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Research article

Elephant pathway use in a human-dominated landscape

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Habitat loss and fragmentation are two of the biggest threats facing wildlife today. Understanding the role of wildlife pathways in connecting resource areas is key for maintaining landscape connectivity, reducing the impacts of habitat loss and helping address human–wildlife conflict. In this study, we used sign surveys and camera trapping to understand the fine scale movement of elephants moving between a protected area and agricultural zone in the Masai Mara, Kenya. We used generalised linear models to determine factors driving high frequency of pathway use by elephants. Our results showed strong seasonal trends in pathway use, with peaks coinciding with the dry season. However, no correlations between rainfall and pathway use were found. Temporal patterns of pathway use indicate that elephants use risk avoidance strategies by moving between the two areas at times of low human disturbance. Spatial analysis revealed that the most frequently used pathways were closer to farms, saltlicks and forest and those that had a higher percentage of forest cover. Our models also showed a positive relationship between pathway use and the number of elephant crop raiding incidents, highlighting that pathways can play a role in human–elephant conflict. As habitat loss continues, pathways may become more important for linking resources. However, they are also likely to facilitate movement into farmland. The results from this study provide an opportunity for planned management activities to ensure connectivity and to mitigated conflict.

Keywords: connectivity, human–wildlife conflict, land-use planning, *Loxodonta africana*, pathways

Introduction

Habitat connectivity is extremely important for maintaining biodiversity (Haddad et al. 2015, Powers and Jetz 2019), as it underpins dispersal and colonization between habitat patches and so impacts population demography and genetic diversity (Hanski 1998). Therefore, retaining and restoring landscape connectivity has become a crucial goal for

conservation practitioners, especially in the face of continued habitat loss and climate change (Crooks and Sanjayan 2006, Heller and Zavaleta 2009). In heterogenous landscapes, this connectivity often involves wildlife corridors or pathways (Vasudev et al. 2015). These pathways are created by wide-ranging wildlife repeatedly following the same routes when travelling between favoured habitat patches. They can act as least-effort routes to resources (Blake and Inkamba-Nkulu 2004), where individual animals optimise their foraging strategy to gain the most energy for the lowest cost (Stephens and Krebs 1986). Thus, understanding the factors that influence these pathways provides insight into habitat quality and connectivity within a landscape (Von Gerhardt et al. 2014)

Pathways can be particularly important in human-dominated landscapes, where habitat patches are increasingly isolated by the spread of agriculture. They also play a large role in determining the likelihood of wildlife encountering people. This is especially the case in areas where cropland borders protected areas, as the pathways can determine where wildlife enter fields and consume and/or trample crops (Naughton-Treves 1997, Thirgood et al. 2005). Monitoring wildlife movement along pathways and understanding specific pathway usage may offer key insights into patterns of habitat requirements of wildlife in fragmented landscapes. Therefore, there is a need to better understand the role of these pathways in agricultural landscapes and how they influence negative interactions between wildlife and people (Von Gerhardt et al. 2014, Smit et al. 2019). Here we present a case study from Kenya that investigates what predicts the fine scale movement of elephants in an agricultural landscape and how it impacts crop raiding.

African savanna elephants *Loxodonta africana* and forest elephants *Loxodonta cyclotis* are well known for using pathways to move between valuable resources such as water sources, saltlicks and fruiting trees (Vanleeuwe and Gautier-Hion 1998, Blake and Inkamba-Nkulu 2004, Shannon et al. 2009, Von Gerhardt et al. 2014). They also rely on pathways to move through agricultural landscapes, as elephants have large ranges that commonly go beyond the existing network of protected areas (Thouless et al. 2016). Elephants can show deliberate risk avoidance behaviour when using in agricultural areas, as they travel at night to avoid people (Adams et al. 2022). They can also select resources such as water access points with less human development to avoid interacting with people (Buchholtz et al. 2021)

This means that maintaining connectivity for resource access is vital for the long-term viability of elephants and a range of other wildlife species. However, elephants often use these pathways when visiting fields to eat crops, which can have negative impacts on both species as it can severely affect people's livelihoods and lead to retaliatory killing (Choudhury 2004, Linkie et al. 2007, Mariki et al. 2015). Therefore, there is a need to understand the role of pathways in driving these crop raiding patterns, as an important step in land-use planning and managing these interactions (Von Gerhardt et al. 2014, Songhurst et al. 2015, Adams et al. 2017, Smit et al. 2019).

In this study, we used sign surveys and camera trapping to understand the fine scale movement of elephants moving between a protected area and an agricultural zone in the Masai Mara, Kenya. Specifically, we sought to: 1) identify elephant pathways in the study area; 2) understand seasonal and temporal patterns of pathway use by elephants 3) determine elephant group types using the pathways; 4) understand the spatial factors driving pathway use and; 5) determine if high pathway use is correlated with high elephant crop raiding incidents.

