

**Elephant space use is not a good predictor of crop damage.**

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## 51 **ABSTRACT**

52 Elephant crop-damage is a consequence of interactions between people and  
53 elephants that impact people's livelihoods and biodiversity conservation  
54 efforts. Conflicts between people and elephants usually occur when there is  
55 overlap in elephant and human space-use leading to competition for  
56 resources. Therefore, understanding space-use patterns by elephants is key  
57 to alleviating negative human-elephant interactions. In the eastern Okavango  
58 Panhandle (Botswana), more than 16 000 people share resources with 18  
59 000 elephants. Using data from 20 GPS-collared elephants, we investigated  
60 elephant space-use in relation to landscape variables during the day and night  
61 throughout the year and during the dry, wet and crop-damage seasons. We  
62 compared elephant space-use and crop-damage occurrence during the crop-  
63 damage seasons of 2014-2016. We found that elephant space-use was  
64 determined primarily by distance to waterholes and areas away from  
65 agricultural fields. However, predicting elephant space-use at the large scale  
66 was challenging. In particular, during the crop-damage season when the  
67 relationship between crop-damage events and elephant distribution was found  
68 to be non-linear. This revealed that areas that elephants frequently use might  
69 not be good indicators of the likelihood of crop-damage. Based on our  
70 findings, we suggest deterring elephants from peoples' crops at the local  
71 scale is the most appropriate strategy for reducing elephant impacts on crops,  
72 alongside landscape scale interventions. We encourage future studies to use  
73 combinations of spatiotemporal methods, as well as practitioners to focus  
74 their efforts at the local scale, protecting elephant corridors, and supporting  
75 farmers to collaboratively work to decrease elephant crop-loss.

76  
77 **KEYWORDS** Human-wildlife conflict; crop-raiding; crop-loss; movement;  
78 satellite collar; Botswana.

## 80 **1. INTRODUCTION**

81 Human-wildlife interactions have increased in the last decades as a result of  
82 expanding human activities and a concurrent loss of natural habitats for  
83 wildlife (Barnosky et al. 2011; Liu et al. 2003). Increased interactions between  
84 people and wildlife can result in competition for natural resources. Over time,  
85 this competition may develop into conflict between those affected by wildlife  
86 and groups wishing to conserve biodiversity (Redpath et al. 2015; Young et al.  
87 2010). 'Conservation conflicts' are not only one of the most pressing  
88 challenges facing biodiversity conservation (Redpath et al. 2013; Woodroffe et  
89 al. 2005), but they are also hugely detrimental to the economic development  
90 and wellbeing of local people (Redpath et al. 2015; Thirdgood et al. 2005).  
91 Although numerous factors make each conflict unique (Redpath et al. 2013), a  
92 common aspect across conflicts is that species frequently move across  
93 human dominated landscapes, which highlights the fact that these conflicts  
94 are often spatial in nature. Thus, studying the space use of species is a key  
95 step in understanding how and why conflicts might occur, providing vital  
96 information for conservation strategies aimed at reconciling the interests of  
97 wildlife conservation and those of local stakeholders (Douglas-Hamilton et al.  
98 2005; Treves et al. 2004).

99 Crop-damage by elephants is a significant problem in many countries  
100 in Africa, affecting the local livelihoods of countless rural human populations

(Hoare 2000; Sitati et al. 2003). Elephant crop-damage (ECD) generally takes place during the night (Barnes et al. 2007; Jackson et al. 2008), and occurs particularly in isolated fields rather than in populated areas (Graham et al. 2010; Songhurst and Coulson 2014). Bulls have been more frequently recorded damaging crops (Hoare 1999; Sitati et al. 2003; Smit et al. 2017), because of their risk-taking behaviour to maximise reproductive success (Sukumar 1991), although cow-calf groups have also been observed to feed on crops (Sitati et al. 2003; Smith and Kasiki 1999). It is extremely dangerous for farmers to defend their fields because – unlike other species – elephants can cause severe harm, and even death, to people (Naughton-Treves et al. 1999; Thirgood et al. 2005). In retaliation for ECD, farmers will sometimes kill elephants, closing in this way a cycle of conflict affecting both humans and elephants. Negative perceptions and lethal retaliation as a result of ECD are some of the most important threats to elephant populations worldwide (Hoare 1999; Lamarque et al. 2009).

