

1 **Abstract**

2 Human-wildlife conflict is increasing due to rapid natural vegetation loss and fragmentation.  
3 We investigated seasonal, temporal and spatial trends of elephant crop-raiding in the Trans  
4 Mara, Kenya during 2014-2015 and compared our results with a previous study from 1999-  
5 2000. Our results show extensive changes in crop-raiding patterns. There was a 49% increase  
6 in incidents between 1999-2000 and 2014-2015 but an 83% decline in the amount of damage  
7 per farm. Crop-raiding went from highly seasonal during 1999-2000 to year-round during  
8 2014-2015, with crops being damaged at all growth stages. Additionally, we identified a new  
9 elephant group type involved in crop-raiding, comprising of mixed groups. Spatial patterns of  
10 crop-raiding also changed, with more incidents during 2014-2015 neighbouring the protected  
11 area, especially by bull groups. Crop-raiding intensity during 2014-15 increased with farmland  
12 area until a threshold of 0.4 km<sup>2</sup> within a 1 km<sup>2</sup> grid square, and farms within 1 km from the  
13 forest boundary, <5 km from the protected area boundary and >2 km from village centres were  
14 most at risk of crop-raiding. In the last 20 years the Mara Ecosystem has been impacted by  
15 climate change, agricultural expansion and increased cattle grazing within protected areas.  
16 Elephants seem to have responded by crop-raiding closer to refuges, more frequently and  
17 throughout the year but cause less damage overall. While this means the direct economic  
18 impact has dropped, more farmers must spend more time protecting their fields, further  
19 reducing support for conservation in communities who currently receive few benefits from  
20 living with wildlife.

## 21 **Introduction**

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

35

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

46 behaviour can vary across sites, by elephant group type and over time, depending on the  
47 landscape and the behaviour of people towards elephants.

48

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

58

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

70

71 **Methods**

72 *Study Area*

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

94

95

**Table 1**

96

97 ***Data collection***

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

112

113 ***Analysing characteristics of elephant crop-raiding***

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

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

124

#### 125 *Analysing temporal and seasonal patterns of crop-raiding*

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

133

#### 134 *Analysing spatial patterns of crop-raiding*

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

143

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

146 Wallis and Mann-Whitney U tests. Second, we repeated the approach by Sitati et al. (2003)  
147 using logistic regression to determine the factors that best predict the occurrence of crop-  
148 raiding in a series of 5 x 5 km grid squares. We carried out three separate analyses based on  
149 the three group types, using ArcGIS to calculate the spatial characteristics of each grid square.  
150 There was no serious collinearity between our predictor variables (Supplementary Materials)  
151 so we rescaled them to have a mean of zero and a standard deviation of 1, as this puts the  
152 predictors on a common scale and improves the convergence of statistical models (Gelman et  
153 al. 2008). To find which factors predicted crop-raiding presence we used R (R Development  
154 Core Team 2013) and the lme4 package (Bates et al. 2016) to carry out the logistic regression,  
155 using a binomial error structure and logit link function. We used the package MuMIn (Barton  
156 2016) to evaluate all candidate models; examine the averaged parameter estimates (Beta),  
157 standard errors and confidence intervals of the predictor variables, and; compare models using  
158 the Akaike Information Criteria (AICc), restricting the models to  $\Delta AICc < 4$  to remove  
159 implausible models.

160

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

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

177

## 178 **Results**

### 179 *Characteristics of elephant crop-raiding*

180 Crop-raiding in the Trans Mara increased from 263 incidents per annum during 1999-2000 to  
181 392 incidents per annum during 2014-2015, a rise of 49%, (Table ). Despite the increase in the  
182 number of incidents, there was a decline in the area of damage per incident, as mean damage  
183 of all incidents (including where the group type was Unknown) during 1999-2000 was  $1.17 \pm$   
184  $0.0096$  ha compared to  $0.20 \pm 0.014$  ha during 2014-2015. The percentage of each field  
185 damaged during 2014-2015 was generally low: 67% of incidents involved damage of <10% of  
186 the total cultivated area being damaged, 5% of incidents led to >50% of cultivated area being  
187 damaged, and 2% of incidents led to the entire cultivated area being damaged. Maize was the  
188 main crop eaten during both study periods, and during 2014-2015, maize was damaged in  
189 68.8% of crop-raiding incidents. Additionally, the number of different crops eaten increased  
190 from 18 during 1999-2000 to 26 during 2014-2015.

