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REPORT

Smallholder Farms as Stepping Stone Corridors for Crop-Raiding Elephant in Northern Tanzania: Integration of Bayesian Expert System and Network Simulator

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Abstract Crop-raiding elephants affect local livelihoods, undermining conservation efforts. Yet, crop-raiding patterns are poorly understood, making prediction and protection difficult. We hypothesized that raiding elephants use corridors between daytime refuges and farmland. Elephant counts, crop-raiding records, household surveys, Bayesian expert system, and least-cost path simulation were used to predict four alternative categories of daily corridors: (1) footpaths, (2) dry river beds, (3) stepping stones along scattered small farms, and (4) trajectories of shortest distance to refuges. The corridor alignments were compared in terms of their minimum cumulative resistance to elephant movement and related to crop-raiding zones quantified by a kernel density function. The "stepping stone" corridors predicted the crop-raiding patterns. Elephant presence was confirmed along these corridors, demonstrating that small farms located between refuges and contiguous farmland increase habitat connectivity for elephant. Our analysis successfully predicted elephant occurrence in farmland where daytime counts failed to detect nocturnal presence. These results have conservation management implications.

Keywords Ecological corridors · Bayesian expert system · Human–elephant conflict · Crop damage control · Farms · Movement behavior

INTRODUCTION

Crop raiding is a major cause of human–wildlife conflict worldwide. Many wildlife species regularly raid fields: e.g., deer and raccoon in North America; wild boar in Europe; primates and elephant in Africa and Asia; kangaroo in Australia as well as rodent and bird species throughout the world (Lamarque et al. 2009). Crop-raiding animals impact local livelihoods and undermine conservation efforts, particularly in developing countries (Naughton et al. 1999). Yet, spatial patterns of crop raiding are poorly understood, making prediction and protection difficult. The African elephant (*Loxodonta africana* Blumenbach), is a vulnerable keystone species of the savanna ecosystem as well as being a crop raider (Hoare 1999b) and represents an appropriate model to investigate crop raiding patterns by wildlife. Crop raiding is the most common form of human–elephant conflict (Hoare 2000) occurring mainly at night (Graham et al. 2009) and when food crops are ripe (Chiyo et al. 2005). Mostly small farms are affected (Graham et al. 2010b) due to insufficient protection (Sitati et al. 2005). Spatial patterns of crop raiding by elephant have been associated with human population density (Newmark et al. 1994), amount of cultivated land (Sitati et al. 2003), elevation (Smith and Kasiki 2000), slope (Wall et al. 2006), and proximity to settlements (Hoare 1999b), roads (Sitati et al. 2003), water sources (Smith and Kasiki 2000), protected areas (Hoare 1999b), and daytime elephant refuges (Graham et al. 2010b). Yet, the uneven distribution of crop raiding amongst farms remains poorly understood (Sitati et al. 2005). The poor spatial predictions of crop raiding have been attributed to insufficient analysis of the sexual composition of raiding herds (Hoare 1999b), palatability of cultivated crops (Chiyo et al. 2005), farm protection methods (Sitati et al. 2005), and farm size (Sitati et al.

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2005), as well as to the spatial resolution of the data (Sitati et al. 2003; Graham et al. 2010b). Anecdotal evidence suggests that proximity to elephant corridors also influences crop-raiding patterns (Smith and Kasiki 2000). Studies on elephant movement show that corridors may follow linear environmental features such as footpaths (Ngene et al. 2010), dry river beds with dense riverine vegetation (Kikoti 2009), and least relief resistance, such as flatter terrain and lower elevations (Smith and Kasiki 2000; Wall et al. 2006; Ngene et al. 2010). However, we provide evidence here that elephants may also move along "stepping stone" corridors. Stepping stones are an array of small habitat patches offering shelter, food, and rest during movement and dispersal (Bennett and Mulongoy 2006). The effectiveness of these corridors depends on patch size and inter-patch distance, as well as the relief resistance of the landscape around these patches (Uezu et al. 2008). Birds (Fischer and Lindenmayer 2002), frogs (Vos 1999), insects (Haddad 2000), and mammals (Kramer-Schadt et al. 2011) have been found to successfully move and disperse along "stepping stone" corridors. Outside protected areas, and particularly within small-scale farming land, elephants move between refuges and feeding grounds at night and at high speed to avoid people (Galanti et al. 2006; Ngene et al. 2010). Because elephants are attracted to ripe food crops (Chiyo et al. 2005), small farms that are surrounded by savanna are particularly vulnerable to crop raiding (Graham et al. 2010a). Therefore, in this study, we hypothesized that the spatial distribution of scattered small farms surrounded by savanna enhances landscape connectivity for elephants, connecting elephant refuges with crop-raiding zones. In other words, scattered small farms act as "stepping stone" corridors, increasing the vulnerability of farms along and at the termini of these corridors. Large farms on the other hand, which employ effective protection methods and often cultivate less palatable cash crops such as coffee and tea, may hamper elephant movement by acting as barriers, and may thereby further amplify the vulnerability of neighboring small farms.

We propose a "daily refuge-to-crop raid corridor" hypothesis to predict patterns of crop raiding by elephant. Our hypothesis was tested in the Tarangire–Manyara ecosystem (TME), northern Tanzania, using elephant movement data obtained from total elephant counts, expert knowledge, and crop-raiding events. Total counts have been successfully used to predict elephant migration routes and dispersal areas, but have failed to predict the presence of elephant in farming areas which report frequent raids (Pittiglio et al. 2012). Expert systems (Skidmore 1989) have been shown to successfully predict wildlife distribution in the absence of direct field observations (Murray et al. 2009). The UNIversal CORridor network simulator (UNICOR; Landguth et al. 2012) was used to predict four alternative categories of "daily refuge-to-crop raid corridors" along: (1) footpaths, (2) dry river beds, (3) stepping stone farms, and (4) "control corridors"; the latter based on proximity to refuges and following trajectories of low relief. An independent dataset of elephant presence (Msoffe et al. 2007) was used to validate the simulated corridors. We believe that this is the first study demonstrating the corridor hypothesis with crop raiding, and in particular the effect of stepping stone farms on elephant movement behavior.