The incidence of ECD has increased in recent decades partly because of the expansion of agricultural land into natural habitats. This increase is reflected in the number of studies describing the distribution and drivers of crop-damage (see Chiyo et al. 2005; Graham et al. 2010; Sitati et al. 2003, 2005; Songhurst and Coulson 2014). However, those studies that have focused on the spatial factors determining crop-damage incidence have not necessarily combined these insights with observed space-use by elephants. On the other hand, elephant movement studies have predominantly focused on ecological questions relating to home ranges, individual trajectories, and the speed of elephants in relation to specific landscape features such as water sources or protected areas (see Birkett et al. 2012; Loarie et al. 2009; Polansky et al. 2015). Few studies have used the whereabouts of elephants to better understand their spatial preferences and whether these relate to ECD locations at different times of the year (Graham et al. 2010; Jackson et al. 2008). Such a spatiotemporal approach may be far more useful to land-use planning efforts, as well as to better understand if the spatial overlap of elephant populations with people is a good indicator of the level of conflict with agricultural activities (Pozo et al. 2017a; Neumann et al. 2012).

The eastern Okavango Panhandle (Botswana) is home to the largest unprotected populations of African elephants (*Loxodonta africana*) in the world (Chase et al. 2016). The size of this population has increased in recent years (DWNP 2013; Pozo et al. 2017a; Songhurst et al. 2016), having benefitted from the continuous supply of water from the Okavango River and a low level of poaching relative to neighbouring countries (Chase et al. 2016). Here, more than 18 000 elephants share resources with an increasing number of people (CSO 2011; Pozo et al. 2017a) throughout the dry (May-October) and wet (November-April) seasons. In this area, farmers plough their fields in fertile soils away from the Okavango River, close to which land is of less good quality for crops. Ploughing takes place at the beginning of the wet season, and the harvest happens between January and April, a period known as the cropping season (Songhurst and Coulson 2014). This is also the time when elephants are more likely to forage in fields, and thus this period is also known as the crop-damage season. To minimise ECD, a number of mitigation strategies have been implemented in recent years (Pozo et al. 2017b), such as land-use management and the identification and protection of elephant

corridors (Songhurst et al. 2015). All of these would benefit from a clearer understanding of elephant space-use in the region (Pozo et al. 2017a,b).

In this study, we analysed and predicted elephant space-use patterns across the eastern Panhandle from Global Positioning System (GPS) telemetry data, and compared these to the distribution of contemporaneous crop-damage incidents. Our goal was first to characterise elephant distribution in the eastern Panhandle across seasons (dry, wet and crop-damage), as well as during the day and at night. Secondly, we used the distribution of reported crop-damage locations to identify vulnerable agricultural land and predict a risk map of crop-damage in the study area. Lastly, we combined both predictions (distribution of elephants and crop-damage locations) to determine the intensity of space-use by elephants at which crop-damage incidents are more likely to occur in the study area.

## 2. MATERIALS AND METHODS

### 2.1 Study area

The 8 732 km<sup>2</sup> non-protected study area is located in the eastern Okavango Panhandle, in northern Botswana. Deep Kalahari sands cover the majority of the region, with fertile soils away from the Okavango River. Vegetation cover is represented by mopane (*Colophospermum mopane*) and acacia (*Acacia erioloba*, *Acacia tortillis*) woodlands, and mixed marginal floodplain (*Acacia nigrescens*, *Hyphaene petersiana*) (Roodt 1998). The Delta has a continental climate with 360-500 mm annual rainfall during the wet season (November-April) (Ramberg et al. 2006). Daily temperatures range from 25-35°C during the day to an average of 8°C during the night (Ramberg et al. 2006). The hottest month of the year is October, at the end of the dry season (May-October).

The study area is delimited by the Namibian border to the north, the Okavango River to the southwest and the northern buffalo fence on the south-eastern edge (Fig. 1). Elephants stay in this area due to the presence of artificial (veterinary fencing) and natural (the Okavango River) barriers. More than 16 000 people live in 13 villages along the Okavango River (CSO 2011; Fig. 1). Local farmers cultivate fields from the river edge up to 15 km inland. Ploughing takes place during the wet season and crops are harvested every year between April-June (Jackson et al. 2008). Most ECD events take place at the end of the wet season between January-April (Songhurst 2017).

### 2.2 Data collection

Elephant relocations were collected by the Ecoexist Project from GPS collars (Iridium Vectronic) fitted to 10 females and 10 males in April 2014 (Appendix, Table A1). Each collar was set to give hourly GPS fixes. Individuals were selected using a spotter plane, and subsequently darted and immobilized from a helicopter. All collaring procedures were supervised by a veterinarian and performed under the research permit EWT 8/36/4 XVII (79) as well as affiliated immobilization permits. To reduce bias towards any specific area within the eastern Panhandle, individuals were selected from independent herds. Females were selected based on their body size (larger individuals were preferred) and on the age of their calf (>3 years) if any. All collared males were older than 20 years (Songhurst 2014). For this study, we considered data collected between April 2014 and April 2016.