191

192 Historically, crop-raiding was carried out by two different types of elephant group: (1) family  
193 groups and (2) bull groups, including lone bulls. However, we recorded an additional group  
194 type consisting of a family group and bulls involved in crop-raiding. These mixed groups were



195 involved in the most incidents and caused the highest amount of damage per incident (Table  
196 2).

197

198 **Table 2**

199 ***Temporal and seasonal patterns of crop-raiding***

200 The time each group spent crop-raiding declined between 1999-2000 and 2014-2015, with the  
201 median time for family groups dropping from 3 hours to 1.5 hours and the median time for bull  
202 groups dropping from 1.5 hours to 1 hour (Table 2). The crop raiding incident duration during  
203 2014-2015 for mixed groups was the same as for family groups.

204

205 During 1999-2000 there were clear peaks in crop-raiding, one month experienced no crop-  
206 raiding, and the majority of crops damaged were mature or dry crops (Figure 1). During 2014-  
207 2015, crop-raiding occurred in every month during the 18-month monitoring period and  
208 affected crops at every growth stage. There was a decline in crop-raiding incidents in February  
209 2015, September 2015 and October 2015 related to the period after maize harvesting. Monthly  
210 rainfall fluctuated more during 2014-2015, ranging from 5.9 mm to 230.4 mm as compared to  
211 more consistent monthly rainfall between 44.6 and 113.2mm during 1999-2000 (Figure 1).  
212 Although, the 1999-2000 data only represented 12 months of rainfall compared to 18 months  
213 from 2014-2015.

214

215 ***Spatial patterns of crop-raiding***

216 Crop-raiding incidents were spatially clustered in both 1999-2000 and 2014-2015 but their  
217 locations partially changed (Figure 2). During 1999-2000, more incidents occurred in the  
218 northwest of the Trans Mara, whereas crop-raiding during 2014-2015 occurred along the edge

219 of the protected area and close to the forest. The cluster of crop-raiding incidents in the east of  
220 the region was the same for both time periods.

221

### 222 **Figure 1**

223

224 There were differences in the distances that groups travelled from the forest to crop-raid ( $n =$   
225  $373$ ,  $\chi^2 = 12.393$ ,  $df = 2$ ,  $p = 0.002$ , Figure S5), with family groups raiding closest to the forest,  
226 followed by mixed groups and then bull groups (Table S1). The opposite pattern was shown  
227 for distance to protected areas, with family groups raiding furthest from the protected areas ( $n$   
228  $= 373$ ,  $\chi^2 = 12.315$ ,  $df = 2$ ,  $p = 0.002$ , Table S1).

229

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

236

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

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

249

250

### **Table 3 and Figure 4**

## **251 Discussion**

### **252 *Characteristics of elephant crop-raiding***

253 Elephant crop-raiding in the Trans Mara has changed markedly since 1999-2000, with incidents  
254 per annum increasing by 49%. This is most likely due to the 63% increase in human population  
255 in the region and agricultural expansion, as farmland increased by 42.5% (Table 1, Tiller,  
256 2018). Despite the increase in the number of crop-raiding incidents, the actual amount of  
257 damage per farm during 2014-2015 was much lower than during 1999-2000. The mean damage  
258 per incident was 1.17 ha during 1999-2000, compared to 0.20 ha during 2014-2015, and so the  
259 total amount of damage per annum dropped from 308 ha to 78 ha. There could be a number of  
260 reasons for this. First, the mean farm size decreased from 3.4 ha during 1999-2000 to 2.2 ha  
261 during 2014-2015, potentially reducing food availability and making it more difficult to crop-  
262 raid undetected. Second, the recorded increase in retaliatory killings (Table 1) may have made  
263 elephants more risk averse and more likely to curtail a crop-raiding incident. Third, farmers  
264 may have become more effective at guarding their fields, using the same tried and tested  
265 approaches based on guarding their fields throughout the night and using deterrents, such as  
266 fences, fire and fireworks (Sitati et al. 2005; Sitati & Walpole 2006). Fourth, recent estimates  
267 suggest the Trans Mara elephant population has declined since 1999-2000, although the Masai

