



# Validating movement corridors for African elephants predicted from resistance-based landscape connectivity models

Liudmila Osipova · Moses M. Okello · Steven J. Njumbi · Shadrack Ngene · David Western · Matt W. Hayward · Niko Balkenhol

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## Abstract

**Context** Resistance-based connectivity models are widely used conservation tools for spatial prioritization and corridor planning, but there are no generally accepted methods and recommendations for validating whether these models accurately predict actual movement routes. Hence, despite growing interest and recognition of the importance of protecting landscape connectivity, the practical utility of predictions derived from connectivity models remains unclear.

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L. Osipova (✉) · N. Balkenhol  
Wildlife Sciences, University of Göttingen, Göttingen,  
Germany  
e-mail: [afp48e@bangor.ac.uk](mailto:afp48e@bangor.ac.uk);  
[bominosh@gmail.com](mailto:bominosh@gmail.com)

N. Balkenhol  
e-mail: [nbalken@gwdg.de](mailto:nbalken@gwdg.de)

L. Osipova  
Bangor University, Bangor, UK

M. M. Okello  
Department of Tourism Management, Moi University,  
Nairobi, Kenya  
e-mail: [mokello@fieldstudies.org](mailto:mokello@fieldstudies.org)

**Objectives** The difficulties in validations are mainly related to the unavailability of independent data and lack of appropriate, easily applied statistical frameworks. Here, we present a case study where two independently collected datasets were used to validate resistance-based landscape connectivity models and movement corridors identified by these models.

**Methods** We used annual aerial counts to evaluate the connectivity model, and a field survey to assess the performance of predicted corridors. We applied these two independent datasets to validate a previously developed connectivity model for the African elephant (*Loxodonta africana*) in the Borderland region between Kenya and Tanzania.

S. J. Njumbi  
International Fund for Animal Welfare (IFAW), Nairobi,  
Kenya  
e-mail: [snjumbi@ifaw.org](mailto:snjumbi@ifaw.org)

S. Ngene  
Kenya Wildlife Service, Nairobi, Kenya  
e-mail: [sngene@kws.go.ke](mailto:sngene@kws.go.ke)

D. Western  
African Conservation Centre, Nairobi, Kenya  
e-mail: [jonahwestern@gmail.com](mailto:jonahwestern@gmail.com)

M. W. Hayward  
University of Newcastle, Newcastle, Australia  
e-mail: [matthew.hayward@newcastle.edu.au](mailto:matthew.hayward@newcastle.edu.au)

**Results** The results of this study confirm that the resistance-based connectivity model is a valid approach for predicting movement corridors for the African elephant. We show that high connectivity values are a strong predictor of the presence of large numbers of the elephants across the years. The probability of observing elephants increased with increasing connectivity values, while accounting for seasonality is an important factor for accurately predicting movements from connectivity models.

**Conclusion** Movement corridors derived from resistance-based connectivity models have a strong predictive power and can be successfully used in spatial conservation prioritization.

**Keywords** African elephant · Conservation planning · Resistance surface · Landscape connectivity · Movement corridors · Step-selection function

## Introduction

Habitat fragmentation and species range shifts caused by changing bioclimatic envelopes cast doubt on the conservation benefits of static protected areas and require new methods and concepts (Sanderson et al. 2006; Bennett et al. 2006; Doerr et al. 2010; Donaldson et al. 2017). Preserving connectivity between otherwise isolated habitat patches is essential for conserving species, as it helps to maintain gene flow and viable populations (Haddad and Tewksbury 2006). Reduced landscape connectivity can dramatically affect many ecological processes, and therefore connectivity planning is a valuable complementary method to conventional conservation approaches (Bennett et al. 2006).

The term ‘landscape connectivity’ relates to two different concepts—structural and functional connectivity (Crooks and Sanjayan 2006; Meiklejohn et al. 2009). Structural connectivity refers to the physical connection of habitat patches via habitat-like corridors. In contrast, functional connectivity describes the response of organisms to landscape structure and the patterns of ecological flows that result from these individual responses (Brooks 2003). For example, a stretch of forest that structurally connects two forest patches may not be functional for a forest-dwelling

target species, if the species is unwilling or unable to successfully travel through the corridor. Similarly, two patches that are not physically connected by any obvious corridor can still be functionally connected from the perspective of the target species, if it can successfully move through the matrix between the patches. Hence, taking into consideration the functional response of species to landscape structure is becoming a crucial part of contemporary conservation planning approaches (Bennett 2003; Baguette and Van Dyck 2007).

Functionality is especially important for the delineation of conservation corridors. While structural corridors are considered non-dynamic land bridges between suitable patches, functional corridors take into account actual movement behaviours and dispersal abilities and hence are species-specific (Tischendorf and Fahrig 2000; Baguette and Van Dyck 2007; Goswami and Vasudev 2017). While identifying structural corridors is straightforward, especially when working within habitat-matrix-corridor landscapes (Forman 1995), delineating functional corridors is more challenging, particularly when working in gradient landscapes with spatially and temporally varying matrix qualities. In such landscapes, models of functional connectivity are often based on resistance surfaces, which contain values that predict how environmental conditions in any cell of the study landscape will impede the willingness or ability of an individual to move through that cell (Beier et al. 2008; Zeller et al. 2012).