Using Quantum Geographic Information System (QGIS version 2.12.1-Lyon) and Google Earth (v 7.1.5.1557, 2016) images, we digitised layers pertaining to human land-use (i.e. settlements and agricultural fields), water sources (i.e. the Okavango River and waterholes) and elephant corridors. The resulting layers were ground-truthed using GPS locations taken on the ground as well as from aerial surveys and large-scale aerial photographs (1: 50 000). Elephant corridors were determined using ground monitoring, field vulnerability surveys and participatory land-use planning (Songhurst et al. 2015).

In addition, we analysed crop-damage data collected in the study area during the same time as elephant movements were recorded. Crop-damage data was collected following Hoare (1999), by selecting local enumerators and training them to identify crop-damage events in each village. Enumerators visited damaged fields throughout the year, taking a GPS location and additional data on the scale of foraging damage at each crop-damaged plot (Songhurst 2017).

## **2.3 Data analysis**

### **2.3.1 Elephant distribution**

We estimated a utilization probability distribution (UD; Worton 1995) for each of the 20 collared elephants using a Brownian bridge movement model (BBMM, hereafter; Horne et al. 2007) applied to the corresponding trajectory. The BBMM is a continuous-time stochastic model of movement in which the probability of being in an area is conditioned on the time between consecutive locations of an individual and its estimated mobility. It uses a sequence of time-specific location data, the estimated error associated with the location data, and a grid-cell size for the output UD (Sawyer et al. 2009) to estimate animal space-use. Given elephants move between 2-6 km a day in our study area (Loarie et al. 2009), we use grid-cells of 5 km<sup>2</sup> to facilitate data analysis, provide realistic space use patterns and adequate mapping resolution.

Assumptions of the BBMM are that location errors correspond to a bivariate normal distribution, and that relocations are not independent. Given that our GPS relocations are recorded every hour and that the assumption of normally distributed errors is appropriate for GPS data (Horne et al. 2007; Sawyer et al. 2009), our dataset fulfilled both BBMM requirements. Due to satellite failure, 8.4% of all fixes were collected with more than 1-hour interval. This was not considered a problem because BBMMs accounts for unequal time intervals between locations (Horne et al. 2007). We implemented BBMMs using functions in the R packages *adehabitatHR* and *BBMM*. Specifically, we used the function *brownian.bridge* to estimate UD across the grid. The *brownian.bridge* function estimates the motion variance given an individual trajectory and a specified location error (here set to 100 m). In the following analyses, we consider UD conditional on the corresponding 99% home range contours in order to avoid estimating utilisation probabilities in areas outside the study area (e.g. the western Panhandle).

We first estimated four different UD per individual elephant, each of these representing one of four temporal periods: all study years combined, dry (May-October), wet (November-April) and crop-damage (January-April) seasons. In our study area, elephants use space differently during the day and night (Loarie et al. 2009; Pozo et al. 2017b), therefore joint UD for all

elephants (hereafter, population UD) during the day (06:00-18:00) and night (18:00-06:00) were created. These describe the probability of finding any of the collared elephants, in a given grid-cell and period of time. Joint UDs were obtained by summing individual UDs and re-scaling to sum to one. We repeated the same procedure across years to obtain a single population UD per season. This approach resulted in a single probability map for all individuals throughout the year, as well as during the day and night of the dry, wet and crop-damage seasons. All UDs were projected onto a 1 112-cell grid (i.e. excluding grid-cells not occupied by elephants), each with a specific probability of finding at least one individual from a particular category (e.g. elephants during the day in the dry season).

We performed our statistical analysis in 2 stages. As a first step, we used generalised linear models (GLMs) with binomial errors to model the probability of cell use by each of the 20 collared elephants across all years, as well as during the dry, wet and crop-damage seasons. Our response in this case consisted of a binary variable indicating occurrence (1) or not (0) of each individual in each cell. Secondly, to determine the drivers of space-use intensity, we used beta regressions (Ferrari and Cribari-Neto 2004) to model population UD values (excluding cells with UD=0) against the distance to five landscape features: peoples' settlements, agricultural fields, elephant corridors, waterholes and the Okavango River. However, we found high levels of multicollinearity among some of the explanatory variables (i.e. variance inflation factor, VIF > 5) and as a result our final models across seasons only considered distance to agricultural fields, elephant corridors and waterholes as predictor variables. We used the *betareg* function (betareg R package) applied to each population UD throughout the year and per season during the night and day (i.e. 7 models). For all seasons, Moran's I test revealed significant spatial auto-correlation (Legendre and Legendre 1998) between neighbouring UD probabilities, and as a result we included a distance-weighted autocovariate obtained using the function *autocov\_dist* (spdep R package) as an additional explanatory variable in all regressions (Chen et al. 2015; Dorman et al. 2007). Lastly, we predicted the expected distribution for the entire population of elephants (i.e. not only the 20 collared individuals) in each season. To do this, we used our full models (i.e. those including agricultural fields, corridors and waterholes) across years, and for each season (i.e. dry, wet and crop-damage). In doing this, we assumed all of the explanatory variables influenced elephant space-use.