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

270

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

282

283 We also found that the types of elephant group involved in crop-raiding has changed, as there  
284 was an additional group type of mixed groups comprising of family groups plus one or more  
285 bulls. Family groups have traditionally been most responsible for crop-raiding in the Trans  
286 Mara (Sitati et al. 2003) which is in contrast to studies from other parts of Africa where raiding  
287 is mostly by bull groups (Hoare 1999a; Chiyo & Cochrane 2005). Three possibilities could  
288 explain this finding : (1) family groups in the Trans Mara are less risk averse; (2) food quality  
289 is lower in the Trans Mara and so family groups have to adopt more risky behaviour to meet  
290 their nutritional requirements; (3) risks are lower, possibly because the long boundary between  
291 farmland and elephant refuges makes it easier to remain undetected. Thus, the formation of  
292 mixed groups could be because these risks have further reduced, allowing bigger groups to

293 successfully avoid detection. Alternatively, it could be that risks have increased and so family  
294 groups prefer to crop-raid with bulls that may have more experience of encountering people.  
295 Also, it may be safer to crop-raid in larger groups (Songhurst et al. 2015), which is reflected in  
296 the larger elephant group size that we recorded during 2014-2015 compared to 1999-2000. The  
297 fact that incidents were shorter and caused less damage supports the hypothesis that this is a  
298 response to increased risks, but further research is needed to understand this change and its  
299 implications for mitigation management.

300

### 301 *Seasonal patterns of crop-raiding*

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

316

317 *Spatial patterns of crop-raiding*

318 Crop-raiding incidents in the Trans Mara were highly clustered, as is widely reported  
319 throughout Africa (Graham et al. 2010; Songhurst & Coulson 2014). However, the locations  
320 of crop-raiding partly changed, with fewer incidents in the northwest as compared to 1999-  
321 2000, and more along the edge of the protected areas and close to large forest patches. Land  
322 cover data suggest this shift is due to the spread of agricultural land since 1999-2000 (Tiller,  
323 2018), fragmenting the forest and leaving the northwest of the region largely transformed  
324 (Table 1), leaving fewer forest patches in which elephants can seek refuge before or after crop-  
325 raiding (Graham et al. 2009; Wilson et al. 2013). We also found there were differences between  
326 elephant group types, as family groups crop-raided closest to the forest, followed by mixed  
327 groups and then bull groups. In this case, bull groups could be greater risk-takers than family  
328 groups as they travel further from the forest to crop-raid. The opposite pattern was shown for  
329 distance to protected areas, with bull groups crop-raiding closest to the protected area, although  
330 in general incidents were much further from the protected area than from forest patches. This  
331 suggests the Masai Mara National Reserve is acting as a source, rather than a staging post, for  
332 crop-raiding elephants.

333

334 To look at spatial predictors of crop-raiding, we first investigated changes since 1999-2000 by  
335 repeating the analysis of Sitati et al (2003), based on 25 km<sup>2</sup> sampling units. Like this previous  
336 study, we found that area under cultivation was a predictor of crop-raiding, but in our case, this  
337 only applied to family and mixed groups and the relationship was opposite, with more crop-  
338 raiding in units with the least farmland cover. A possible explanation is that during 1999-2000  
339 many of the sampling units were completely forested, so the units with the highest amount of  
340 farmland contained the most crops but were also close to forest patch refuges. In contrast, by  
341 2014-2015 deforestation meant the sampling units with the most farmland tended to be much

342 further from forest patches. Instead, the units that were raided tended to include forest patches  
343 and so had less farmland cover (Sitati et al. 2003; Graham et al. 2010; Wilson et al. 2013;  
344 Goswami et al. 2015). Thus, in effect both the 1999-2000 and 2014-2015 models predicted that  
345 elephant crop-raiding depended on the presence of elephants and crops, although how this  
346 correlated with the measured factors changed with time. This intuitive result provides little  
347 information to help inform mitigation, highlighting the need for new, more-detailed spatial  
348 analyses at a much finer scale.