MATERIALS AND METHODS

Study Area Selection

The TME (between 3°36′S and 4°7′S, and 35°82′E and 36°74′E) is part of the Maasai Steppe (Prins 1987) and hosts the largest population of elephant in northern Tanzania. The TME includes protected (Tarangire and Lake Manyara National Parks), semi-protected (Manyara Ranch, Lolkisale, and Mkungunero Game Controlled Areas) and unprotected areas (Fig. 1). The area is a gently undulating plateau with an elevation between 1000 and 2000 m a.s.l. The landscape is dotted with steep rocky outcrops and carved by seasonal rivers with dense riverine vegetation. Steep rocky outcrops act as barriers to elephant movement (Edkins et al. 2008), whereas the dry river beds with dense riverine vegetation provide cover and connectivity for elephants outside the protected areas (Kikoti 2009). Within the TME, elephants move seasonally from the National Parks to the dispersal areas outside the Parks in response to seasonal vegetation biomass and drinking water (Pittiglio et al. 2012). Elephant seasonal migration corridors are well-defined in the TME (Galanti et al. 2006; Pittiglio et al. 2012), but "daily refuge-crop raid" corridors are not.

Recent household surveys reveal a low tolerance toward elephants by villagers living in the dispersal areas because of the crop raiding (Kaswamila 2009). Crop farming expanded in the TME over the past 30 years, whereas the elephant population remained stable over the same period (Pittiglio et al. 2013). The research area (1940 km^2) was selected in the north-eastern TME, to include an important elephant dispersal area located inside the administrative boundary of three adjacent villages, namely Loborsoit A, Naitolya, and Lolkisale (Galanti et al. 2006), which are characterized by rapid agriculture expansion and an increasingly fragmented landscape (Pittiglio et al. 2013). These villages have similar land use (i.e., both small and large crop farms), cultivated crops (mostly maize and beans), and human population densities (<17 inhabitants km^2) (National Bureau of Statistics Tanzania 2006). The dominant vegetation type is open savanna (Kahurananga 1979).

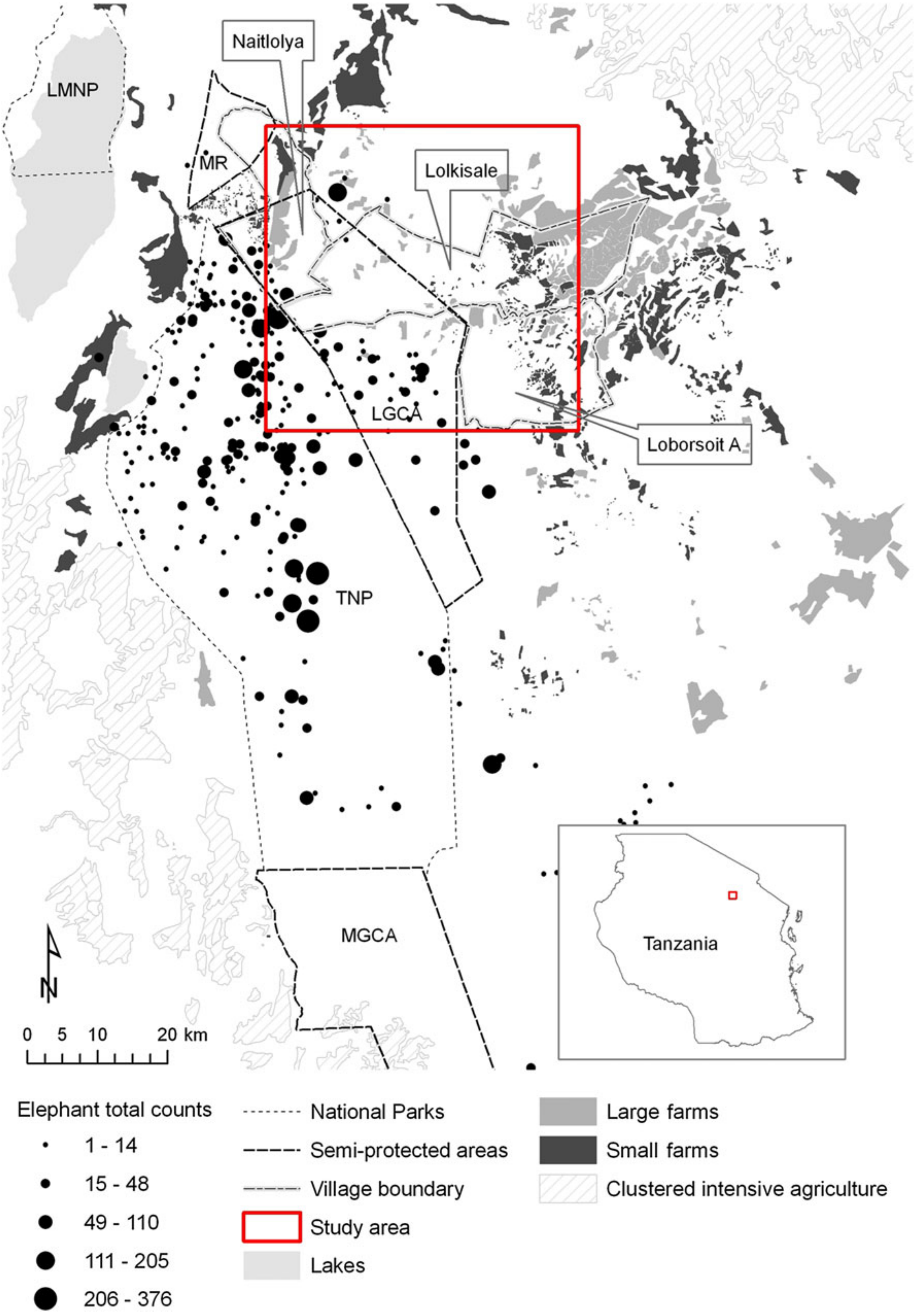

Fig. 1 Selected study area within the Tarangire–Manyara ecosystem in Tanzania. Elephant total counts, the boundaries of Tarangire (TNP) and Lake Manyara (LMNP) National Parks; Lolkisale (LGCA) and Mkungunero (MGCA) Game Controlled Areas; Manyara Ranch (MR), and the villages of Naitolya, Lolkisale, and Loborsoit A, are shown