Because of the suspected variation in space-use across individual elephants, we additionally performed an analysis at the individual level. To do this, we used beta regressions to determine the relative influence of the distance to each of the three landscape variables on cell UD for collared females and males. To avoid bias due to spatial autocorrelation, we calculated and included a spatial autocovariate as an explanatory variable in each individual model. In both cases (population and individual analysis), we scaled continuous variables to a mean of zero and standard deviation of one prior to model implementation so that resulting coefficient estimates could be compared.

### 2.3.2 Crop-damage distribution

We used crop-damage incidence data to: a) calculate a traditional fixed kernel

distribution (Calenge 2015) and contour isopleths of 50%, 20% and 10% of foraging incidents in the study area; and b) to predict a risk map of ECD occurrence for the eastern Panhandle. To compare the distribution of damage incidents with that of elephants, we mapped crop-damage data onto the same 1 112-cell grid as for the elephant space-use analysis. For each cell, we allocated a 0 when no foraging incidents had been recorded, and a 1 if they had (i.e. binary response). We applied a traditional kernel method via the *kernelUD* function in the *adehabitatHR* package in R to produce a distribution of crop-damage events across the study grid (Calenge 2011; Chen et al. 2015), and subset the 50%, 20% and 10% contours to identify areas that had been more affected by ECD. To predict crop-damage incidents we used generalised linear models (GLMs) with quasibinomial errors and a logit link function to regress the binomial crop-damage response against the same landscape features used for the elephant distribution analysis (i.e. distance to agricultural fields, elephant corridors and waterholes). Moran's I test revealed spatial auto-correlation between ECD locations, and so we added an autocovariate as explanatory variable to the global model. Lastly, we used our full models to predict the likelihood of crop-damage occurring throughout the eastern Panhandle.

To better understand the spatial relation between the likelihood of ECD events and elephant space-use, we used Generalised Additive Models (GAMs; Hastie and Tibshirani 1990) with Gaussian error structure and identity link function. For this analysis, we used the *mgcv* package in R to regress predicted ECD values against the predicted distribution of elephants during the crop-damage season. We used R (ver. 0.13.17) for all analyses.

## 4. RESULTS

### 4.1 Elephant distribution

Elephant occurrence throughout the year was primarily determined by proximity to waterholes and increased distances to agricultural fields (Table 1). In addition, our most general model (i.e. all seasons at all times) showed that, within areas used by elephants, the intensity of space-use by the species was significantly determined by shorter distances to elephant corridors (Fig. 2; Table 2). Despite providing an overview of the occurrence and use of space by collared elephants in our study area, both general models (all season at all times; Tables 1 & 2) provided little information on seasonal processes. This is the reason why we also investigated each season separately.

Without exception, all models (i.e. across seasons and during the day and night times) showed a negative effect of distance to waterholes on elephant occurrence, and a positive effect of distance to agricultural fields (Table 1). Similarly, all models regardless of the season showed a negative effect of distance to corridors on the presence of elephants (Table 1). However, the effect of distance to elephant corridors on the occurrence of the species was only significant during the crop-damage season (Table 1; crop-damage season, day & night). The dry season analysis showed that elephants spent time in areas close to waterholes throughout the day and night (Fig. 2; Table 1). During the driest months of the year (May-October), the intensity of elephant space-use was restricted to areas close to water sources in comparison to other seasons, with highly used sites more likely to be 'inter-connected' via pathways (Fig. 2).

During the wet season (November-April), our analysis showed that the space-use patterns of collared elephants were more dispersed across the study area than during the dry season (Fig. 2). Our GLMs and beta regression models revealed elephants prioritised areas close to waterholes throughout the wet season, and collared individuals only stayed away from agricultural land during the day (Table 1) and used corridors more intensively at night (Table 2). Lastly, during the crop-damage season (January-April), elephants showed a clear spatial avoidance of the north-eastern section of the study area, as well as of some of the villages along the Okavango River (Fig. 2). The local elephant population showed significant spatial preferences for areas closer to waterholes and corridors, and away from agricultural fields during the day and night (Table 1). However, our analysis suggested an absence of effect of any of the landscape features on intensity of use during the months of the crop-damage season (Table 2).