Material and methods

Study site

The Trans Mara District (2900 km²) is situated in south-west Kenya. It lies next to the world famous Masai Mara National Reserve, which is part of the Serengeti–Mara ecosystem that sees the annual migration of > 1.2 million wildebeest (Sinclair and Norton-Griffiths 1979) and is home to an estimated elephant population of 2595 individuals (Waweru et al. 2021). The Mara ecosystem is approximately 6000 km², of which ca 25% represents the Masai Mara National Reserve and 75% is unprotected, privately and communally owned land (Walpole et al. 2003). The Trans Mara District's human population is approximately 274 500 (KNBS 2010), which is a 63% increase from 1999. This increase, together with a switch from pastoralism to subsistence farming, has led to rapid land-use change and agricultural expansion (Ogutu et al. 2011, Tiller et al. 2021). Subsistence agriculture is now an important livelihood strategy and, the planting of crops is dependent on rainfall, with planting during the rains, and crop harvesting occurring after the rains. Rainfall is typically bimodal, falling in general in two seasons, the 'long rains' between February and June and the 'short rains' in November and December. A steep escarpment divides the Trans Mara and the Masai Mara National Reserve, which contains a series of natural pathways that allow wildlife to move between them (Fig. 1). Wildlife migrates into the Trans Mara because it contains the Nyakweri Forest, an important area for food, water and saltlicks. However, the forest is declining through land being cleared for charcoal and agriculture (Liyama et al. 2017, Tiller 2018).

Data collection

We identified active pathways along the escarpment with the assistance of local rangers and farmers (Fig. 2). We assumed pathways were in use if the path was devoid of vegetation (Blake and Inkamba-Nkulu 2004), marked with elephant dung or footprints and showed signs of elephant browsing on the bordering vegetation (Von Gerhardt et al. 2014). Pathways that did not show any of these signs were not included in this study. We then mapped each pathway using a Garmin Etrek30 Global Positioning System (GPS). The GPS track was taken from the bottom of the escarpment on the border of the Masai
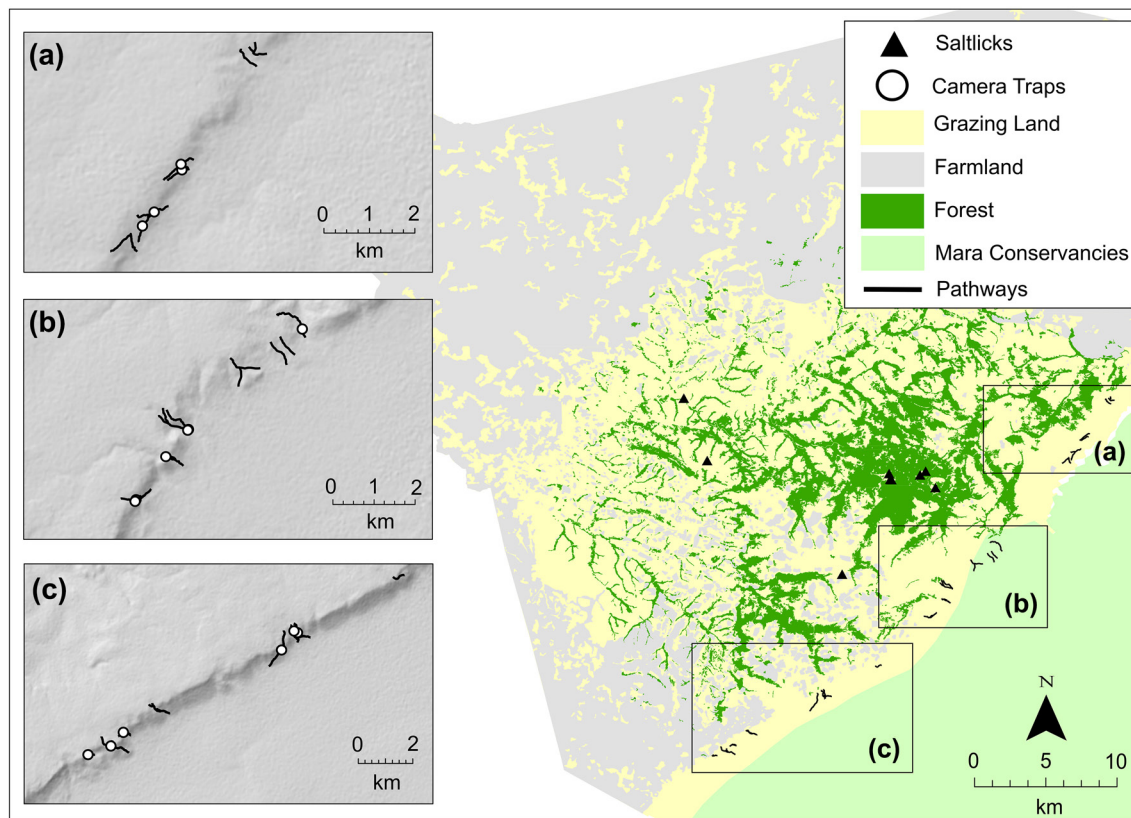
Figure 1. Location of the 22 elephant pathways along the escarpment connecting the Masai Mara to the Trans Mara District. Forest cover is from 2015 (Tiller 2018). Pathways are shown at a finer scale on inserts (a), (b) and (c) which also show the location of the camera traps on 14 of the pathways. Each circle represents 2 camera traps, 1 camera trap facing up the escarpment and 1 camera trap facing down the escarpment to capture the direction of movement of the elephants.