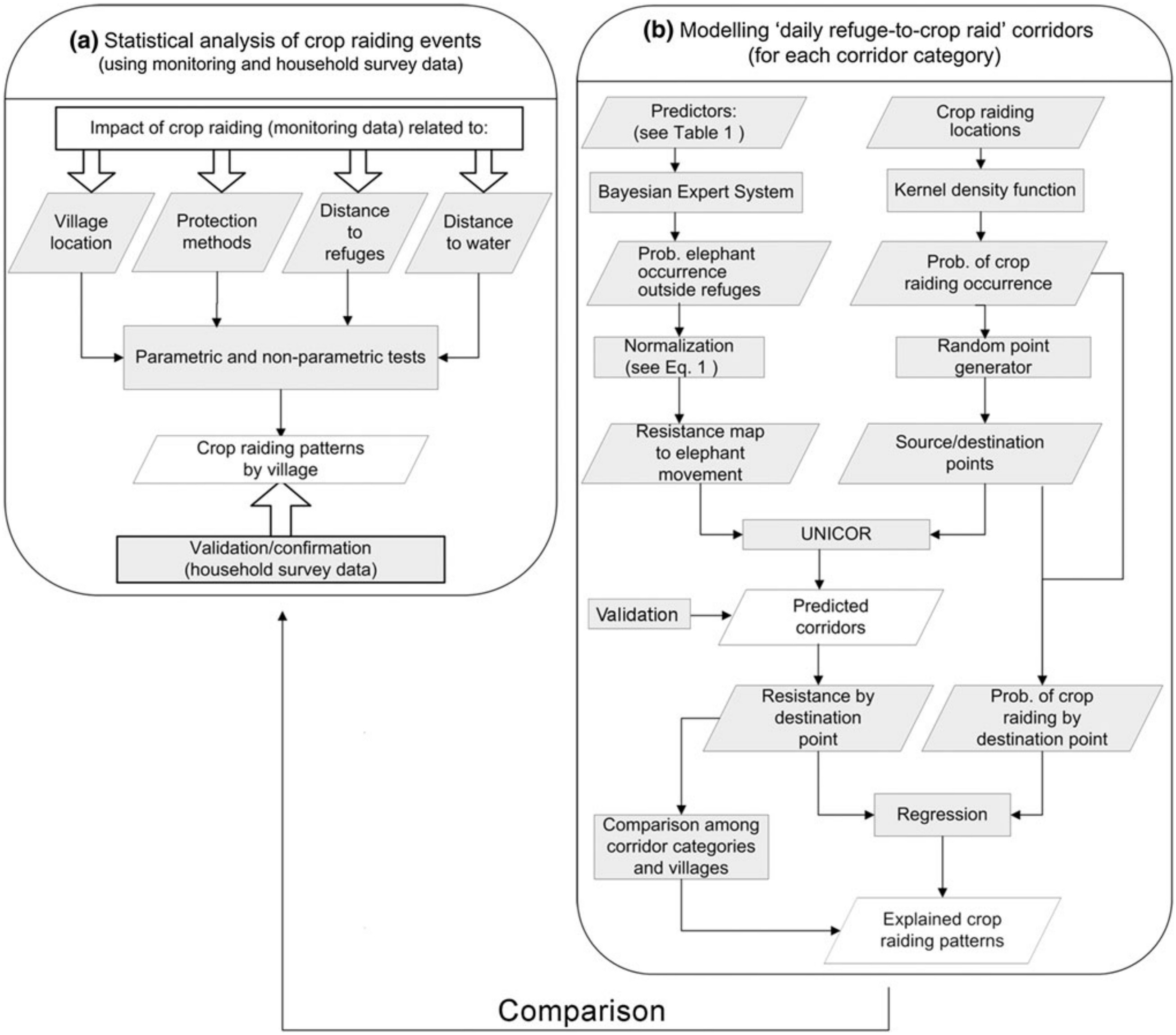

Fig. 2 Flowchart of the research approach: **a** statistical analysis of crop-raiding patterns and their validation; **b** prediction and validation of daily refuge-crop raid corridors and their analysis in relation to crop-raiding patterns

Research Approach

A flowchart illustrates the research approach (Fig. 2). First, we tested whether the impact (i.e., the rate and characteristics) of crop raiding was different between years and villages, and whether it was related to proximity to water and elephant refuges. The results of this statistical analysis were validated using household survey data. Second, we integrated a Bayesian expert system with a corridor network simulator to predict four alternative corridor categories between the daytime refuges and the nighttime crop raided zones. The corridors were validated using an independent dataset of elephant presence, with the comparison between corridors measured by their resistance to elephant movement. Then, we tested whether the impact of crop raiding at a given destination point was related to the resistance of the corridors heading to that point for each category of corridor. Lastly, the predicted pattern of crop raiding was compared with the pattern obtained from the statistical analysis.

Statistical Analysis of Crop-Raiding Events

Wildlife crop-raiding events were recorded by a local canvasser for each village using a standardized form (Hoare 1999a), immediately before and during the crop ripening period (Chiyo et al. 2005) from May 2006 to September 2008. Farmers reported the raiding events to the canvasser who then visited the farms for verification and quantification (Hoare 1999a). The recorded information was: name of the farmer; date of raiding event; GPS location of the raid; type of damaged crop(s); farm size; spatial extent of damage; raiding species; protection methods. The protection methods employed by the farmers were surveyed following the approach of Sitati et al. (2005) and Osborn and Parker (2002), and included: (a) active deterrents—presence of a watchman, bonfires on the property boundary, shouting, torches, tins and drums, smoke from burning hot chillies or from burning livestock or elephant dung; (b) passive deterrents—home-made barriers/fences of vegetation, wire, rope; or (c) a combination of the two (mixed methods). Because large farms (>40 ha) were only occasionally damaged by elephants, the statistical analysis focused on crop-raiding events for small farms (<40 ha) in 2006 and 2008. This farm class boundary was based on expert knowledge (Kibebe 2005). The damaged area and the proportion of the damaged area per farm were calculated to reflect actual and relative losses (Sitati et al. 2005). The statistical analysis of crop raiding consisted of: (1) a two-way ANOVA to test whether the average damaged area per farm and the average proportion of damaged area, as well as the average farm size, were related to the specific village locations (Naitolya, Lolkisale, and Loborsoit A) for both years (2006 and 2008), and then tested for their interaction. Because the data were not normally distributed, we applied a rank transformation. Subsequently, the ranks were analyzed with ANOVA (Conover and Iman 1981). The Tamhane T2 post hoc multiple comparison test was used to test differences among the three villages; (2) a non-parametric Kruskal–Wallis test to analyze differences in median damaged area as well as the proportion of damaged area per farm between the types of protection methods (active, passive, and mixed) at village level. This non-parametric test was required because the data were not normally distributed; (3) a one-way ANOVA to compare the average distance of raided farms to the nearest boundary of elephant refuges (described below) and to water sources (dams) among the three villages. These distances were $\log_{10}$-transformed to approximate a normal distribution. The average elephant daytime travel distance outside the protected areas, i.e., 5 km, was extrapolated from the average speed of 7 radio-collared elephants in TME (Galanti et al. 2006) and used as an explanatory factor of the pattern of crop raiding observed in the villages. In other words, those villages where the average distance of crop raided farms was less than 5 km from refuges and water were excluded from further analysis.

The crop-raiding patterns were validated with the household survey data. Four canvassers conducted two socio-economic surveys in 2006 and 2008 for 363 and 359 surveyed households, respectively. The recorded information on crop raiding was: farm size and percentage of farm area damaged (5 classes: no damage; <25; 25–50; 50–75; >75 %), frequency and time of crop raiding, type of damaged crops, and raiding species.