To parameterize resistance surfaces, empirical genetic or animal movement data (GPS or VHF telemetry datasets) should ideally be used (Zeller et al. 2012; LaPoint et al. 2013; Ziđkowska et al. 2016). Step-selection functions (SSFs) are particularly suitable to estimate resistance surface values (Richard and Armstrong 2010; Zeller et al. 2012; Thurfjell et al. 2014; Carvalho et al. 2015). This method allows calculating the strength of species’ habitat selection using steps reflecting actual animal movements (Zeller et al. 2012, 2015; Keeley et al. 2016). SSFs are based on real animal movement data and therefore reflect animal knowledge of the environment, limit resource selection by modelling realistic habitat availability around each step, and allow us to predict landscape resistance based on movements rather than habitat suitability. SSFs have been successfully applied to a variety of species and conservation problems (Forester

et al. 2009; Roever et al. 2013; Thurfjell et al. 2014; Signer et al. 2017).

Once resistance surfaces have been parameterized based on empirical data, functional connectivity models can be constructed by estimating a spatially-explicit probability that any cell of the landscape will be used by individuals that move from one specific location to another. Thus, while underlying resistance surfaces depict the *local* (i.e., cell-specific) cost to individual movement across the entire study landscape, resulting connectivity models show how this cost shapes movement *among* selected locations within the landscape. The resulting connectivity models can then also be used to predict and delineate functional corridors, by identifying those areas that have the highest, species-specific probability of being used for movement between specific locations of interest (e.g., protected or management areas).

Numerous studies have shown that using resistance-based connectivity models for corridor planning is effective and that they have significant potential in conservation management (Gilbert-Norton et al. 2010; Doerr et al. 2010; Abrahms et al. 2016). Nevertheless, some concerns regarding the usefulness of landscape corridors and their overall performance remain (Beier and Noss 1998; Hodgson et al. 2009). Hence, it is pivotal to validate whether resistance-based connectivity models and the corridors predicted from them are actually suitable for predicting occurrence and movement of the target species.

Thurfjell et al. (2014) reviewed connectivity studies based on step-selection functions, and emphasized that most of these studies neglected validation, and concluded that more research is required to ensure their successful realization in conservation practices. The same conclusion has been made by Wade et al. (2015) in the revision of using resistance-based wildlife connectivity modelling across the United States. Validating the model with independently collected data is challenging as it always requires an additional dataset and the methodological framework for validation has not yet been standardized or applied across a sufficient number of studies.

Indeed, few researchers have attempted to evaluate the predictive performance of connectivity models. These studies used species occurrence and GPS datasets for validating either already existing ‘historical’ structural corridors (Clevenger et al. 2002; Naidoo et al. 2018) or corridors designed via

individual-based modelling (Brooker et al. 1999). Some researchers used genetic data to evaluate the suitability of structural corridors in maintaining dispersal in fragmented landscapes (Mech and Hallett 2001) or validated structural landscape corridors with functional connectivity models (Wang et al. 2008; Mateo-Sánchez et al. 2015; Naidoo et al. 2018). Functional connectivity models and corridors predicted from animal movement data have rarely been evaluated (e.g. LaPoint et al. 2013). Potential datasets for effective validation of functional connectivity and corridors should ideally incorporate long-term observations of movements through the landscape. Animal movements from GPS telemetry are highly suitable for this and, when the sample size is large enough, the data can be split into predictions and validation subsets (Bond et al. 2017). A good alternative to telemetry data are repeated population counts collected in the same area where the predictions were made. Count data allows derivation of the species’ spatial preferences and the identification of fidelity to certain areas, especially if collected over a long period. Large mammals in open areas are often counted during aerial census surveys (Jolly 1969; Western et al. 1976). This method provides high accuracy estimates in areas with sparse vegetation because of good visibility of the animals and high certainty in species recognition (Jachmann 2002; Ndaimani et al. 2016). Hence, aerial census surveys are widely used in animal population studies (Prins and Douglas-Hamilton 1990; Stoner et al. 2007; Singh and Milner-Gulland 2011; Okello et al. 2016). As aerial survey data include a spatial component, it has also been used to identify prominent migration corridors (Pittiglio et al. 2012; Mose et al. 2013), and it is highly informative for validating connectivity models.

In this study, we used an independent data set and conducted a field survey to validate functional connectivity models based on telemetry data for the African elephant (*Loxodonta africana*). Specifically, we built connectivity models for wet and dry seasons based on SSFs-based resistance surfaces and predicted the most probable movement corridors based on these surfaces. Then, we used aerial count data to fit a generalized linear mixed-effect model (GLMM) to predict the probability of observing elephants in the study area and test whether adding connectivity values together with other environmental variables would significantly improve the predictive performance of

the regression model. Finally, we complemented this approach with a fine-scale validation of predicted corridors using an indirect animal sign (spoor/footprint) survey. The first validation approach showed that including a connectivity estimate as a model covariate significantly improved our ability to predict the presence of elephants in our study area. The second validation approach confirmed that the corridors predicted from the seasonal connectivity models were used more frequently than areas outside predicted corridors.