Mara to the top of the escarpment. The end of the pathway was determined by the point at which the pathway widened and became open habitat. Habitat type was also recorded on each pathway using a classification system from Kindt et al. (2011). As each pathway went through a number of different habitats, we used a GPS to record the co-ordinate at which there was a change in habitat type. To determine seasonal pathway use, we conducted bi-weekly elephant dung surveys on each pathway from September 2014 to August 2015. Each survey took 1 to 2 hours, during which we counted dung piles along two predefined transects (one going down the pathway and one going up) to ensure we covered the pathway. We assumed each dung pile represents a single individual. Dung was removed after each count to avoid recounting.

To determine temporal patterns of pathway use and elephant group type using the pathways, we placed 32 heat and motion camera traps (Bushnell Trophy Cam HD 2013) on 14 pathways during two sampling periods: September 2014 – October 2014 and February 2015 – August 2015 (Fig. 2). We were unable to place cameras on all the pathways due to limited camera availability and the unsuitability of some pathways for camera trap placement; i.e. some pathways were too wide or too open to place camera traps. To ensure elephants were captured on the 14 pathways, we placed cameras on the narrowest part or sections where we knew elephants would

cross (e.g. by small water bodies). To obtain suitable photographs of elephants for group type identification, the camera traps were mounted on trees or erected posts at varying heights between 1–3 m depending on the pathway slope. The height of the camera > 1 m was to ensure the best capture of the head, pinnae, and tusks of elephants (Smit et al. 2019). Each pathway had at least one camera facing up the escarpment and one facing down the escarpment to capture the frontal area of the elephant to aid identification of the elephants. There were two pathways which split, so two cameras were placed on each sub-pathway to ensure elephants were captured. Cameras were set at a 5 s trigger interval with three colour images taken per trigger event. At night the camera used infrared and had the same trigger speed. We downloaded the images from memory cards and changed the camera batteries every three weeks.

We created a database of the camera trap images and recorded the site (pathway name), the position of the camera trap (up or down), the type of photo (e.g. wildlife, people or false trigger), the wildlife species in the photo and the date and time the image was taken. Specifically, for the elephant images, we recorded additional information including: 1) the direction in which the elephant was travelling; 2) the number of elephants in the image and; 3) the group type. Group type was classified as i) bull groups, ii) female-led family groups or iii) family + bull groups. Group type was
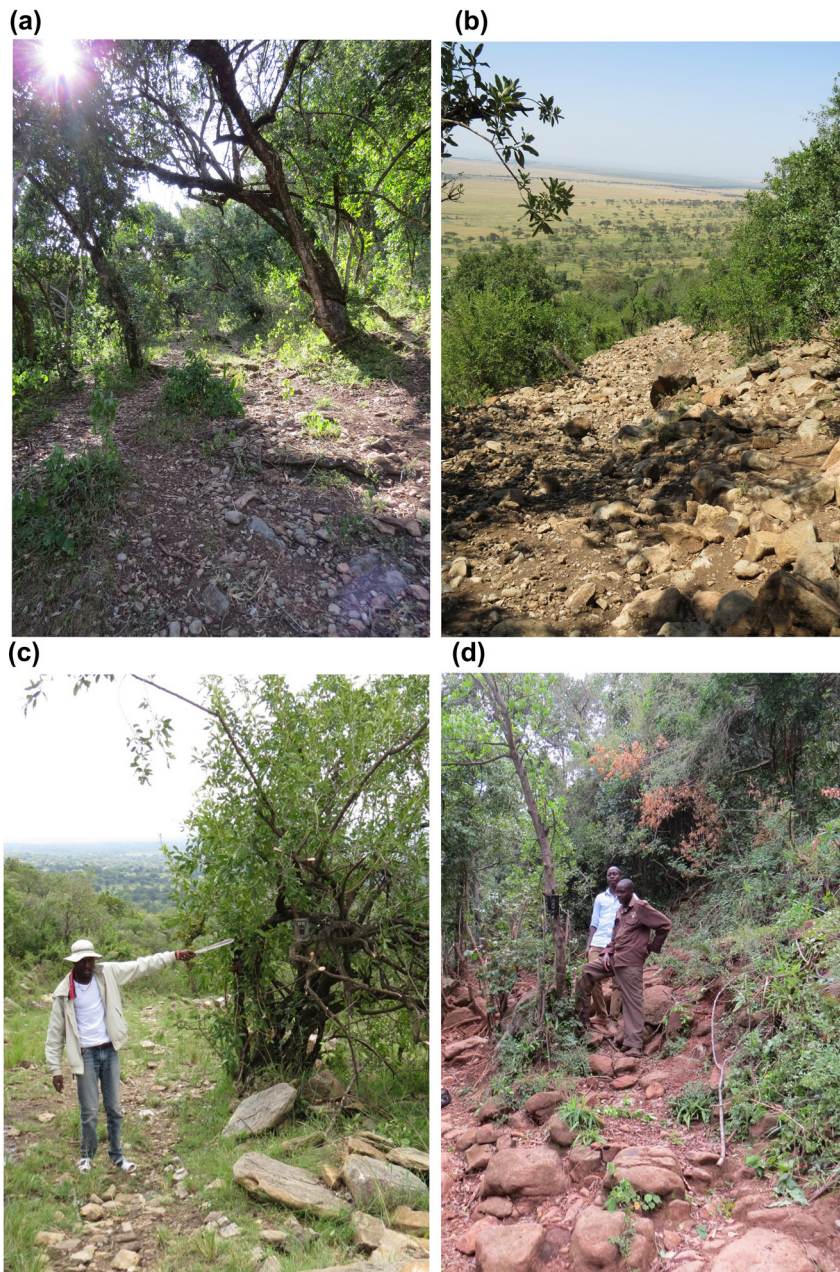
Figure 2. Four (a, b, c, d) of the 22 elephant *Loxodonta Africana* pathways along the escarpment connecting the Masai Mara to the Trans Mara District. We placed 32 camera traps on 14 of the pathways. At least one camera on each pathway pointed up the escarpment and at least one camera pointed down the escarpment to determine the direction of movement of elephant groups into and out of the Masai Mara.

