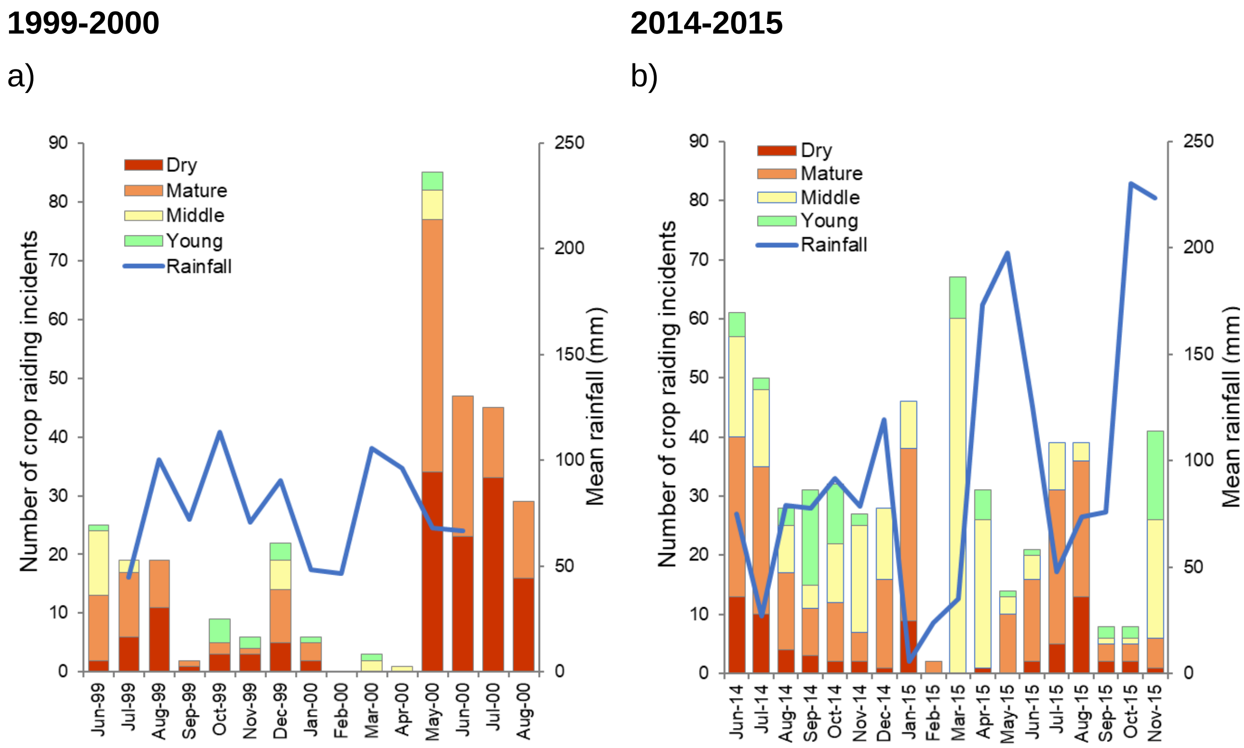
Table 2. Elephant crop-raiding characteristics during 1999-2000 and 2014-2015.

Crop-raiding Characteristics	**1999-2000** (329 incidents in 15 months)		**2014-2015** (589 incidents in 18 months)		
	Family	Bull	Family	Bull	Mixed
Percent of incidents	64%	32%	24%	11%	28%
Median % crop damage per farm	30	25	5.2	1.7	6.0
Mean area of damage (ha) + SE	1.18 ± 0.122	0.60 ± 0.060	0.20 ± 0.025	0.10 ± 0.020	0.22 ± 0.032
Median elephant group size	8	3	6	3	10
Elephant group size range	3-40	1-9	3-50	1-6	4-65
Median incident duration (Hours)	3	1.5	1.5	1	1.5

*The percentages do not sum up to 100, as the remaining percent is from the group ‘Unknown’

Table 3. GAM model outputs for the family group and the mixed group analyses. GAM models provide a technique that fits a smooth relationship between the explanatory variables and the response variable. The greater the value of the estimated degrees of freedom (edf), the more the model had to smooth the data.