## Methods

### Study area

The 8300 km<sup>2</sup> study area is within the Greater Amboseli Ecosystem in borderland between Kenya and Tanzania (Fig. 1a). It is a semi-arid area prone to the droughts and with irregular rainfall with short rains from October to December, and a long rainy season from March to May. The water sources are mostly seasonal streams and minor rivers (Okello et al. 2016). The area includes three large national parks (NPs) and three community conservancies.

### Resistance surface and connectivity modelling

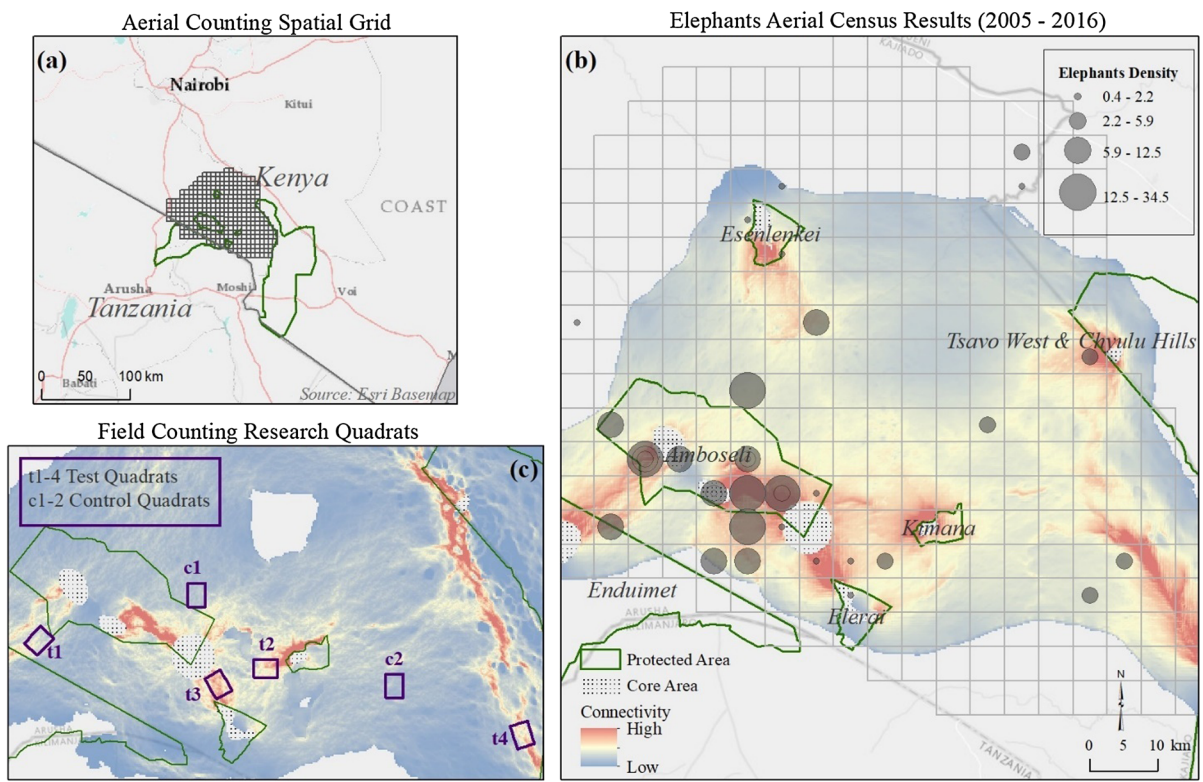
We used a methodological framework fully described in Osipova et al. (2018) for modelling seasonal resistance maps with 250 m resolution. We calculated resistance to movement surfaces using movement data obtained from 12 individuals of African elephants collared in the study area. The data were collected over two consecutive years (2013–2014). We fitted SSFs (Manly et al. 2002; Fortin et al. 2005; Johnson et al. 2006) to the movement data and 11 environmental variables obtained from publicly available sources or derived from remote sensing data and resampled to 250 m resolution (Supplement 1, Table S1). For seasonal models, we fitted SSFs using the same set of environmental variables, but with the different NDVI layers (MODIS) for each month. For that, we subset the movement data for each month and extracted corresponding NDVI values for the movement steps. Thereafter, the whole dataset was split into wet and dry seasons. We used monthly rainfall data obtained from the Tropical Rainfall Measuring

Mission (TRMM; TMPA/3B43 dataset) to define wet and dry seasons. Months with rainfall less than 30 mm/month were assigned to the dry season.

The data were fitted using penalized conditional logistic regression with least absolute shrinkage and selection operator (LASSO) (Reid and Tibshirani 2014). This approach avoided autocorrelation and biases in covariates, which is a general issue for telemetry data (Beyer et al. 2010; Street et al. 2016). The inverse of movement probabilities estimated with SSFs were interpolated to the resistance surfaces whose values range from 0 to 1, where lower values represent a higher probability that an elephant will move through this area (Zeller et al. 2012).