determined by sexing elephants based on their genitalia (if visible), body size, shape of their head and length and configuration of tusk size (Moss 1996). During the period in which an elephant group crossed a camera, depending on the size of the group, many images were captured. Thus, to avoid double counting elephant groups, we developed a Python script to select images from our database that were taken more than 15 min apart. This time marker was determined after reviewing all the images and calculating the average time between each independent group. Group type was then determined by reviewing the series of images within the 15 min time frame.

To understand the relationship between pathway use and crop raiding, we collected data on elephant incursions into agricultural fields in the Trans Mara District from September 2014 to September 2015 (Tiller et al. 2021).

Analysing patterns of pathway usage

All the data analysis was carried out using the statistical software R (www.r-project.org). We assessed the seasonal patterns of pathway use by totalling the number of dung piles counted across all pathways for each month and averaging rainfall readings from weather stations across the Trans Mara

and Masai Mara National Reserve (8 rain stations in total). We then carried out a Spearman's Rank Correlation test with dung counts and rainfall. Due to the potentially delayed effects of rainfall on the ripening of crops and greening of vegetation, we also ran correlations between dung counts and rainfall from the previous month.

To look at the temporal patterns of elephant groups travelling up the pathways into the Trans Mara and down the pathways into the Masai Mara, we sorted the camera trap data into time and direction. Images were grouped into time stamps of 24 one-hour intervals so that we had a frequency distribution of each elephants travelling up and elephants travelling down the pathways.

Analysing the factors determining pathway use

To determine whether higher pathway activity predicted high human–elephant conflict incidents, we fitted a linear model based on the number of crop raiding incidents per month as our response variable and the total number of dung piles across all pathways as our predictor variable. Our assumption was that during high human–elephant conflict months there would be more elephants using the pathways to access farms, with a certain proportion of this population involved in the incidents.

We used descriptive statistics to summarise the number of elephant detections on each pathway. To investigate the factors driving high elephant pathway use, we used five predictor variables: distance of pathway to nearest farm, continuous forest outside the pathway, saltlicks (eight in total which are permanent), the percentage of forest cover along pathways and slope. To measure the percentage of forest on each pathway, we calculated the length of the pathway and then used the GPS co-ordinates from the habitat survey to work out the proportion of the pathway that we had classified as forest. We mapped farmland and forest cover and locations of saltlicks by on-screen digitising of 5 m CNES/Astrium satellite imagery from 2015 using QGIS (QGIS Development Team 2015). We then calculated the distance from the end of each pathway to the nearest farm, continuous forest in the Trans Mara and saltlicks using the *Generate Near Table* function in 'ArcMap' ver. 10.4.

We then carried out exploratory analysis including graphical inspection, correlation matrices and bivariate tests. Variance inflation factors (VIFs) and Pearson correlation coefficient (r) were used to test for collinearity amongst the predictor variables and we found no evidence of collinearity between our predictor variables (VIF < 5; r < 0.7; Dormann et al. 2013). Exploratory modelling identified persistent over dispersion between the response and predictor variables. Thus, to overcome this problem, we fitted a GLM with a negative binomial error structure and all predictor variables were scaled to have a mean of zero and a standard deviation of 0.5 (Gelman 2008). For model selection, we used a model averaging approach (Burnham and Anderson 2002) using the 'MuMin' package (Barton 2016), which examines average parameter estimates, standard errors and confidence intervals of the predictor variables. First, we constructed a global model containing all

predictor variables but after inspecting the output we found slope did not significantly influence the number of dung piles and we therefore removed it from our global model to avoid overfitting. We then applied the Dredge function to the global model, producing a model set containing all possible model permutations. Models were then ranked based on their AICc (Akaike information criterion) score, where the lowest score signifies the most parsimonious model, and calculated the delta AICc (the difference in AICc between each model and the best preforming model). We then averaged parameter estimates for models with a delta AICc < 2, as this suggests a similar level of support among models (Burnham and Anderson 2002). The relative importance (RI) of explanatory variables was then calculated by summing the Akaike weights across all models in which the variable was present, resulting in an estimate of probability that the variable of interest features in the best model. Finally, we applied a goodness of fit test to the model set to determine if the models fitted the data well.