At the individual level our analysis showed a significant variation in space-use patterns across elephants, but a non-significant difference between females and males (Appendix, Fig. A1). In general, across all seasons, females and males stayed closer to waterholes and corridors, but females seemed to use corridors during the dry, wet and crop-damage seasons more intensively than males (Appendix, Fig. A1). Although we found that both females and males were more likely to use areas close to agricultural land at night-time during the dry and wet seasons, respectively (Appendix, Fig. A1), we did not find significant trends for proximity to fields during the crop-damage season. On the contrary, females and males seemed to avoid agricultural land during the day and at night during the busiest harvesting months (Appendix, Fig. A1).

## 4.2 Crop-damage distribution

The analysis of risk of ECD showed that more than 50% of recorded crop-damage events took place in the north-west and southern parts of our study area (Fig. 3). Our risk map predicted that agricultural land close to Tobera and Mohembo-East, as well as fields between Gunotsoga and Beetsha represented areas of high risk (Fig. 3). The GLM analysis showed that fields close to waterholes ( $-3.8621 \pm 0.89$ ,  $P < 0.001$ ) were more likely to be damaged by elephants, and that distance to corridors did not have a significant effect on the likelihood of elephants damaging crops ( $-0.0355 \pm 0.19$ ,  $P > 0.05$ ).

Our GAMs revealed a non-linear effect of predicted elephant distribution on crop-damage events during the day (*Deviance explained* = 29.6%;  $N=1112$ ;  $P < 0.001$ ) and at night (*Deviance explained* = 33.2%;  $N=1112$ ;  $P < 0.001$ ). The non-linear association between elephant distribution and crop-damage incidence during the night (*smooth term* = 7.185;  $F = 66.04$ ;  $P < 0.001$ ; Fig. 4) was stronger than the effect during the day-time (*smooth term* = 5.634;  $F = 67.42$ ;  $P < 0.001$ ; Fig. 4). This translates as a higher likelihood of ECD in areas with intermediate to low levels of elephant space-use intensity during the night.

## 5. DISCUSSION

Our findings are in agreement with previous research showing that the use of space by elephants is influenced by water availability (Jackson et al. 2008;



Loarie et al. 2009; Polansky et al. 2015) and the presence of corridors as a risk avoidance strategy in proximity to people's settlements (Douglas-Hamilton 2005; Graham et al. 2009; Songhurst et al. 2015). During the crop-damage season, collared individuals in the eastern Panhandle stayed away from people's fields. To this end, we developed a crop-damage risk map to better understand the relative likelihood of damage incidents and its relation to landscape variables in the study area, and we compared this with the intensity of elephant space-use measured over the same time period. We found elephant space-use to be correlated in a non-linear way with the occurrence of crop-damage events during the day and night throughout the crop-damage season. Our study shows that elephant distribution in the eastern Panhandle is challenging to predict at the population level because of the high variation across individuals. Although observed patterns were primarily related to the availability of water, the presence of elephant corridors, and the absence of people's fields, our analysis explained comparatively little variance in elephant space-use. Equally, the non-linearity in the relationship between elephant space-use and the occurrence of crop-damage events signifies that the intensity of space-use by elephants is not a good predictor of the likelihood of crop-loss.

Although our models explained a small amount of variation, they suggest that throughout the year elephant distribution is primarily determined by proximity to waterholes and areas away from agricultural fields. We expected elephants to be away from waterholes during the dry season when there is little water available in them, and close to them during the wet season when more water resources are available away from the Okavango River. In addition, since most human settlements in our study area are close to the river, we also expected elephants to show a preference for waterholes during the wet and the crop-damage seasons to minimise contact with human activities. Nevertheless, our study agrees with previous work suggesting elephants rely primarily on water sources throughout the year, and that they avoid the risk associated with human inhabited areas by adapting their spatial behaviour (Douglas-Hamilton et al. 2005; Sitati et al. 2003).

Elephant space-use during the dry season hinted at a reliance on "routes" connecting highly used areas. This may arise from pre-existing knowledge of reliable water and foraging sources during the driest months (Polansky et al. 2015). Moreover, owing to a drop in temperature during the wet season, elephants may be able to cover greater distances during the day and not only move during the coolest hours as they usually do during the dry season (Wittermyer et al. 2008). These contrasting patterns of elephant space-use between the dry and wet seasons are consistent with previous data collected in the eastern Panhandle and elsewhere in Africa (Birkett et al. 2012; Jackson et al. 2008; Loarie et al. 2009). Consequently, future land-use planning should aim to maintain connectivity between key sources of water in the region (Goswami and Vasudev 2017).