349

350 To analyse the 2014-2015 data at a finer scale, we used Generalised Additive Models that  
351 accounted for the spatial autocorrelation in the 1 km<sup>2</sup> resolution dataset. We found that crop-  
352 raiding by both family and mixed groups was related to the availability of crops and distance  
353 to forest, and also that family groups raided closer to protected area, and mixed groups raided  
354 further from village centres. For both group types, crop-raiding increased with area of the  
355 planning unit under cultivation until a threshold of 40% of the 1 km<sup>2</sup> sample unit was farmland,  
356 after which it declined. At this point, the risk of human retaliation may have been too high  
357 because refuges were too far away (Graham et al. 2009), providing more evidence that  
358 deforestation has driven the observed change in crop-raiding spatial patterns. Our analysis also  
359 showed that farms 1 km from the forest boundary, 5 km from the protected area boundary and  
360 >2 km from village centres were most at risk of crop-raiding, although there was a multimodal  
361 pattern at larger distances which supports anecdotal evidence that elephants based inside the  
362 protected area show different crop-raiding patterns than those found outside (Figure 3d and  
363 3e). These findings are consistent with other studies showing that more crop-raiding occurs  
364 within 6 km of the forest or protected area (Graham et al. 2010; Gubbi 2012; Guerbois et al.  
365 2012), and in areas with lower densities of people (Graham et al. 2010; Chen et al. 2016).  
366 Therefore, targeting mitigation in these ‘hotspots’ could be effective. These results also show

367 the advantage of using a Generalised Additive Model to analyse crop-raiding patterns, as it  
368 provides more nuanced information about the spatial patterns. However, it also requires more  
369 data, so in this case we could not analyse crop-raiding by bull groups and so could only gain  
370 insights from the univariate and logistic regression analyses.

371

### 372 *The future co-existence of humans and elephants*

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

382

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





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

<b>Types of changes in the Trans Mara</b>	<b>1999-2000</b>	<b>2014-2015</b>
Number of people	168,721 (1999 census)	274,500 (2009 census)
Area of farmland (km <sup>2</sup> )	945.7	1347.8
Mean farm size (ha)	3.4	2.2
Forest cover (km <sup>2</sup> )	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

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

<b>Crop-raiding Characteristics</b>	<b>1999-2000</b>		<b>2014-2015</b>		
	(329 incidents in 15 months)		(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

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

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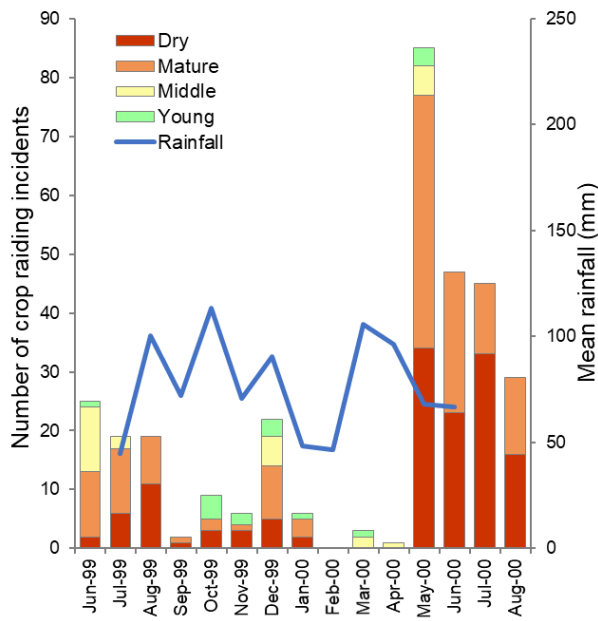
541 **Table 3.** GAM model outputs for the family group and the mixed group analyses. GAM  
 542 models provide a technique that fits a smooth relationship between the explanatory variables  
 543 and the response variable. The greater the value of the estimated degrees of freedom (edf),  
 544 the more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

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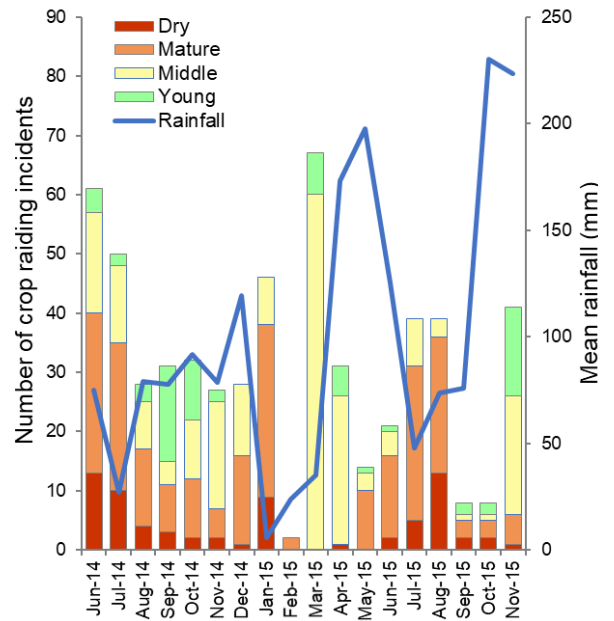
**1999-2000**

a)