Results

We identified 22 active elephant pathways along the escarpment. The mean ($\pm$ 1 SE) pathway length of was 878.5 $\pm$ 62.59 m, the mean minimum slope was 4.12 $\pm$ 0.52° and mean maximum slope was 27.70 $\pm$ 1.80°. Forest cover on the pathways ranged between 0 and 74.06 % (mean 20.12% $\pm$ 5.57).

Temporal and seasonal patterns of pathway usage

There were strong seasonal trends in elephant pathway use, with two peaks in elephant activity in September 2014 and August 2015, with over 1000 dung piles recorded in each of these months (Fig. 3). Signs were lowest in November 2014 and May 2015 and non-existent in June 2015 when no dung piles were recorded, suggesting that elephants did not use the pathways during this month. Average monthly rainfall ranged from a minimum of 14.1 mm in January 2015 to a maximum of 191.37 mm in April 2015 and there was no relationship between rainfall and total number of dung piles (pathway use) (Spearman's Rank correlation: $r_s = -0.006$, $p = 0.991$, Fig. 3).

The camera trapping data revealed a distinct pattern in the times when elephants travelled up and down the pathways (Fig. 4). Elephants were photographed travelling up the pathways into the Trans Mara predominantly during 17:00–24:00 h (median = 19:00) and back down the pathways into the Masai Mara National Reserve during 04:00–09:00 h (median = 06:00).

Elephant group types using pathways

During the nine months of camera trapping, we recorded all three elephant group types (bull groups, female-led family groups and family + bull groups) using the pathways 825 times (341 moving down and 484 moving up). There was a mean of 72 $\pm$ 26.49 groups per pathway and the mean size of an
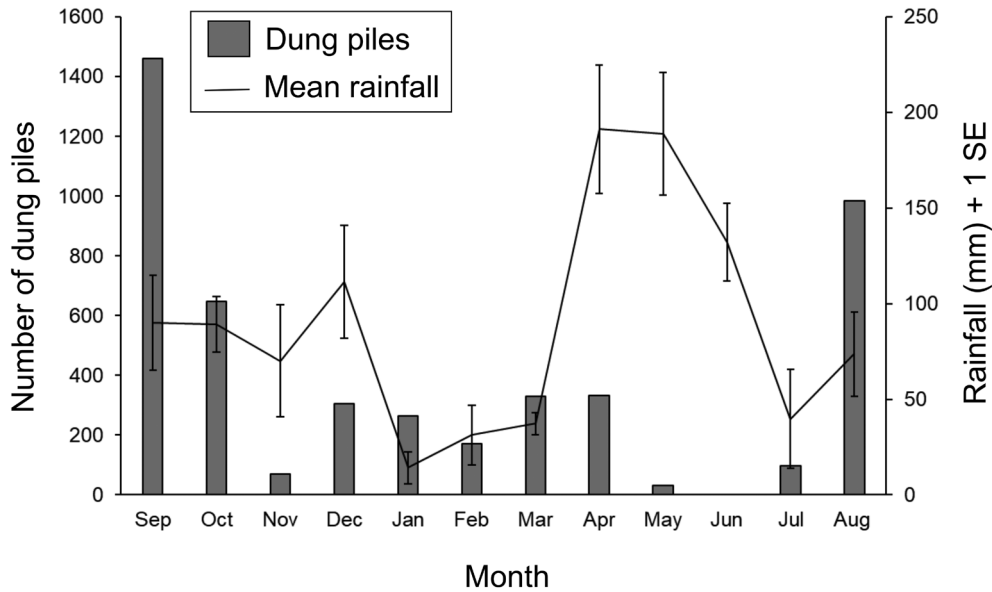
Figure 3. Seasonal patterns of elephant pathway use as measured by the total amount of dung piles recorded each month from September 2014 to August 2015.

elephant group was 4.25 ± 0.13. Pathways Enkiu and Mara West were used more frequently than other pathways (Fig. 5).

Human–elephant conflict and factors determining pathway use

The number of HEC incidents was significantly and positively associated with the number of dung piles on pathways ($\beta = 0.656$, SE $= 0.238$, p < 0.05, Fig. 6).