Mapping Small and Large Farms

A shapefile of crop farming in 2000 (Pittiglio et al. 2013) was updated to 2006 by digitizing new farms and deleting abandoned farms using three adjacent ASTER 1B level (EOS, 15 m) cloudless images from January 21 and February 5, 2006 and 14 IKONOS-2 images (GeoEye, 1 m) acquired between September 12 and November 28, 2005. The farms were classified as small farms or large farms by using village land use maps and by visual image interpretation.

Daytime Refuges, Nighttime Crop-Raiding Zones, and Connecting Corridors

A standard bivariate normal kernel density function (Silverman 1986) was used for estimating the daytime wet season elephant refuges, and the nighttime crop-raiding zones, as well as vulnerability subzones within the crop-raiding zones. This method was applied to minimize false absences due to the spatial and temporal discontinuity of total counts as well as account for elephant vagility and environmental context (Pittiglio et al. 2012) as well as missed or unreported crop-raiding events. The probabilities of crop raiding were estimated from 259 GPS locations of crop-raiding events recorded in 2006, 2007, and 2008. The probabilities of elephant occurrence were estimated from 223 GPS locations of the total counts aerial surveys in the wet season from 1996 to 2001 (see Pittiglio et al. 2012). These counts can be assumed to represent elephant refuges during the crop-monitoring period because the elephant population size and spatial distribution did not change significantly during the study period (Lobora 2010; Pittiglio et al. 2013). The kernel smoothing parameter h was selected through the likelihood cross validation method (Horne and Garton 2006) using Animal Space Use 1.3. beta (Horne and Garton 2009). A threshold of 95 % of the probability volume contour (Kernohan et al. 2001) defined the boundaries of the elephant refuges and of the crop-raiding zones. “High” and “very high” vulnerable subzones were defined as the probabilities of crop raiding being within the 50 and 10 % volume contours, respectively.

We generated two input data: (1) source/destination points, and (2) a “resistance raster” for each corridor category. Each pixel in this resistance raster has a value representing the resistance to an elephant movement across the pixel in any direction. We used UNICOR (Landguth

Table 1 Predictors used to generate the maps of resistance to elephant movement for each corridor category

Corridor category	*N* predictors	Description of predictors
Footpaths	6	Distance and direction from boundary of elephant refuges; inside/outside elephant refuges; slope, elevation, and distance from footpaths
Dry river beds	6	Distance and direction from boundary of elephant refuges, inside/outside elephant refuges, slope, elevation, and distance from the dry river beds
Stepping stone farms	9	Distance and direction from small farms, large farms, and boundary of elephant refuges; inside/outside elephant refuges, slope, and elevation
Control	4	Distance and direction from boundary of elephant refuges, slope, and elevation

et al. 2012) to simulate daily corridors for elephants between the refuges and the crop-raiding zones. UNICOR estimates least-resistance movement paths (i.e., optimal paths) between all pairs of source points and destination points, given a number of source and destination points and a raster of "landscape resistance" to animal movement. Then, a kernel density function is applied on these paths to generate a corridor density map (Landguth et al. 2012): the higher the density, the higher the expectation (probability) of an animal movement along the predicted corridor.

The kernel probabilities of elephant occurrence and of crop raiding were used as weights in randomly generating 10 source points within refuges and 10 destination points in crop-raiding zones. That is, points with higher probabilities of elephant occurrence (or of crop raiding) had a higher chance of being selected as starting (or ending) nodes of the corridors. Points were placed at least 5 km apart in the elephant refuges, and 3 km apart in the conflict zones, using Hawth's analysis tools 3.27 (Beyer 2004). These two distances approximate to the average elephant travel distance by day and by night (Galanti et al. 2006). Because elephant refuges and crop-raiding zones were estimated from daytime counts and nighttime crop-raiding events, respectively, the source and destination points were considered to be spatially and temporally independent within the daytime elephant refuges and nighttime crop-raiding zones.

Species distribution models have been used to generate species suitability maps that are converted into resistance maps of animal movement using least-cost path modeling (Chetkiewicz et al. 2006). In this study, a Bayesian expert system (Skidmore 1989; Murray et al. 2009) was used to generate a map of suitability to elephant movement between refuges and crop-raiding zones for each corridor category. The Bayesian method and conditional probabilities are provided in the Electronic Supplementary Material (Supplementary Material Box S1 and Table S1). Predictors are reported for each corridor category in Table 1. The "control" corridor is based on predictors that are shared with the other corridors. Rocky outcrops (Edkins et al. 2008) and large farms were considered to be barriers in all corridors and were classified as "no data." Three predictors were based on the direction of elephant movements from refuges to raiding zones. We assigned higher probabilities to angular directions close to 0° and to 180° because it indicates traveling along stepping stones (Fischer and Lindenmayer 2002) and implies a straightforward movement from the refuges to the crop-raiding zones and vice versa. Predictors with a variance inflation factor (VIF) larger than 2.5 were excluded from the analysis to avoid multicollinearity (Allison 1999).

The probabilities of elephant occurrence generated by the expert system were normalized between 0 (low resistance; i.e., high suitability) and 100 (high resistance; i.e., low suitability), such that low probabilities reflect higher movement resistance (Chetkiewicz et al. 2006). Specifically, the movement resistance for a theoretical elephant to cross a pixel at location ($X_{i,j}$) was:

$$\text{Resistance}_{(X_{i,j})} = \frac{(x_{\max} - x_{i,j})}{(x_{\max} - x_{\min})} \times 100 \qquad (1)$$

where $x_{\max}$ and $x_{\min}$ are the maximum and minimum predicted probabilities of elephant occurrence and $x_{i,j}$ is the predicted probability at pixel ($X_{i,j}$). The resistance raster map was imported into the UNICOR software and the corridors were predicted for each combination of source/destination pairs of points based on their minimum cumulative resistance to elephant movement. The (minimum) cumulative resistance for a corridor is the Euclidean distance weighted by the cumulative resistance of all cells traversed (Pinto and Keitt 2009). The average cumulative resistance of the predicted corridors heading to the same destination point was calculated for each corridor category and $\log_{10}$-transformed to approximate a normal distribution. This measure, hereafter named "cumulative resistance" reflects the resistance for an elephant to move from any source point in the refuges to any given destination point in the crop-raiding zones following the predicted corridors. Specifically because the elephant is an opportunistic and generalist species and moves along paths of least resistance (Ngene et al. 2010), then the higher resistance the less likely elephants will choose that path. Similarly, if