We found marginally different patterns of elephant space-use during the night than during daylight hours, which could be a consequence of elephants moving at times of lower temperatures in the dry season. However, because this pattern was present throughout the year, we argue this behaviour may also be the result of elephants prioritising times of low human activity (Douglas-Hamilton et al. 2005; Hoare and Du Toit 1999; Songhurst et

al. 2015). Such a risk-avoidance strategy, whereby elephants use the cover of darkness, has been demonstrated previously. For instance, Graham et al. (2009) showed elephants in Tanzania and Kenya were more active at night outside protected areas. It is interesting to find free-ranging elephants using the same strategies in an unprotected area such as the eastern Panhandle.

Our individual-level analysis showed that, during the crop-damage season, elephants stayed close to waterholes, tended to stay away from people's fields and used corridors significantly more than during any other time of the year. This contradicts our expectation of finding a strong effect of proximity to fields on elephant space-use. A possible explanation for this behaviour might be that none of the 20 collared elephants feed on crops, and they remain in areas further away from human activities. However, we found this to be unlikely because of the strong correlation our results showed between the likelihood of ECD and the distribution of the local population during the crop-damage season. We, therefore, think that if any of the collared individuals in our study feed on crops, they probably do it opportunistically and for short periods of time, which cannot be represented as trends in our individual space-use analysis. In addition, elephants are probably using corridors more intensively to move away from areas of high risk during the harvesting months, as has been found in previous studies in the same area (Songhurst et al. 2015). An alternative explanation to the field-avoidance behaviour might be that elephants are also using the higher availability of natural resources away from fields exclusively during the crop-damage season, which are less risky to forage on than are crops from fields. This is also supported by our results in the dry and wet seasons when elephants occurred more often close to agricultural land. It is important to emphasise that we were unable to account for additional environmental variables, such as vegetation types and rainfall across seasons. Given that vegetation and crop growth in northern Botswana rely on seasonality (i.e. variation on temperature, rainfall, etc.), our findings should be taken with some caution. Nevertheless, they provide a much-needed starting point to understand elephant space-use patterns and their relation with the levels of crop-damage in the region.

In this context, our study suggests that the relationship between the distribution of crop-damage and elephant space-use is non-linear. We found that ECD had a higher probability to occur within a low intensity of elephant space-use, rather than at the highest levels. This likely reflects that ECD occurs opportunistically when elephants transit through highly used sites (e.g. water sources, vegetation patches) across the study area. This finding could have consequences for future mitigation strategies to reduce ECD. Indeed, studies that only consider elephant distribution as a direct indicator of ECD make the underlying assumption that mitigation should be targeted at areas that are most highly used by the species. Such a strategy would overlook the pathways between highly used areas, where elephants might opportunistically damage crops. Our study highlights the importance of considering elephant and ECD distributions when focusing mitigation efforts across space, and validates the protection of elephant corridors in the eastern Panhandle as a strategy to minimise ECD.

Despite finding that certain landscape covariates determined elephant space-use better than others, predicting the use of space by the species

remained challenging, particularly during the crop-damage season (Pittiglio et al. 2014; Sitati et al. 2003). Our results revealed spatial variation in the distribution of crop-damage based on ECD events, but we did not find strong evidence that elephants were attracted to people's crops. Moreover, high variation in space-use patterns across individual elephants suggests larger sample sizes would be needed to reliably predict crop-damage. Our findings also support the idea that to effectively manage ECD and inform appropriate land-use planning interventions it is important to focus on deterring elephants from people's crops at the local scale alongside understanding elephant space-use patterns (Pozo et al. 2017b).

## 6. CONCLUSION

Our study shows that elephant distribution in the eastern Panhandle is primarily determined by the proximity to waterholes and areas away from agricultural land. Elephants tended to stay away from people's fields and close to elephant corridors during the crop-season; suggesting crop-damage may be an opportunistic behaviour. This was also reflected in a non-linear, negative relationship between the likelihood of ECD and elephant space-use intensity. Thus, we concur with previous studies that high elephant space-use may not be a good indicator of the likelihood of ECD. We highlight that a combination of different spatiotemporal methods, such as those used in this study, represents an integrated and more reliable approach to better understand crop-damage dynamics and tackle ECD issues. This will help prevent negative human-elephant interactions and perceptions developing into conflicts.