The most frequently used pathways were closer to farms, saltlicks and forest in the Trans Mara and those that had a higher percentage of forest cover. Distance to farms was the strongest predictor as it appeared in all models prior to averaging (RI 1.0). Distance to saltlick and percentage of forest cover on pathways appeared in 70% (RI 0.70) of models, while distance to forest appeared in 30% (RI 0.3) of models prior to averaging (Table 1; for model selection results see Supporting information).
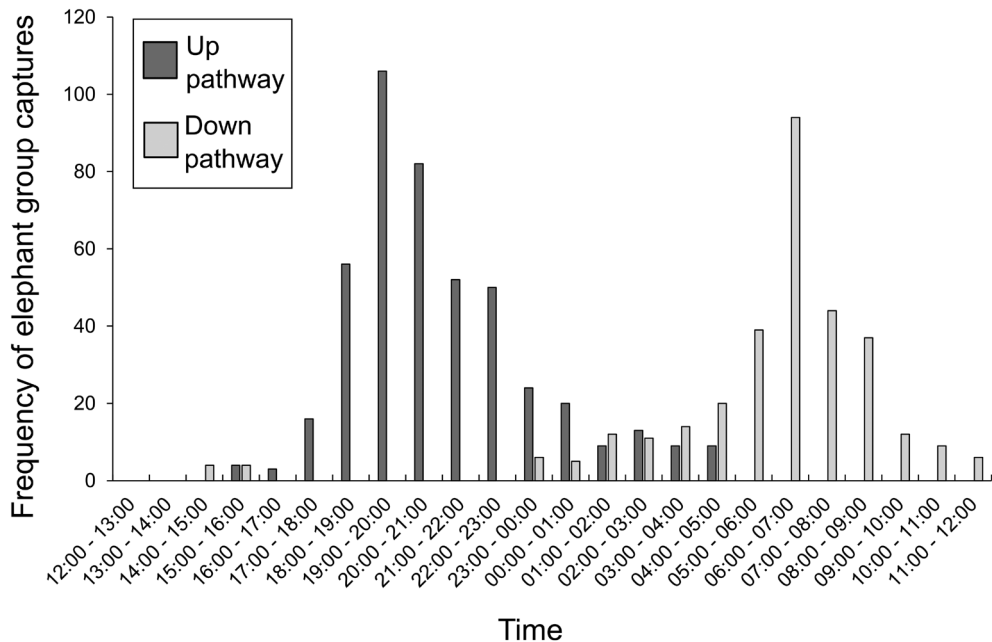

Figure 4. Temporal patterns of elephants travelling up the pathways into the Trans Mara District and down the pathways into the Masai Mara National Reserve, as determined through camera traps. Frequency of captures is the total number of elephant groups detected over the whole study period.
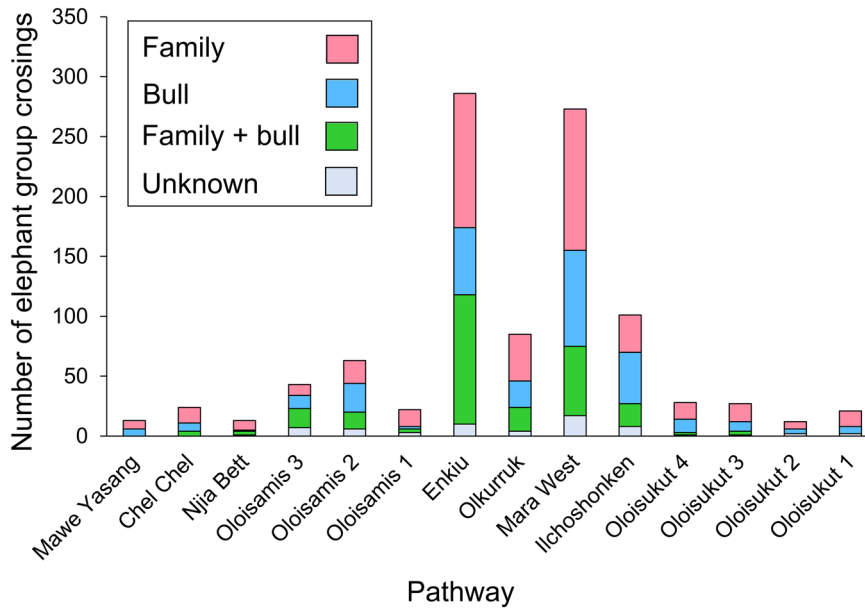
Figure 5. The number of elephant captures on camera trap pathways of each elephant group type.

Discussion

Understanding the role of wildlife pathways as conduits for movement among resource areas is key for addressing human–wildlife conflict and maintaining landscape connectivity (IUCN 2023). In this study, we used camera trapping and elephant sign surveys to understand the fine-scale movements of elephants to determine pathway use and their role in human–elephant conflict.
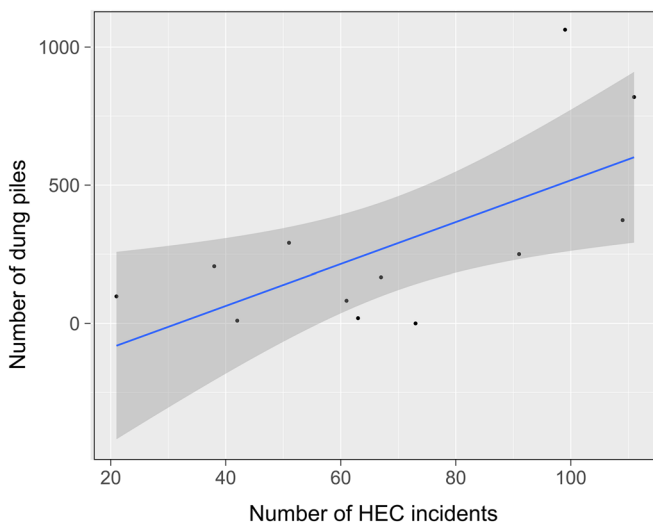

Figure 6. The positive relationship between the number of human–elephant conflict incidents and the number of dung piles recorded across the pathways each month. The blue line represents the regression line, the grey shading represents the 95% confidence intervals and the points represent the monthly data.