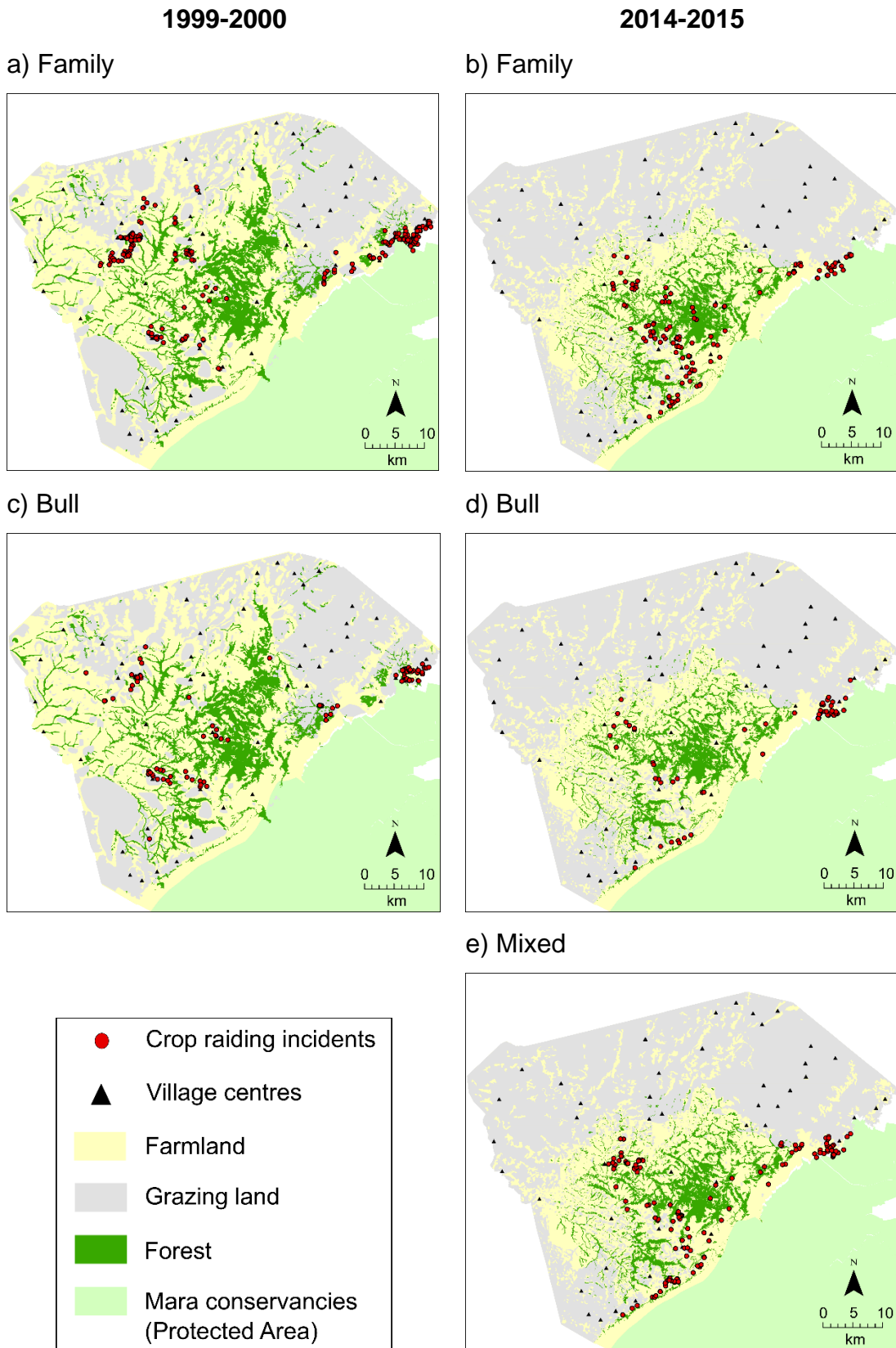


**2014-2015**

b)