As the resistance surface is pixel-based (each pixel represents one resistance value) and connectivity has a route-specific nature (Cushman et al. 2009), we applied least-cost paths (LCP) and circuit theory to model connectivity and delineate the most likely movement corridors (McRae et al. 2008; Carroll et al. 2012). LCP assume optimal movement of organisms across the heterogeneous landscape (i.e., the resistance surface) while circuit-theory assumes random movement of individuals across the entire resistance surface (McRae et al. 2008). The two approaches are complementary, because LCP predict a single optimal movement path between patches, while circuit theory identifies alternative pathways and small areas that are disproportionately important for connectivity ('pinch-points'). To combine the two approaches, the LinkageMapper toolkit (McRae and Kavanagh 2011) provides an option to first delineate corridors based on least-cost calculations (by combining and mosaicking the cost-weighted distance grids for all pairwise least-cost path calculations; see Supplement 4) and then to restrict the circuit-theoretic calculations to within these corridors. The result of these calculations are predictions of the most likely movement paths within the delineated corridors. Specifically, the amount of current running through the least-cost corridors reflects the likelihood of random walks within the corridors and represent the amount of connectivity between the patches (Shah and McRae 2008; Carroll et al. 2012). Cells with higher current flows are predicted to be used more frequently by organisms moving through the corridor network. This combination of least-cost and circuit-theoretic connectivity modeling has been successfully applied to studies in movement ecology, landscape genetics and

## Greater Amboseli Ecosystem. Elephants Aerial Census and The Ground Counts



**Fig. 1** **a** Study area in the borderland between Kenya and Tanzania with the spatial grid used for the elephants' aerial census; **b** connectivity model with the core areas estimated from the elephant movement data using a 50% threshold of kernel densities. Elephant density is estimated with annual aerial census implemented by African Conservation Center in

2005–2016; **c** connectivity model estimated using a subset of the elephant movement data (March) and validation research quadrats. Quadrats t1–t4 are test quadrats placed in the area with predicted high connectivity flows (probable movement corridors); c1–2 are control quadrats placed in the area with low predicted connectivity

wildlife corridor design (e.g. Yumnam et al. 2014; Bowman and Cordes 2015; Dutta et al. 2016; Jackson et al. 2016; Hofman et al. 2018).

We defined patches as the core areas used by the elephants in protected lands. We estimated these areas as the 50% threshold of the kernel density calculated from the elephants' GPS fixes within the NPs and community conservancies. The LinkageMapper analysis was performed in ArcGIS 10.5.1 (ESRI 2017) and output rasters were further processed in the *raster* package in R, version 2.7.15 (Hijmans et al. 2016).

#### Connectivity model validation methods

##### *Connectivity model validation using aerial counts*

We used the elephant counts collected by the Amboseli Conservation Program (ACP) from aerial surveys conducted between 2005 and 2016. The entire study area of 8300 km<sup>2</sup> was surveyed using a block sampling method with a spatial grid with 332 grid cells of 5 × 5 km size (Fig. 1a). Each grid cell was systematically traversed by the aircraft using straight flight lines at a nominal height of 91 m with counting strips approximately 150–200 m wide (Norton-Griffiths 1978). The aircraft crew included a pilot and two observers (front and rear). The total number of elephants estimated per grid cell was spatially attributed to the coordinates of each cells' center

(see Western et al. 1976 for further details). The surveys were repeated for wet and dry seasons in the corresponding years (Fig. 1b).

We hypothesized that if the connectivity model performed well and the grid cells with higher connectivity values representing higher likelihood of elephants' movements between habitat patches, they would be more frequently used by elephants compared with a cell of similar characteristics with lower connectivity values. Connectivity values extracted from the surfaces represent cumulative electrical currents calculated from electrical connectivity theory and reflecting the likelihood of random walks between each pair of patches (Shah and McRae 2008).

For testing this hypothesis, we regressed aerial observations of elephants per grid cell with various environmental variables and connectivity values. We fitted a GLMM with a set of environmental covariates and connectivity values per grid as fixed effects, and the years of observations as a random effect using R software version 3.4.3 (R Core Team 2017) and a package lme4 version 1.1.15 (Bates et al. 2015). The environmental variables were chosen based on ecological relevance and tested for collinearity (Table 1). The final set of environmental variables used for model fitting had Pearson correlation coefficients less than 0.6 (Supplement 2) and are presented in Table 1. We also tested the count data for spatial autocorrelation with a spline correlogram for each sampling year to ensure that the sampling cells were spatially independent.