Temporal and seasonal patterns of pathway usage

There were strong seasonal trends in elephant pathway use, with two peaks in elephant activity in September 2014 and August 2015. These peaks coincided with the dry season, which is between June and October in the Masai Mara (Sitati 2003). During the dry season, elephants are constrained by limited forage and water (Birkett et al. 2012, Bohrer et al. 2014) and may need to use the pathways to access different resources found in the Trans Mara. The increase in pathway use during September 2014 and August 2015 also coincided with the peak movement of the wildebeest migration from the Serengeti ecosystem in Tanzania to the Masai Mara (Boone et al. 2006). Anecdotal evidence suggests that, during this time, elephants seek refuge in the Trans Mara to avoid the large numbers of wildebeest who compete for grass (Sitati 2003). Despite these seasonal patterns, we found

Table 1. Results of model averaged GLM fitted with negative binomial errors to investigate predictors of high pathway use by elephants from September 2014–September 2015. Significant predictor variables from our averaged models where confidence intervals do not cross zero. Averaged parameter estimates (β), unconditional standards errors (SE) and relative variable importance factors (RI) are also reported. The Akaike information criterion correction (AICc) was used to rank models and any model that ranked ΔAICc < 2 was averaged to obtain final estimates presented. Relative importance (RI) refers to the summed Akaike weights across all models in which the variables were present.

Predictor	B	SE	LCI	UCI	RI
(Intercept)	5.610	0.116	5.354	5.865	
Distance to farm	−0.418	0.135	−0.720	−0.115	1.0
Distance to saltlick	−0.677	0.145	−0.999	−0.354	0.70
Distance to forest	−0.438	0.138	−0.741	−0.135	0.30
Forest cover on pathways (%)	0.540	0.139	0.231	0.849	0.70

no relationship between pathway use and rainfall. This was unexpected as previous studies found elephant movement increased during high periods of rainfall (Cushman et al. 2005, Loarie et al. 2009, Bohrer et al. 2014b). However, the absence of such a relationship in our study could be due to elephants seeking resources in the Trans Mara all year round, as the quality and quantity of grass in the Masai Mara National Reserve has dropped due to cattle overgrazing (Ogutu et al. 2011, 2016). It could also reflect changes in elephant crop raiding patterns, as this is now occurring in the Trans Mara throughout the year and at all stages of crop growth (Tiller et al. 2021), and peaks in pathway use were associated with slight peaks in human–elephant conflict incidents, including crop raiding.

There was a distinct pattern of elephant activity on the pathways, as elephants travelled up the pathways into the Trans Mara at night and travelled down the pathways into the Masai Mara in the early morning. These travel times are consistent with other studies (Von Gerhardt et al. 2014, Smit et al. 2019, Adams et al. 2022) and suggest risk avoidance behaviour, as human activity is low during these times, and darkness makes it easier for elephants to go undetected (Graham et al. 2010, Von Gerhardt et al. 2014, Ihawagi et al. 2018). Travelling during these times also minimises time spent in high-risk areas, i.e. where there are high human densities (Douglas-Hamilton et al. 2005). A greater understanding of pathway use, as well as risk-avoidance behaviours used by wildlife, can greatly improve the effectiveness of land-use zoning to achieve 'landscapes of coexistence' (IUCN 2023). For example, elephants in Assam India would use forest refuges in the day to avoid humans, leaving these forest patches in the evening to crop raid on farms. Based on this understanding, mitigation was targeted at the edges of these refuges (Wilson et al. 2013).

All elephant group types (bull groups, female-led family groups and family + bull groups) used pathways and the results suggest that there are no differences in pathway use by group type. This is similar to Botswana where all group types used the pathways (Adams et al. 2017). However, one caveat is that we do not know the proportions of the group types in the resident Trans Mara population compared to the proportions using the pathways. Bull groups in other parts of Africa (e.g. Tanzania) have been reported to use pathways more than female-led family groups, especially when pathways lead to farmland (Smit et al. 2019). Other studies have indicated that bulls use specific pathways closer to human settlements, whereas female-led family groups tend to avoid such pathways (Von Gerhardt et al. 2014, Songhurst et al. 2015). We know from Tiller et al. (2021) that females as well as male elephants are involved in crop raiding incidents in the Trans Mara, which could also explain why all group types use the pathways.