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## 9. TABLES

**Table 1.** Summary of generalized linear models (GLMs) for elephant occurrence at all seasons, and during the dry, wet and crop-damage seasons. Each model shows elephant binomial response (i.e. presence or not) as a function of the effect of distance to waterholes, elephant corridors and agricultural fields; as well as its respective distance-weighted autocovariate. The period column shows models including data collected 24 hours a day, during the day (6:00-18:00) and night (18:00-6:00).

Binomial GLMs							
Season	Period	Explanatory variable	Estimate	Std. Error	z-value	Pr(> z )	
all	all times	intercept	6.453	0.548	11.782	< 2e-16	***
		distance to waterholes	-1.160	0.237	-4.900	0.000	***
		distance to corridors	0.132	0.217	0.608	0.543	
		distance to fields	0.533	0.186	2.868	0.004	**
		autocovariate	9.571	0.898	10.664	< 2e-16	***
dry	day	intercept	-0.820	0.104	-7.901	0.000	***
		distance to waterholes	-0.673	0.189	-3.562	0.000	***
		distance to corridors	-0.237	0.172	-1.372	0.170	
		distance to fields	0.265	0.117	2.264	0.024	*
		autocovariate	2.217	0.224	9.901	< 2e-16	***
dry	night	intercept	-0.894	0.103	-8.713	< 2e-16	***
		distance to waterholes	-0.596	0.199	-2.994	0.003	**
		distance to corridors	-0.124	0.161	-0.767	0.443	
		distance to fields	0.266	0.119	-2.235	0.254	*
		autocovariate	1.687	0.184	9.167	< 2e-16	***
wet	day	intercept	1.043	0.121	8.652	< 2e-16	***
		distance to waterholes	-0.620	0.143	-4.326	0.000	***
		distance to corridors	-0.180	0.148	-1.216	0.224	
		distance to fields	0.414	0.110	3.777	0.000	***
		autocovariate	2.695	0.270	9.989	< 2e-16	***
wet	night	intercept	1.018	0.110	9.263	< 2e-16	***
		distance to waterholes	-0.691	0.144	-4.795	0.000	***
		distance to corridors	-0.242	0.146	-1.658	0.097	.
		distance to fields	0.201	0.107	1.876	0.061	.
		autocovariate	1.983	0.225	8.811	< 2e-16	***
crop-damage	day	intercept	0.134	0.093	1.438	0.150	
		distance to waterholes	-0.472	0.160	-2.948	0.003	**
		distance to corridors	-0.663	0.181	-3.669	0.000	***
		distance to fields	0.903	0.130	6.931	0.000	***
		autocovariate	1.925	0.167	11.524	< 2e-16	***
crop-damage	night	intercept	-0.012	0.080	-0.144	0.886	
		distance to waterholes	-0.566	0.154	-3.673	0.000	***
		distance to corridors	-0.822	0.170	-4.848	0.000	***
		distance to fields	0.868	0.121	7.187	0.000	***
		autocovariate	1.234	0.122	10.104	< 2e-16	***



759 **Table 2.** Summary of beta regression models for the intensity of elephant  
760 space-use at all seasons, and during the dry, wet and crop-damage seasons.  
761 Each model shows the elephant population UD<sub>s</sub> as a function of the effect of  
762 distance to waterholes, elephant corridors and agricultural fields; as well as its  
763 respective distance-weighted autocovariate. The period column shows  
764 models including data collected 24 hours a day, during the day (6:00-18:00)  
765 and night (18:00-6:00).  
766

Beta Regression Models							
Season	Period	Explanatory variable	Estimate	Std. Error	z-value	Pr(> z )	
all	all times	intercept	-7.098	0.029	-243.200	< 2e-16	***
		distance to waterholes	-0.080	0.057	-1.416	0.157	
		distance to corridors	-0.170	0.050	-3.386	0.001	***
		distance to fields	0.062	0.032	1.924	0.054	
		autocovariate	0.422	0.013	31.342	< 2e-16	***
dry	day	intercept	-6.155	0.082	-74.959	< 2e-16	***
		distance to waterholes	0.015	0.140	0.105	0.917	
		distance to corridors	-0.181	0.110	-1.641	0.101	
		distance to fields	-0.112	0.071	-1.574	0.116	
		autocovariate	0.170	0.025	6.687	0.000	***
dry	night	intercept	-6.238	0.078	-79.519	< 2e-16	***
		distance to waterholes	-0.045	0.142	-0.315	0.753	
		distance to corridors	-0.171	0.095	-1.812	0.070	.
		distance to fields	-0.047	0.070	-0.672	0.501	
		autocovariate	0.207	0.023	8.889	< 2e-16	***
wet	day	intercept	-6.708	0.043	-155.842	< 2e-16	***
		distance to waterholes	-0.094	0.077	-1.217	0.224	
		distance to corridors	-0.123	0.072	-1.706	0.088	.
		distance to fields	0.040	0.046	0.087	0.386	
		autocovariate	0.253	0.020	12.868	< 2e-16	***
wet	night	intercept	-6.767	0.039	-175.014	< 2e-16	***
		distance to waterholes	-0.002	0.073	-0.021	0.983	
		distance to corridors	-0.147	0.064	-2.275	0.023	*
		distance to fields	0.021	0.042	0.494	0.622	
		autocovariate	0.292	0.019	15.637	< 2e-16	***
crop-damage	day	intercept	-6.438	0.052	-122.672	< 2e-16	***
		distance to waterholes	-0.052	0.084	-0.620	0.536	
		distance to corridors	-0.126	0.092	-1.370	0.171	
		distance to fields	0.108	0.064	1.675	0.094	.
		autocovariate	0.167	0.028	5.938	0.000	***
crop-damage	night	intercept	-6.396	0.052	-123.764	< 2e-16	***
		distance to waterholes	0.052	0.088	0.592	0.554	
		distance to corridors	-0.148	0.096	-1.546	0.122	
		distance to fields	0.078	0.062	1.249	0.212	
		autocovariate	0.133	0.031	4.336	0.000	***