Elephant group type	Model		Distance to villages	Distance to protected area	Distance to forest edge	Area under cultivation
Family	GAM (poisson)	edf	< 0.001	6.795	2.235	1.944
		p value	0.459	0.001	0.063	0.035
		f statistic	0.000	26.453	4.893	5.636
Mixed	GAM (negative binomial)	edf	1.023	< 0.001	4.394	1.691
		p value	0.029	0.358	< 0.001	0.043
		f statistic	0.457	0.000	4.075	0.546



546 **Figure 2.** Elephant crop-raiding (a) seasonal patterns during 1999-2000 and (b) seasonal
547 patterns during 2014-2015. The seasonal patterns show the number of incidents for each crop
548 age group and mean rainfall per month (mm).

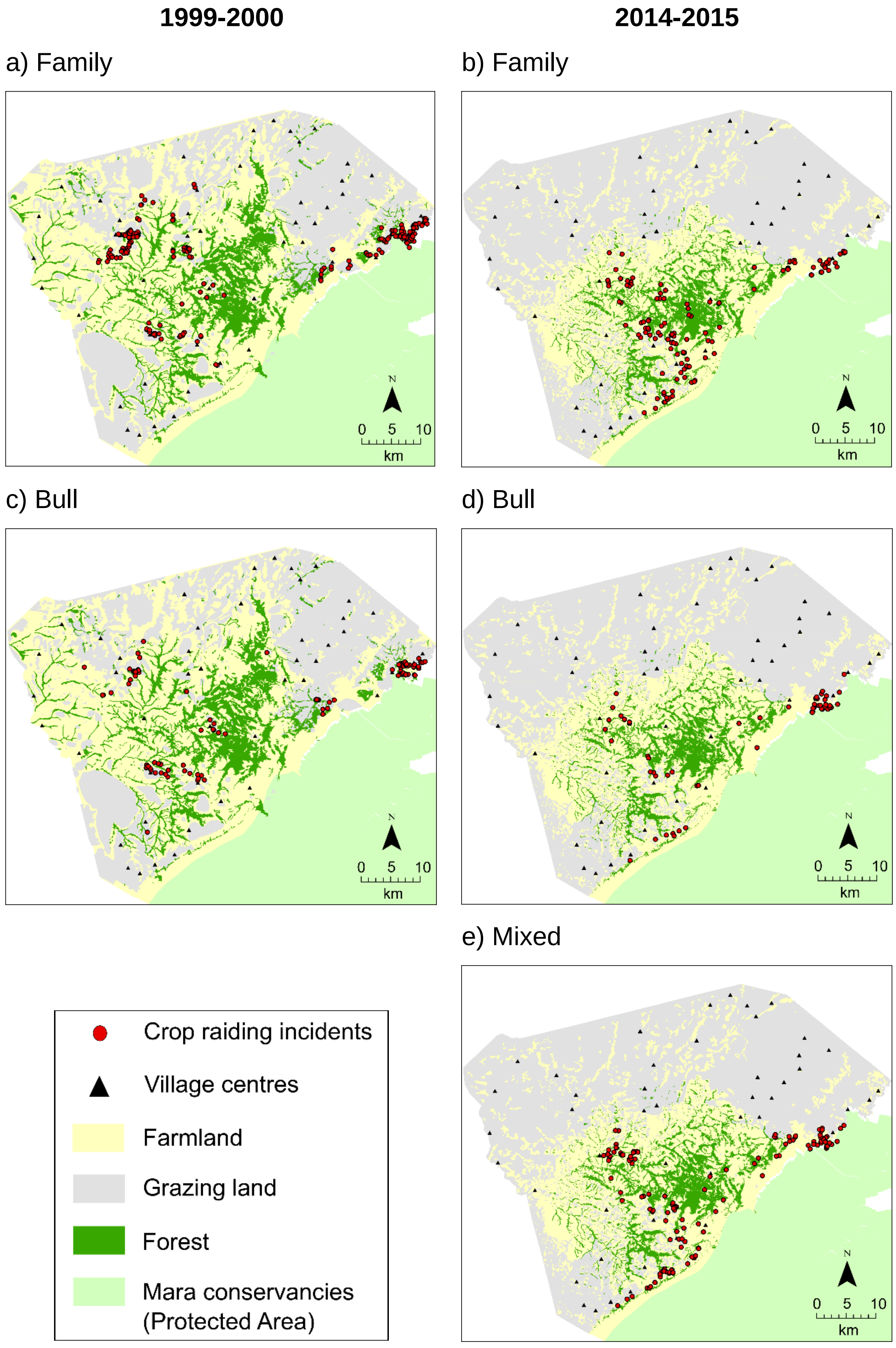


Figure 3. Locations of crop-raiding incidents of the different elephant group types and land cover in the Trans Mara District during 1999- 2000 and 2014-2015.