Human–elephant conflict and factors determining pathway use

Pathways play an important role in human–elephant conflict as our model showed a positive relationship between the total number of dung piles recorded on the pathways each month and the number of crop raiding incidents in the Trans Mara. The temporal patterns of elephant pathway use also coincided with crop raiding incidents, which occurred between the hours of 18:00 and 09:00 (Tiller et al. 2021).

All pathways were used by elephants, but some pathways were used more than others. Our results show that high pathway use was driven by distance to farmland, distance to saltlicks, distance to forest and percentage of forest cover on pathways. The strongest predictor was distance to farmland, with a substantially higher frequency of elephant pathway use nearer to farms. Pathway location strongly influences elephant movement (Songhurst et al. 2015) and, in the Trans Mara, elephants are using the pathways to access farmland. Farmland is the most dominant landcover type in the Trans Mara (Tiller 2018), and the average distance from the end of a pathway to farmland is 1.64 ± 0.25 km. Thus, farmland is easily accessible for elephants and the pathways play an important role in elephant crop raiding, suggesting they help facilitate movement into farmland. Other studies across Africa have reported similar findings, with farms closest to pathways experiencing a higher frequency of crop raiding and damage due to elephants (Guerbois et al. 2012, Von Gerhardt et al. 2014, Songhurst et al. 2015, Smit et al. 2019). Pathways can also act as crop raiding staging posts. 'Staging' is pre-conflict movement behaviour described in other species, such as American black bears (Marchinton 1995), monkeys (Mekonnen et al. 2012), and Asian elephants (Wilson et al. 2013). More recently, it has been quantitatively defined and assessed in African elephants using GPS tracking data, where authors were able to identify staging behaviour prior to agricultural incursions (Hahn et al. 2023).

Our study also suggests that distance to forest and saltlicks are important predictors of pathway use, although they were not as strong a predictor as distance to farmland. It should be noted that there have been high levels of illegal forest clearance in the Trans Mara District since we collected our data, and there is a need for follow-up research to investigate how this has impacted current patterns of elephant movement and conflict. However, the use of these pathways to access resources, such as saltlicks and browse in the forest, is known to continue (Hahn et al. 2023) and suggests that the Trans Mara continues to be an important dispersal area for elephants. Thus, the pathways are likely to play a crucial role in resource access, which has been reported in other parts of Africa, where pathways lead to favoured areas such as water, saltlicks and preferred trees (Vanleeuwe and Gautier-Hion 1998, Blake and Inkamba-Nkulu 2004, Shannon et al. 2009, Von Gerhardt et al. 2014).

Optimal foraging theory would suggest that elephants use pathways as least-effort routes between food resources (Blake and Inkamba-Nkulu 2004, Von Gerhardt et al. 2014). Another low energy foraging strategy is to avoid travelling on steep slopes (Wall et al. 2006). However, the pathways along the escarpment are steep, ranging from 4.1° to 27.7°, and so elephants used a high amount of energy climbing these pathways. Moreover, slope did not determine pathway use

suggesting that elephants were willing to climb the different ranges of slope. Thus, our results suggest that there must be a high nutritional gain for elephants to travel into the Trans Mara to compensate. In particular, elephants could be targeting crops, as they are highly nutritious and more palatable compared to wild forage (Sukumar 1990, 2003), and therefore offer a high reward for climbing the pathways. Further research should be conducted looking into these energetic costs and benefits in regard to optimal foraging. Finally, percentage of forest cover on the pathways was an important predictor of pathway activity, which could be due to elephants using the forest as cover to avoid detection and/or feeding on the vegetation on the pathways (Wilson et al. 2013).

Our results provide an opportunity for planned management activities to ensure connectivity and to mitigate conflict. First, the key resource areas (forest patches and saltlicks) and pathways could be incorporated into land-use planning to provide protection for these areas, providing safe passage for elephants and wildlife into these important dispersal areas (IUCN 2023). Second, for pathways leading directly to farms, mitigation could be specifically targeted along these pathways (Songhurst et al. 2015). For example, pathways could be regularly monitored during the peak crop season to warn famers about potential conflict and proactively deploying deterrent mitigations. In addition, long-term mitigation planning, such as the use of unpalatable buffer crops, fencing, and alternative income programs in farms near pathways could be initiated (Songhurst et al. 2015, Henly et al. 2023).

Expanding human development has restricted elephant ranges across Africa (Wall et al. 2021). Kenya's protected areas are not enough to conserve wildlife. Instead, they need to be connected to other areas of critical resources by pathways and corridors and integrated into broader ecological landscapes including human-dominated areas (Nyhus and Tilson 2004) Thus, understanding pathway use, fine scale wildlife movement along pathways and their role in human–wildlife conflict is key for land-use planning and conflict mitigation.

Author contributions

Lydia Tiller: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Tatyana Humle**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Rajan Amin**: Conceptualization (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Amie Humphries**: Formal analysis (supporting); Writing – review and editing (supporting). Dave Seaman: Formal analysis (supporting); Writing – review and editing (supporting). **Noah Sitati**: Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Robert Smith**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

Data availability statement

Supporting information

The Supporting information associated with this article is available with the online version.

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