Table 2 Number of events (n), size (ha), damage (ha), damage per farm (%), and total amount of damaged land (ha) by village per year. Standard deviations [sd] are in brackets

	2006					2008				
	n	Farm size	Damage	%	Total damage	n	Farm size	Damage	%	Total damage
Lolkisale	62	5 [7.3]	0.5 [0.5]	10 [10]	31	79	3 [3]	1 [1]	20 [10]	84
Loborsoit A	11	1.5 [2.3]	0.3 [0.3]	20 [10]	4	14	1.3 [0.8]	0.4 [0.8]	10 [10]	6
Naitolya	22	4 [6.3]	2 [6]	20 [10]	53	21	3 [2]	1 [1]	20 [10]	23
Total	95				88	114				113

Table 3 Households (HHs) surveyed in 2006 and 2008, HHs practicing agriculture, HHs reporting damage by elephants, and their average farm size (ha) in 2006 and 2008

Village	Pop 2002	n HHs	HHs 2006	HHs 2008	HHs farm 2006	HHs farm 2008	Raided HHs 2006	Raided HHs 2008	Farmsize 2006[a]	Farm size 2008[a]
Lolkisale	7599	844	149	140	134	125	45 (34 %)	102 (82 %)	4 [3] (45)	4 [3] (98)
Loborsoit A	5443	825	143	135	80	35	24 (30 %)	7 (20 %)	1 [1] (24)	3 [2](7)
Naitolya	1295	429	71	70	69	64	51 (93 %)	61 (95 %)	2 [1] (51)	2 [1] (60)
Missing				14		2		1		
Total			363	359	283	226	120	171	120	165

[a] [Standard deviation]; (number of farms)

a landscape has higher average cumulative resistance, elephants are assumed to use the (simulated) corridors rather than any other random path. In other words cumulative resistance gives a measure of accessibility (and vulnerability) of the destination point to elephant. A one-way ANOVA was performed to test differences in average cumulative resistances among the four corridor categories, and a t test to compare differences between the villages. Furthermore the cumulative resistance was linearly regressed against the probability of crop raiding at each destination point. Crop-raiding probabilities were $\log_{10}$-transformed to approximate a normal distribution prior to regression analysis. Scatterplots and an ANCOVA were used to compare the slopes of the regression lines. We applied the Gaussian kernel density function on the predicted corridors to generate the corridor density maps (Landguth et al. 2012) and display the corridors most likely used by elephant. An independent dataset of elephant occurrence was collected between 1996 and 2001 during a previous project (Oikos 2002; Msoffe et al. 2007) and used in this study to confirm elephant presence along the simulated corridors. The dataset consisted of geo-referenced presence/absence data collected during participatory land use planning activities in Lolkisale and Loborsoit A, as well as interviews with farmers and hunters. A detailed description of the dataset is given by Msoffe et al. (2007).

The GIS layers were obtained from a Global Environment Facility project (see Pittiglio et al. 2012), re-projected to the UTM zone 37, Spheroid Clarke 1880, Datum Arc 1960, and re-sampled (with the nearest neighbor method) to 30 × 30 m. Subsequently, spatial analysis was performed in ArcGIS 9.3 (ESRI) and statistical analysis in SPSS 16.0.1. The Bayesian expert system algorithm was programmed in ENVI 4.7 (ITT Visual Information Solutions). UNICOR was downloaded from http://cel.dbs.umt.edu/software/UNICOR/.

RESULTS

Statistical Analysis of Crop Raiding

A total of 406 crop-raiding events were recorded. About 300 ha were damaged by wildlife, affecting 27 % of the monitored farms, and 3 % of all small farms in the area. The most frequently damaged crops were: maize (55 %), lablab beans (22 %), beans (9 %), and green gram (7 %). Crop raids were mostly at night (92 %) and often caused by more than one species: elephant (65 %), warthog (37 %), zebra (31 %), wild pig (27 %), and antelope (17 %). Elephant crop-raiding statistics are reported in Table 2. The damaged area per farm, as well as farm size, was significantly smaller in Loborsoit A than in Lolkisale and Naitolya, while the proportion of damaged area per farm was significantly higher in Naitolya than in Loborsoit A and Lolkisale (see Supplementary Material, Table S2). In Lolkisale the extent of the damage, as well as the proportion of the damaged area per farm, increased between 2006 and 2008 ($P < 0.1$ and $P < 0.001$), whereas they remained unchanged in Naitolya and Loborsoit A. The median