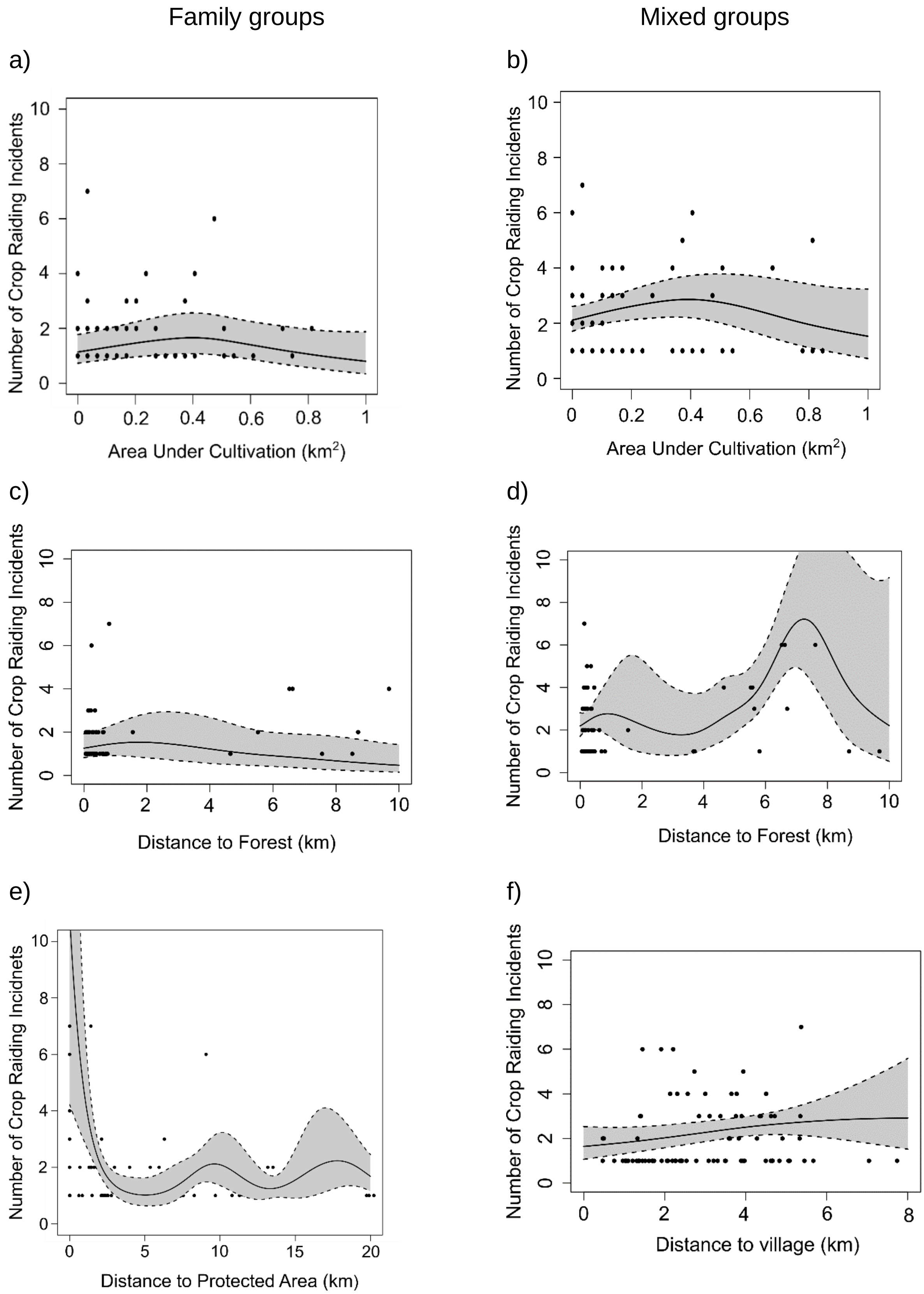


Figure 3. Predicted human-elephant conflict as a function of: (a & b) distance to forest, (c & d) area under cultivation, (e) distance to protected area and (f) distance to village. The dashed lines show the upper and lower confidence limits and the points represent the 1km^2 grid squares in which the data were analysed.