To assess the effect of seasonality, we used two resistance surfaces, and hence, two connectivity models for wet and dry seasons. We excluded 12 grid cells covering the core areas that were intensively used by the elephants within the protected lands, which assured that we were testing the connectivity model for non-protected areas only (Fig. 1b). Animal count data are often overdispersed due to zero-inflation (high proportion of zeros in relation to the actual counts) (Zuur et al. 2009). The recommended method of dealing with zero-inflated datasets is using a mixture model consisting of two parts. The binomial aspect modelled the probability of obtaining zero values; while the count aspect takes only values larger than zero and fits the model assuming a Poisson distribution (Zuur et al. 2009; O'Hara and Kotze 2010). Therefore, we fitted a Poisson model with a log link function for the count part, and logit link for the binary part (Bolker

et al. 2012). We used wet and dry seasons as categorical interaction terms, assuming the effects of connectivity may differ with seasonality.

We began by fitting the full model incorporating all explanatory variables, and then tested the importance of each variable by gradually excluding them from the model (stepwise AIC selection procedure). We calculated joint AIC values (for zero-inflated and count parts), and estimated goodness-of-fit of each model by calculating  $R^2$ , marginal  $R_m^2$  (variance explained by fixed terms) and conditional  $R_c^2$  (variance explained by fixed and random terms) (Nakagawa and Schielzeth 2013). We verified the top selected model fit by plotting of Pearson residuals against fitted values and each covariate, and the residuals were checked for spatial autocorrelation (Zuur et al. 2010).

#### *Predicted corridors validation using indirect field counts*

To evaluate if the predicted corridors were intensively used by the elephants, we placed six 12 km<sup>2</sup> research quadrats in the study area. We applied a connectivity model built only on a subset of the GPS movement and NDVI layers from March 2015. We used the subset because we aimed to refine the prediction to the corresponding time of year when the field data were collected (i.e., March 2017).

Four 'test quadrats' were positioned within the predicted corridors (high connectivity values), and two 'control quadrats' were placed outside of the corridors (Fig. 1c). Each quadrat consisted of 4 parallel transects 3 km long with a 1 km gap between them. To account for potential biases caused by human disturbance, we placed two quadrats (one test and one control) in an area of intensive agriculture (Fig. 1c). We attempted to allocate the quadrats in areas with similar environmental conditions to ensure that there were no physical or ecological barriers for the elephants to traverse while travelling from one protected area to another. We assumed that if the predicted higher connectivity values were 'working' corridors for the elephants, then elephant track density and abundance estimates would be higher in the test quadrats.

We collected and georeferenced all elephant tracks from the walking transects (overall length of the survey transects was 12 km within each quadrat and

**Table 1** Stepwise models' selection goodness-of-fit comparisons for zero-inflated GLMM fitted to the elephants counts data

Dropped fixed terms	AIC <sub>j</sub>	log lik	Count part		Binary part	
			R <sub>m</sub> <sup>2</sup>	R <sub>c</sub> <sup>2</sup>	R <sub>m</sub> <sup>2</sup>	R <sub>c</sub> <sup>2</sup>
None (full model)	3289.8	− 1434.0	0.31	0.44	0.18	0.18
Connectivity × season	4471.9	− 1815.5	0.17	0.31	0.08	0.08
Season (interaction term)	4055.5	− 1818.9	0.21	0.33	0	0
All but connectivity × season	4146.8	− 1866.3	0.18	0.23	0	0
Slope	4073.6	− 1827.4	0.2	0.25	0.17	0.17
NDVI	3432.7	− 1507.2	0.29	0.4	0.003	0.01
Grasslands	3381.0	− 1480.9	0.29	0.45	0.12	0.12

Joint Akaike information criterion for the count and binary fitted models (AIC<sub>j</sub>), log likelihood (log lik), variance explained by fixed term only (marginal variance R<sub>m</sub><sup>2</sup>) and variance explained by fixed and random terms (conditional variance R<sub>c</sub><sup>2</sup>)

*Full model:* Number of elephants ~ Slope + NDVI + Proportion of Grasslands + Connectivity + (Connectivity × Seasons) + (1year)

72 km in total). The survey area included mainly open savannah with a sparse vegetation or local-scale agriculture (Table 2). Elephant tracks are highly visible in this flat area and easy to identify; they are only washed away during heavy rain. Therefore, collecting the data over a short time period at the end of the dry season assured counting most crossings from at least the last 2 months (no rain had fallen within the study area in that time). The data were collected with the help of an experienced tracker who identified footprints. Due to the large size of elephant footprints and their persistence over time, we were able to estimate an approximate age of crossings deductively by the level of track disturbance (1–2 days ago; 3–7 days; 7–14 days; more than 2 weeks ago). Stander et al. (1997) showed that spoor tracking using local knowledge had a 98% accuracy. Using local knowledge for animal tracking has been successfully applied in numerous studies on a suite of species, including African elephants (Southgate et al. 2005; Norris et al. 2008; Southgate and Moseby 2008; Songhurst et al. 2016).

We estimated track densities per quadrat by calculating the total number of tracks recorded along the transects (groups of individuals travelling together were counted as one) and divided by the quadrat's area. We also calculated the total number of individuals that crossed the research quadrat within the last 2 months. The higher the numbers, the more intensively the elephants moved through the research plot in the last 2 months.