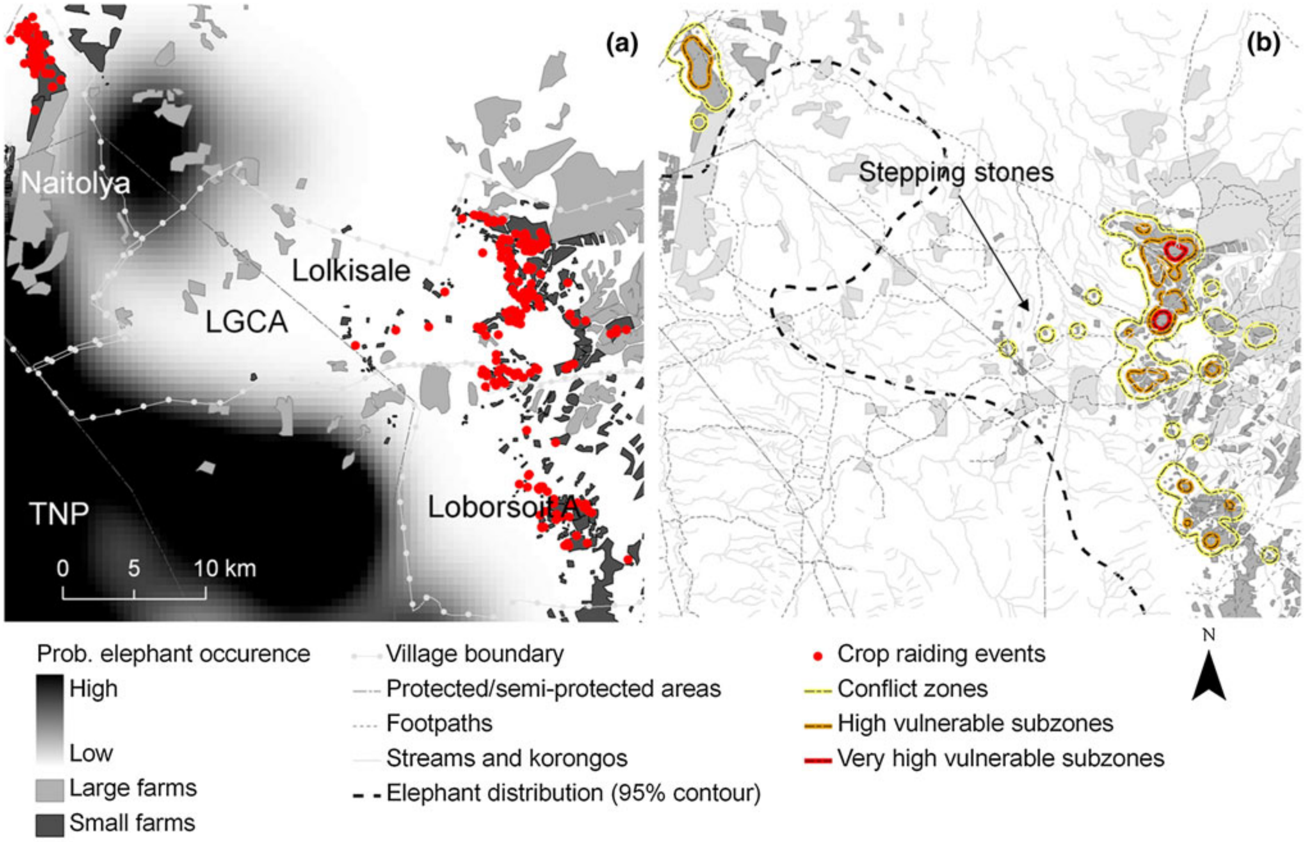

Fig. 3 **a** Crop-raiding events by elephants and probability of elephant occurrence from total counts; **b** elephant refuges (95 % contour), crop-raiding zones (95 % contour) including high and very high vulnerable subzones (50 and 10 % contours, respectively), footpaths, and dry river beds. The *arrow* indicates the stepping stone farms. *TNP* Tarangire National Park, *LGCA* Lolkisale Game Controlled Area

damaged area per farm was not significantly different when comparing between protection methods ($P > 0.05$).

The results of the household survey are shown in Table 3. Agriculture was the main land use in Lolkisale and Naitolya in both years. In Loborsoit A, half of the respondents were mixed crop–livestock farmers, though the number of farmers decreased by 25 % by 2008. Crop raiding mostly occurred at night (for 85 % of the farmers), mainly caused by elephant (75 %), warthog (29 %), and zebra (19 %). The highest percentage of farmers reporting crop raiding by elephant was found in Naitolya and the lowest in Loborsoit A during both years (Table 3). In Lolkisale the number of raided farms more than doubled between 2006 and 2008. Average farm size per village (Table 3) and damage extent (Supplementary Material, Fig. S1) were similar to those obtained from the monitoring data (Table 2).

Daily Refuges, Nighttime Crop-Raiding Zones, and Connecting Corridors

The kernel smoothing parameter h for the refuges was 4000 m, and for the crop-raiding zones 594 m. The distribution of crop-raiding events did not overlap with the elephant occurrence predicted by the total counts (Fig. 3a). The vulnerability to crop raiding was low in Loborsoit A and high in Naitolya and Lolkisale (Fig. 3b).

Figure 4a, b shows a boxplot of the distances from raided farms to elephant refuges and dams. The average distance to refuges was significantly shorter in Naitolya than in Loborsoit A and Lolkisale, whereas the longest distance was in Lolkisale ($F(2,256) = 432.5$, $P < 0.001$; post hoc test, $P < 0.05$ for all pairs). The average distance to dams was significantly shorter in Loborsoit A than in Lolkisale and Naitolya; and the longest distance was in Naitolya ($F(2,256) = 22.4$, $P < 0.001$; post hoc test, $P < 0.05$ for all pairs). Because in Naitolya both distances were less than 5 km, this village was excluded from the corridor analysis.

All environmental predictors ($VIF < 1.2$) were included in the Bayesian expert system to generate 4 resistance maps to elephant movement (Supplementary Material, Fig. S2 and Table S3). The weighted random sampling placed 2 destination points within "very high" vulnerable subzones, 3 points within "high" vulnerable subzones, and 5 points within conflict zones (Fig. 5e). The variation of crop-

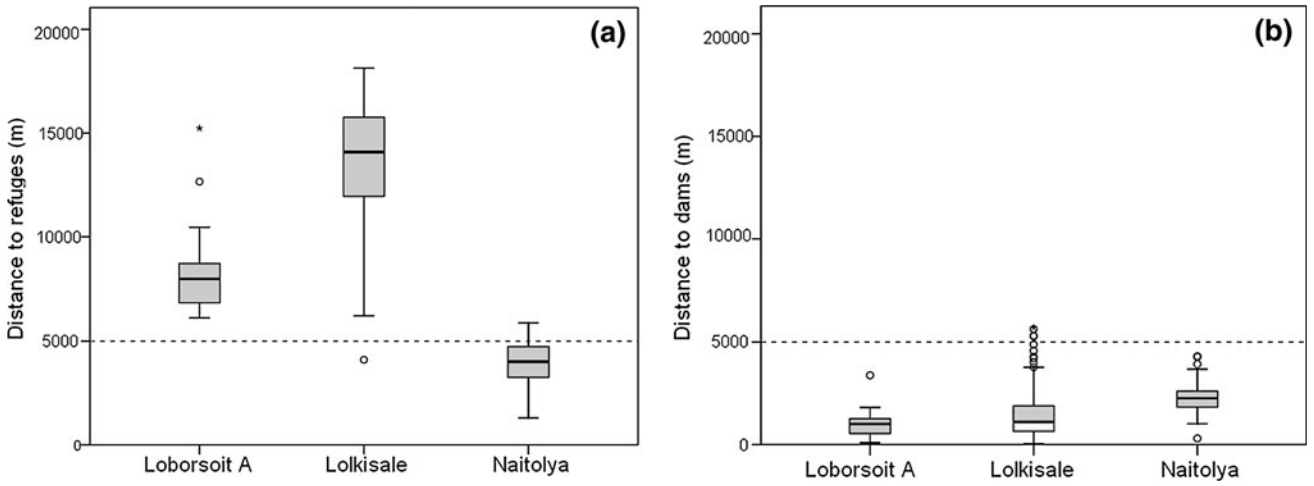

Fig. 4 Boxplot of the distance of raided farms to **a** elephant refuges and **b** dams. The *dotted line* represents the average elephant travel distance in TME

raiding probability among the selected destination points was high such that no crop-raiding zone was over- or under-represented (mean crop-raiding probability = 0.009; sd = 0.009; $n = 10$). Figure 5a–e shows the corridor density maps of each corridor category in Lolkisale and Loborsoit A. Elephant refuges were directly connected with the crop-raiding zones of Lolkisale through two high density footpath corridors (Fig. 5a), two high density dry river bed corridors (Fig. 5b), two high density “stepping stone” corridors (Fig. 5c), and one high density control corridor (Fig. 5d). In contrast, in Loborsoit A the crop-raiding zones were only indirectly connected with the refuges, except for one high density control corridor and one low density dry river bed corridor (Fig. 5a–e). The average size of the stepping stone farms was 8 ha (sd = 7.5, $n = 36$) and the average distance to the next closest stepping stone farm (as calculated using polygon’s centroid) was 1000 m (sd = 1420, $n = 36$). Four stepping stone farms reported crop raiding during the monitoring activity (see Fig. 3a, b). On average, about 55 % of the farm area was damaged by elephant (in one case about 90 %). In the same area (Lemooti subvillage), 7 farmers (out of 8) reported crop raiding during the household survey.