## 10. FIGURE CAPTIONS

**Figure 1.** Study area in the eastern Okavango Delta Panhandle, Botswana (a). White circles represent the thirteen villages (i.e. Mohembo-East, Kauxwi, Tobera, Xakao, Sekondomboro, Ngarange, Mogotho, Mokgacha, Seronga, Gunotsoga, Eretsha, Beetsha and Gudigwa) along the Okavango River (in light grey). White and dark-grey polygons represent the thirteen elephant corridors and agricultural land respectively. Light-grey circles show waterholes. The small southern Africa inset map (b) shows the location of the study area in northern Botswana in white.

**Figure 2.** Utilisation distribution (UD) maps of the elephant population in the eastern Okavango Delta Panhandle. Maps represent population UD during the (a) whole year, (b) the dry (May-October), (c) wet (November-April) and (d) crop-damage (January-April) seasons, at day (06:00-18:00; in orange) and night (18:00-06:00; in light blue) times, respectively. Legend shows symbols for landscape variables (i.e. villages, fields, elephant corridors, waterholes, and the Okavango River) and UD proportions in all maps, respectively.

**Figure 3.** Crop-damage risk map for the eastern Okavango Delta Panhandle. (a) Circled areas show 50% (continuous black line), 20% (dashed black line) and 10% (dotted black line) likelihood of crop-damage events in the study area based on traditional fixed kernel analysis. Risk-map (in red) shows predicted distribution of damage events by elephant during the crop-damage season (January-April), and its spatial overlap with landscape variables (i.e. the Okavango River, waterholes, corridors, fields and villages). Small maps (b and c) represent the overlap between predicted crop-damage events and predicted elephant distribution during the (b) day (06:00-18:00; in orange) and (c) night (18:00-06:00; in blue).

**Figure 4.** Polynomial regression of predicted crop-damage events as a function of predicted elephant distribution. Orange and blue lines represent the best-fitted models for the (a) day (06:00-18:00) and (b) night (18:00-06:00) elephant distributions, respectively.

**11. APPENDIX**

**Table A1.** Summary of the 20 collared elephants in the Easter Okavango Delta Panhandle. Each column gives specific information about individuals ID, sex, number of relocations received between April 2014 and April 2016, and the mean number of relocations per elephant per hour, respectively.

ID	Sex	No. relocations	Mean time between relocations (hours)
E01	male	16839	1.05
E02	male	11814	1.5
E03	male	16193	1.09
E04	female	17133	1.04
E05	female	9848	1.8
E06	female	14239	1.24
E07	male	16951	1.05
E08	male	11783	1.51
E09	female	16831	1.05
E10	female	8668	2.05
E11	male	5150	3.43
E12	female	8484	2.09
E13	male	11444	1.55
E14	male	11135	1.59
E15	female	16606	1.07
E16	female	16210	1.09
E17	female	5924	2.99
E18	male	16724	1.06
E19	male	11426	1.55
E20	female	5878	3.01

**Figure A1.** Individual elephant space use intercepts and standard deviations during the dry (a and b), wet (c and d) and crop-damage (e and f) seasons at day (06:00-18:00; in white) and night (18:00-06:00; in grey) times. Each graph represents one of the three landscape variables included in our analysis (i.e. elephant corridors [Corridors], agricultural fields [Fields], and waterholes [Waterholes]). Black circles and grey squares represent female and male intercepts, respectively. Both separate by a dashed blue line.