As the track density is a naïve estimate (i.e. the sum of the plot counts), we also calculated the elephant abundance value for each plot using the Formozov–Malyshev–Pereleshin formula (Stephens et al. 2006):

$$D = \frac{\pi \cdot x}{2 \cdot SM}$$

where  $D$ -animal density (abundance),  $x$ -number of daily tracks crossing the survey transect;  $S$ -survey transect length; and  $\hat{M}$ -mean daily travel distance of an animal.

This method estimates animal abundance based on the probabilistic relationship between the number of crossings of a transect of given length and an animal's daily travel distance. The formula has been tested with simulations and empirical datasets and showed high performance for the abundance estimate (Stephens et al. 2006; Keeping and Pelletier 2014). For fitting data to the formula, we used only a subset of fresh (1–2 days old) elephant tracks crossing transects. The average travel distance was calculated using the GPS telemetry for the corresponding month (March). We applied non-parametric bootstrap sampling for the standard error calculation (1000 iterations).

## Results

### Connectivity model evaluation using aerial counts

A multicollinearity test revealed correlations between land cover variables (proportion of grassland,

**Table 2** Environmental variables, tracks densities and abundance values estimated in the research quadrats (t1–4 are test quadrats placed in the predicted corridors; c1–2 are control quadrats placed outside of the corridors)

	Low human disturbance				High human disturbance	
<b>No. on map</b> (Fig. 1c)	<b>c1</b>	<b>t1</b>	<b>t2</b>	<b>t3</b>	<b>c2</b>	<b>t4</b>
Dominant vegetation type	open lands/ sparse bushland	sparse bushland/ open lands	sparse bushland	sparse bushland	sparse bushland	sparse bushland
Mean slope	6.16	4.92	5.53	4.91	5.38	5.61
Mean NDVI	0.16	0.19	0.23	0.27	0.24	0.22
Proportion of agriculture	0.00	0.00	0.00	0.01	0.24	0.46
High connectivity values	0.006	0.52	0.99	0.82	0.006	0.92
<b>Elephants density estimates</b>						
Number of individual tracks	15	126	73	108	11	76
Tracks density*	0.5	3.7	1.7	4.25	0.5	1.3
Abundance (mean $\pm$ S.E.)**	0.04 $\pm$ 0.0006	0.75 $\pm$ 0.002	0.32 $\pm$ 0.001	N/A	0.02 $\pm$ 0.000	0.59 $\pm$ 0.004

\*Individuals moving in a group were counted as 1 set of tracks

\*\*Formozov–Malyshev–Pereleshin estimate with bootstrapping

bushland and woodland), so we retained only one land cover variable (proportion of grassland) in the model. The pairwise Pearson correlation coefficients were less than 0.6 for the final set of explanatory variables (Supplement 2). Plotting Pearson residuals against original and fitted values, neither the explanatory variables or the spline correlogram indicated any problems with models fit (Supplement 3) (Zuur and Ieno 2016).

Correlograms of the count data for most years revealed an absence of or only small spatial correlation splines (less than 0.5) at short distances. Only the 2012 dataset had a spline with a correlation larger than 0.5, but only at a distance of  $\sim 1$  km, which then rapidly decreased (Supplement 3). Considering the size of the grid cells ( $5 \times 5$  km) and results of spatial autocorrelation plots, we concluded that the dataset was not spatially correlated.

We fitted models with all explanatory variables through repeated evaluation with unique variables and interaction term recombinations. Connectivity variables with seasonality as the interaction term were retained in the top 5 selected models. The model with the highest joint AIC criteria included connectivity and season as interaction terms and explained 44% of

the variance ( $AIC_j = 3289.83$ ,  $R_c^2 = 0.44$ ). The model including only connectivity as an explanatory variable itself explained 23% of the data's variance ( $AIC_j = 4146.83$ ,  $R_c^2 = 0.23$ ). Stepwise excluding environmental variables from the model showed that the model fitting was most negatively affected after excluding connectivity from the set of fixed terms ( $AIC_j = 4471.94$ ,  $R_c^2 = 0.31$ ). The second and third most influential covariates were slope and seasonality as an interaction term ( $AIC_j = 4073.61$ ,  $R_c^2 = 0.25$  for slope;  $AIC_j = 4055.54$ ,  $R_c^2 = 0.33$  for seasonality) (Table 1). The full model predicted decreasing probability of zero observation and increasing probability of observing higher elephants number with higher connectivity values (Fig. 2).