The average cumulative resistance differed significantly among the corridor categories ($F(3,36) = 79.9$, $P < 0.001$). The resistance was significantly higher for the “stepping stone” corridors, and lower for the dry river bed corridors than for the other corridors (post hoc test, $P < 0.001$) (Fig. 6). No difference was found between the resistance for the footpath corridors and for the control corridors (Fig. 6). The cumulative resistance was significantly and negatively related to the probability of crop raiding at each destination point for the “stepping stone” corridors ($b = -3.8, t(8) = -2.3, P = 0.05; R^2_{\mathrm{adj}} = 0.32, F(1,8) = 5.3, P = 0.05$), but was not significant for the footpath, dry river bed, and control corridors ($P > 0.05$). The slopes of the regression lines were different among the corridor categories (F(3,32) = 2.31, $P < 0.1$; Supplementary Material, Fig. S3 and Table S4). The average cumulative resistance was significantly higher in Loborsoit A than in Lolkisale for both the stepping stone ($t(8) = -3.9$, $P < 0.001$) and the dry river bed corridors ($t(8) = -2.3$, $P = 0.05$). No significant difference was found between the two villages for the footpath and control corridors ($P > 0.05$). The independent dataset of elephant occurrence provided evidence of elephant presence along the stepping stone corridors and at the stepping stone farms. Elephant also occurred in northern Lolkisale and along the corridor connecting Lolkisale and Loborsoit A, but was absent in southern Lolkisale and northern Loborsoit A and in proximity to large farms. Contradictory information emerged along the footpath connecting the refuges to northern Lolkisale (Fig. 5e and Fig. S4).

DISCUSSION

Measurement of actual crop losses is potentially difficult and controversial (Hill et al. 2002). The concordance in patterns of crop raiding that were independently obtained from annual crop-raiding monitoring and the household survey suggests that the data were consistent and representative for the study area. The impact of crop raiding in the three villages does not appear to be consistently related to distance to the elephant refuges or to water sources, which is a different finding from other studies (Naughton-Treves 1998; Graham et al. 2010b). Naitolya is close to the elephant refuges, relatively far away from water sources and heavily raided, whereas Loborsoit A is close to the

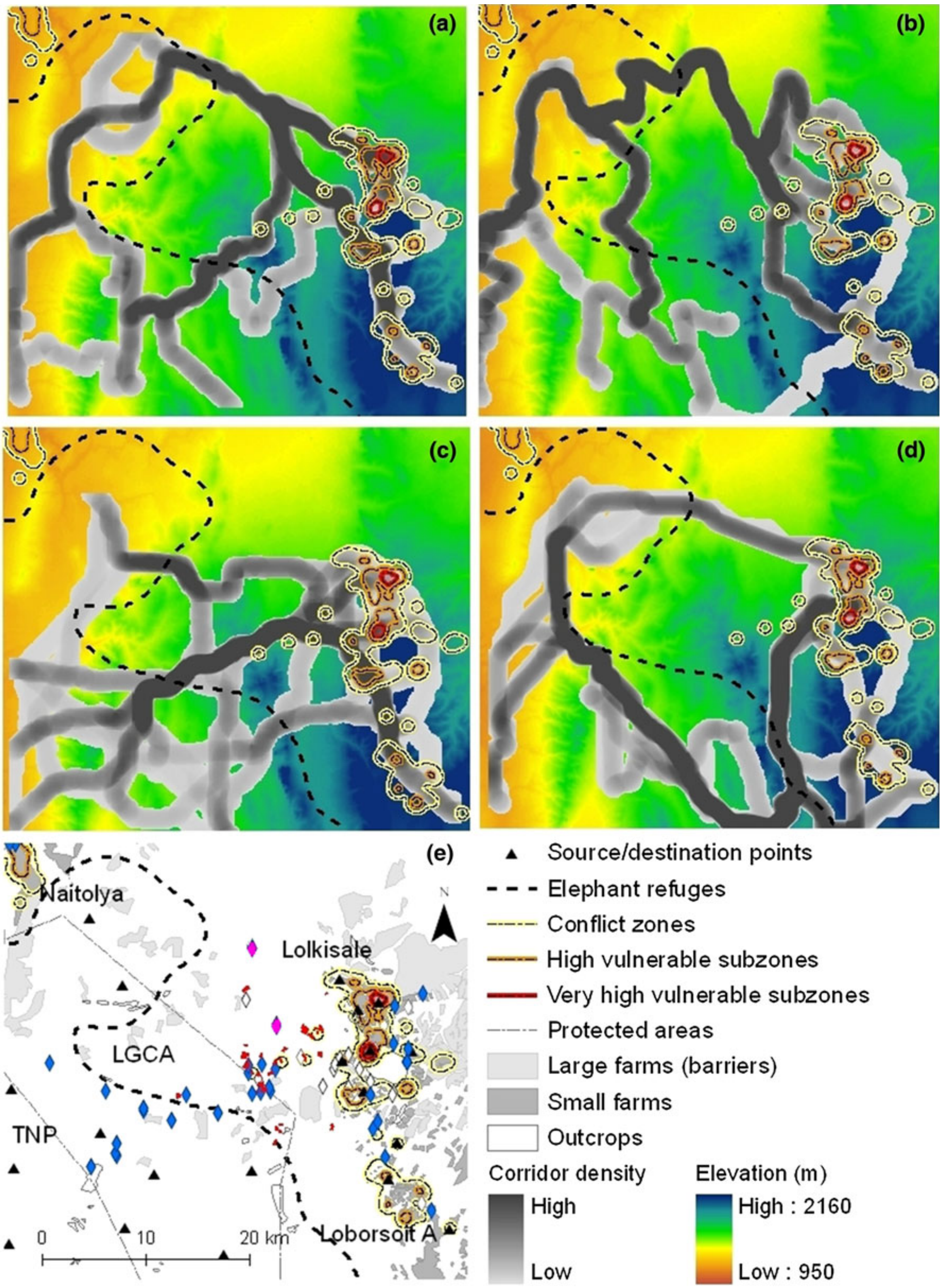

Fig. 5 Predicted elephant corridors along: **a** footpaths, **b** dry river beds, **c** stepping stone farms, **d** control corridors. **e** Shows the boundary of elephant refuges, crop-raiding zones, vulnerability subzones, source/destination points, outcrops, farms potentially acting as stepping stones (in *red*) or barriers (*light gray*) as well as presence (*blue diamond*) and absence (*white diamond*) of elephant from the validation dataset. *Pink diamonds* indicate contradictory information on elephant presence. Higher corridor density reflects higher probability of elephant movement. *TNP* Tarangire National Park, *LGCA* Lolkisale Game Controlled Area