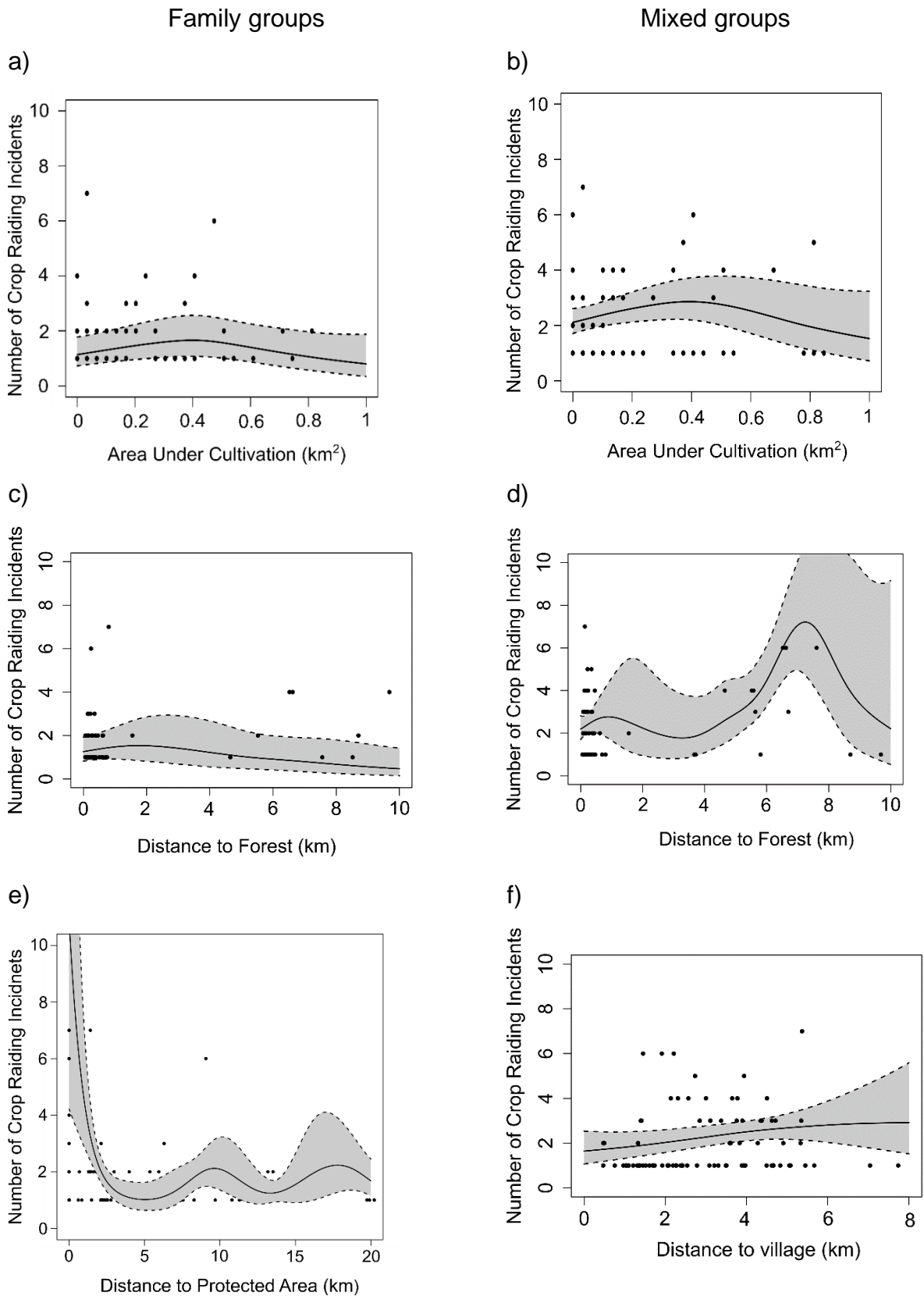


546 **Figure 2.** Elephant crop-raiding (a) seasonal patterns during 1999-2000 and (b) seasonal  
 547 patterns during 2014-2015. The seasonal patterns show the number of incidents for each crop  
 548 age group and mean rainfall per month (mm).



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

551



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