#### Predicted corridors validation using indirect field counts

The research quadrats were placed in the areas with comparably low slope and moderate productivity (NDVI) values (Table 2). The quadrats placed in the area with high human disturbance included at least 24% of small-scale agriculture for the test quadrat, and 46% for the control quadrat. The proportion of higher



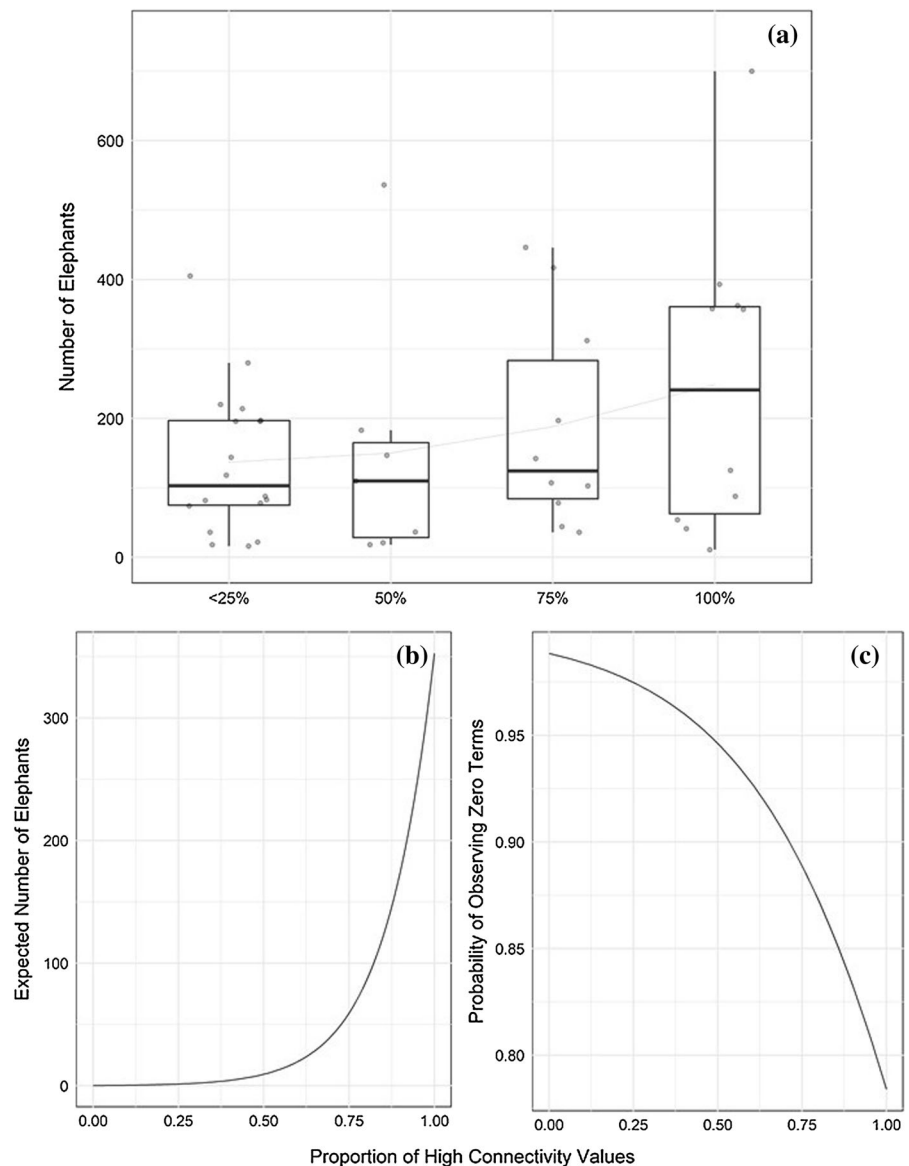
connectivity values (the values higher than 0.2) varies from 50 to 99% for test quadrats, and only 0.06% in both control quadrats (Table 2).

For the Formozov–Malyshev–Pereleshin formula, we used the overall length of the survey transect per quadrat (12 km) and an average daily distance estimated using the telemetry data (5.8 km/day). The range of track densities and abundance values for control quadrats are prominently lower compared to the test quadrats (0.5 vs 1.3–4.25 for tracks density; 0.02–0.05 vs 0.32–0.75 for abundance, Table 2). We could not estimate abundance for the quadrat *t3*

because all counts in this quadrat were older than 2 days, while the formula requires input on only the last day’s tracks. Despite the absence of tracks within the few days prior to the survey, this quadrat actually included the highest track density recorded for the previous 2 months (4.25 tracks/km<sup>2</sup>, Table 2).

The highest track density/abundance ratio was for the corridor connecting Amboseli with Enduimet (quadrat *t1*, Fig. 1c); and the lowest values were for the corridor between Amboseli and Elerai (quadrat *t3*, Fig. 1c). The quadrat *t4* in the high human disturbance area had track density values as high as the quadrats in

**Fig. 2** **a** Number of elephants (non-zero counts) estimated from the aerial census survey (2005–2016) plotted against the proportion of high connectivity values (> 0.2) predicted with a resistance-based SSFs connectivity model; **b** fitted curve for the full zero-inflated GLMM model. The y-axis represents expected number of the elephants, and the x-axis shows the proportion of high connectivity values; **c** fitted curve for the binary part of the model. The y-axis represents probability of observation of zero terms (no elephants in a grid cell), and the y-cell shows the proportion of high connectivity values



the non-disturbed area (e.g. quadrat t2 has a track density 1.7 vs 1.3 for the quadrat t4).