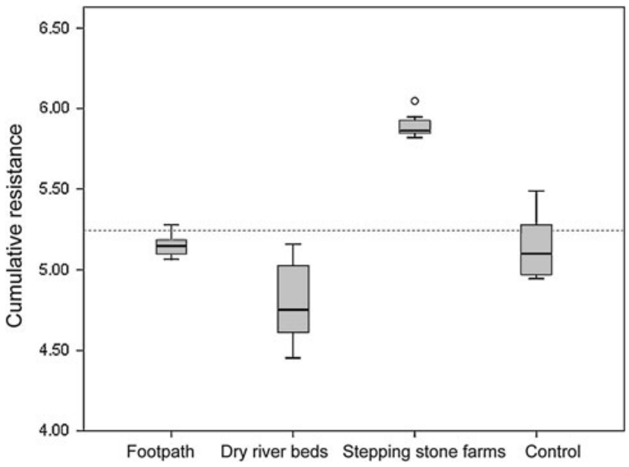

Fig. 6 Boxplot of the cumulative resistance for each corridor category. The *dotted line* represents the average cumulative resistance among all corridors

refuges and water sources, but lightly raided; meanwhile in contrast, Lolkisale is further away from the refuges and water sources and is heavily raided. Contrary to the findings by Sitati et al. (2005), the protection methods of the farms do not appear to influence the levels of crop raiding in our study area. Early surveillance becomes effective when it is reciprocally and simultaneously adopted by several smallholders (Naughton et al. 1999).

The results support our "daily refuge-crop raid corridor" hypothesis for crop-raiding elephants. We found that scattered small farms surrounded by savanna enhance the landscape connectivity for elephants, increasing the accessibility of crop farms to elephants, and thus their vulnerability to raids. There is documented evidence that elephant forage on stepping stone farms and use the simulated stepping stone corridors. These stepping stone farms provide alternative and desirable daily corridors for elephants, even across areas with a high resistance. Since our study found that dry river bed corridors have the lowest resistance for elephants, then these could be expected to be their corridors of choice, in line with the findings of Kikoti (2009). However, our findings show instead a pattern of crop raiding consistent with elephant corridors following stepping stone farms. These results imply crop-raiding elephants travel along corridors of highest resistance. We suggest that the high resistance of the "stepping stone" corridors, which is mostly due to their steeper slopes, is compensated by "easy snacks" from crops in the stepping stone farms. Our analysis shows that these farms are small (about 8 ha) and usually about 1 km apart. Thus, crop raiding may rise if stepping stone farms expand into elephant dispersal areas. Elephant occurrences in farmland (as estimated by the independent dataset) were concordant with the crop-raiding zones estimated by the kernel density function. Absences occurred outside conflict zones or inside low crop raided zones (such as in southern Lolkisale and Loborsoit A).

A novelty of this study is the integration of a Bayesian expert system with a corridor network simulator to predict elephant crop raiding. The Bayesian expert system successfully simulated elephant occurrence outside the refuges where daytime total counts fail because they do not detect nocturnal movement, including crop-raiding behavior. Outside protected areas, elephants are active mostly at night (Galanti et al. 2006; Ngene et al. 2010). Our results imply that daytime animal observations, such as total counts, are sufficient to predict neither crop raiding nor the corridors used at night. Nighttime elephant data can be obtained from radio and satellite-collared elephants (Galanti et al. 2006; Graham et al. 2009). However, because only a few opportunistically selected animals are tracked in such studies, the data may not represent the elephant distribution (Hebblewhite and Haydon 2010), particularly in relation to crop-raiding behavior. The Bayesian expert system successfully modeled the elephant activity during the entire 24 h period, by providing resistance raster maps for the corridor network simulator. An extensive body of literature demonstrates an increasing formal use of Bayesian expert systems to capture expert opinion and model complex ecological systems with limited, inconsistent and lacking measured data (Krueger et al. 2012). In such circumstances, the best available information may often be in the form of expert opinion. Although the method may suffer from a lack of objectivity in relation to the identification of the experts, there is evidence that Bayesian expert systems produce results that are repeatable, robust, accurate, and precise (Skidmore 1989; Murray et al. 2009). Strengths and weaknesses have been clarified as well as ways to reduce the degree of subjectivity and uncertainty (Voinov and Bousquet 2010). In this study, the Bayesian expert system simulated maps of elephant movement resistance. The simulated corridors were validated using crop-raiding records, household surveys, and independent data on elephant occurrence.

"Direction" of travel combined with the distance are important predictors of elephant movements, particularly for the "stepping stone" corridors; similar findings are reported for birds (Fischer and Lindenmayer 2002). Therefore, least-resistance path models based on distance (Chetkiewicz et al. 2006; Pinto and Keitt 2009), may become more accurate by including "direction."

The footpath corridors outside the protected areas did not explain crop-raiding patterns in TME. There is little use of footpaths by elephants in the study area, most likely because these are unpatrolled. Patrolled footpaths elsewhere are used by elephants (Ngene et al. 2010). Finally, the control corridors were poor predictors of routes to crop raiding due to their steepness (see Fig. 5d). Climbing is costly in terms of energetic consumption for heavyweight animals such as elephants and is therefore avoided (Wall et al. 2006).

Crop-raiding by elephant is increasing in Africa, including in the TME (Lobora 2010), which is representative of the increasingly fragmented landscapes surrounding National Parks in Africa. While disruption of connectivity by habitat fragmentation is well-established (Hanski 1998), our study demonstrates that fragmentation caused by small farms can enhance connectivity for elephants, providing alternative corridors and thereby increasing crop-raiding opportunities in villages further away from the elephant refuges. Our findings have conservation and management implications that are important for crop-raiding species. The spatial distribution and size of small farms located between elephant refuges and contiguous farmland which is a target for crop raiding should be considered in land use planning. Small farms may act as stepping stones, and large farms as barriers, and both influence the selection of daily corridors with potential negative consequences for farmers and elephants.

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