## Discussion

Our study demonstrates that connectivity values derived from a landscape resistance model are the most significant predictor of elephant abundance based on a linear mixed effects model derived from aerial census data and environmental covariates and connectivity. Additionally, we implemented on-ground surveys inside and outside of the predicted corridors and calculated elephant density differences between research sites to confirm that the resistance-based connectivity model built on SSFs and circuit theory accurately predicted both at the larger (higher connectivity values predicts higher number of observed animals across the years) and smaller scale (predicted corridors are more intensively used by the focal species).

Repeatable aerial census data is one of the rare examples of an independent dataset that can be used for validation of a connectivity model's predictive power. Systematic block sampling from the air is a well-known and commonly used method for large mammal population trend surveys (Western et al. 1976; Jachmann 2002; Dunham 2011; Ngene et al. 2011). In contrast to the species occurrence data, where the data points represent presence or non-detection of the individual on the ground, aerial counts take 'snapshots' of the ground and estimate the number of individuals and their spatial affiliation over a long period of time. These data characterize the parts of the landscape that are more intensively used for feeding or movements by the animals, and therefore have the potential for capturing regularly used corridors (Pittiglio et al. 2012; Mose et al. 2013). One probable data-related issue would be the high possibility of registering intensively used habitat patches alone with the corridors. To ensure that we are testing movement routes rather than resting/feeding patches, we excluded grid cells corresponding to the intensively used protected lands estimated from the GPS movement data using kernel density (Osipova et al. 2018).

The results of the zero-inflated GLMM model confirmed our hypothesis that connectivity routes are a significant predictor of the presence of elephants in a corresponding spatial grid cells. The goodness-of-fit of the model was most negatively affected when the connectivity predictor was excluded. At the same

time, removing all variables except connectivity leads to improved model fit compared to excluding just connectivity as a predictor. Connectivity with season as an interaction term alone explained 23% of data variance (Table 1). The seasonality influence on model performance is third after the connectivity and slope variables. This leads us to the conclusion that the resistance-based connectivity model is a genuine predictor of elephant presence in the landscape, and adding seasonality to the model significantly improves the predictions.

The predictions from the full zero-inflated model fitting further confirmed the hypothesis that higher connectivity values predicted larger elephant numbers. The shape of the prediction curve captures the patterns observed in the actual data (Fig. 2). When the proportion of higher connectivity values is less than 50% per grid cell, the number of observed elephants remains relatively constant. However, the predicted elephant numbers grew exponentially when the proportion of higher connectivity values reached > 75% per grid cell (Fig. 2). Predictions from the binary section of the model showed that the probability of zero counts (no elephants in a cell) was expected to be high in the data, but the probability decreased with increasing landscape connectivity. Thus, results from the model's predictions are in accordance with our initial hypothesis that the probability of observing large numbers of elephants is higher in areas with higher connectivity potential.

The track counts showed that quadrats in the predicted corridors were crossed by elephants more frequently compared to those off the corridors. Track densities were two to four times higher in the corridors than off them; and the number of individual tracks varied from 73 to 126 in the corridors, versus only 11–15 in the control quadrats. The corridor quadrats placed in the pristine lands adjacent to the large protected areas had the highest movement intensity values (the corridor between Amboseli National Park and Enduimet; the corridor between Tsavo West NP and Chyulu Hills NP). At the same time, the test quadrats placed in the area occupied by small-scale agriculture (46% of the area) were used by elephants at similar rates to the quadrats with no human activity presence. Conversely, the control quadrat with 24% of the agriculture area had only 11 individual crossings (versus 76 individuals in the test quadrat). As the environmental conditions in the quadrats were similar,

we assumed that elephants use the corridors for movement irrespective of human presence. This conclusion corresponds to previous studies that showed that small-scale agriculture attracts elephants for crop raiding, and thereby regularly causes human–wildlife conflict (Graham et al. 2010). The study area has had a long history of human–elephant conflict (Okello 2005; Kioko et al. 2006), and the accurate predictions of movement corridors across such an area with rapidly developing agriculture might be a good predictor of an areas' potential for conflict.

Future studies should expand our validation approach using different datasets and statistical methods. For the field count methods extension, it would be beneficial to use more sample quadrats across the study area and possibly implement repeatable counts within and between seasons. Long-term monitoring of the same predicted corridors would provide valuable information about the prediction accuracy and deliver more data for sensitivity analysis. We found that track density counts were the most convenient on-ground sampling methods for African elephants in savannah biomes. Their tracks are highly visible, easy to identify and stay undisturbed for a long period of time. However, other sampling techniques can be considered for more covered and forested habitats, including distance sampling method (Buckland et al. 2001; Buckland 2004) or camera trapping (Rowcliffe et al. 2008; LaPoint et al. 2013; Burton et al. 2015).

Overall, the results of this research support the hypothesis that resistance-based connectivity modelling is a valuable working tool for predicting movement corridors and has high potential for species connectivity conservation and landscape planning. We demonstrated that the resistance-based connectivity model has a strong predictive power and can be helpful for delineating movement corridors. Additionally, we showed the importance of accounting for seasonality in connectivity studies and confirmed that predicted corridors are intensively used for movement by the elephants.

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