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DOCTOR OF PHILOSOPHY

Functional landscape connectivity models in applied conservation: spatio-temporal variability, on-ground validation and application for African elephants (Loxodonta africana)

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#### UNIVERSITY OF GOETTINGEN & BANGOR UNIVERSITY

### Functional landscape connectivity models in applied conservation: spatio-temporal variability, on-ground validation and application for African elephants (*Loxodonta africana*)

submitted by

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To attain the degree of Doctor of Philosophy (Ph. D.)

in the

Faculty of Forest Sciences and Forest Ecology Department of Wildlife Sciences

&

College of Natural Sciences School of Environment, Natural Resources and Geography

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## Abstract

Faculty of Forest Sciences and Forest Ecology Department of Wildlife Sciences & College of Natural Sciences School of Environment, Natural Resources and Geography

by Liudmila Osipova

Habitat destruction and fragmentation are among the main drivers of global biodiversity loss and developing management approaches that effectively maintain or restore landscape connectivity is one of the major roles of systematic conservation planning. Movement databased functional connectivity models have great potential for applied conservation as they reflect more than just species habitat preferences and can integrate spatial and temporal dynamics. However, there are few challenges for using such dynamic models in wildlife conservation, including a lack of clear up-to-date methodological frameworks and policy guidelines, and insufficient evidence that connectivity-based conservation corridors are effective.

This dissertation aims to demonstrate how resistance-based functional connectivity models accounting for seasonal and individual variability can improve conservation management decisions. Using radio-tracking data from elephants in the Borderland area between Kenya and Tanzania, step-selection functions were applied to create seasonal landscape resistance surfaces. Based on these seasonal models, I predicted movement corridors connecting major protected areas using circuit theory and least-cost path analysis.

In Chapter 2, I demonstrated how incorporating seasonal variability can make a distinct difference in the final outcomes in connectivity modeling, and how disregarding these differences can negatively affect management decisions on the ground, especially in the areas prone to drought. For this, I developed a new analytical framework for incorporating individual and seasonal variability in resistance surface modeling. I compared space-use predictions derived from the novel approach to predictions obtained using a method

typically applied in connectivity research. By comparing empirical elephant movements with simulated movements from both approaches, I demonstrated that my novel framework predicts actual space-use patterns significantly better than the commonly applied models.

In Chapter 3, I applied a time series of seasonally distinct landscape connectivity models to assess how a fence built for human-wildlife mitigation in the study area could affect elephant connectivity in the future. Fence integration into the landscape will cause overuse of habitat patches in other agriculture areas, thereby potentially intensifying human-elephant conflict in new areas. This will likely negate the conservation benefits of fencing across the landscape despite local benefits. These results lead to the conclusion that if fencing is employed on a broader scale, then corridors should be integrated within protected area networks to ensure local connectivity of affected species and the implementation of fencing should be incorporated into the impact assessment process.

The final Chapter 4 focused on the validation of the functional landscape connectivity models and movement corridors using two independently collected datasets. I used multiple-year aerial counts of elephants to evaluate the connectivity model, and a field survey to assess the performance of predicted corridors.

The results of this dissertation confirmed that resistance-based connectivity modeling could have a strong predictive power, provided that seasonality and individual variability are accounted for. Analytically considering seasonal effects and individual movement behavior can significantly improve the performance of connectivity models and their effectiveness in conservation planning and wildlife management.

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## Abbreviations

ACC	African Conservation Center
ACP	Amboseli Conservation Program
AIC	Akaike Information Criterion
AWF	African Wildlife Foundation
CWD	Cost-Weighted Distance
EIA	Environmental Impact Assessment
FMP	Formozov-Malyshev-Pereleshin formula
FONASO	Forests and Nature for Society
GAE	Greater Amboseli Ecosystem
GLMM	Generalized Linear Mixed Effect Model
GPS	Global Positioning System
HEC	Human-Elephant Conflict
HR	Home Range
IFAW	International Fund for Animal Welfare
KWS	Kenya Wildlife Service
Landsat	Land Remote-Sensing Satellite (System)
LASSO	Least Absolute Shrinkage and Selection Operator
LCP	Least-Cost Path
МСР	Minimum Convex Polygon
MODIS	Moderate-resolution Imaging Spectroradiometer
MSPA	Morphological Spatial Pattern Analysis
NASA	National Aeronautics and Space Administration
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NDVI	Normalized Difference Vegetation Index

NP	National Park
PA	Protected Area
PSFs	Path-Selection Functions
ROC	Relative Operating Characteristic Curve
SRTM	Shuttle Radar Topography Mission
SSFs	Step-Selection Functions
TAWIRI	Tanzania Wildlife Research Institute
TRMM	Tropical Rainfall Measuring Mission
UD	Utilization Distributions
UTM	Universal Transverse Mercator Coordinate System
VHF	Very High Frequency Transmitter

# **Chapter 1** Introduction

Current network of protected areas is failing to maintain biodiversity in the face of a rapidly changing environment (Opdam and Wascher 2004; Heller and Zavaleta 2009; Bennett and Saunders 2010a; Dawson et al. 2011). Many countries with biodiversity hotspots are experiencing fast agricultural development and human population growth, which increase the frequency and severity of human-wildlife conflict around the world (Hill et al. 2017; Pozo et al. 2017). Inevitably, conservation science gradually shifts focus from protecting the intact biodiversity hotspots to maintaining connectivity between overwise isolated habitat patches in the human-dominated landscapes. Developing effective management schemes for maintaining landscape connectivity in rapidly changing environments is a major challenge in systematic conservation planning (Margules and Pressey 2000; Rudnick et al. 2012). However, there are a number of conceptual and technical difficulties in integrating the unbalanced nature of the environmental changes into practical conservation decisions (Pressey et al. 2007; Hodgson et al. 2009a; Rubio Lidón et al. 2014).

#### 1.1 Landscape connectivity concept

Landscape connectivity modelling is a relatively new, but popular approach in conservation science and wildlife management because it allow users to simulate fragmented landscapes and prioritized areas essential for unrestricted animal movement and genes transfer (Rouget et al. 2006; Pelletier et al. 2014; Zacarias and Loyola 2018). The term landscape connectivity is often applied to two different concepts - structural and functional connectivity (Crooks and Sanjayan 2006; Meiklejohn et al. 2009). Structural connectivity describes shapes, size and location of features in the landscape, whereas functional connectivity describes the response of individuals to landscape features and the patterns of gene flow that result from these individual responses (Brooks 2003). The concept of structural connectivity is often the basis for building wildlife corridors, which have been widely used in the field of conservation planning (Brooker et al. 1999; Pelletier et al. 2014). However, the corridors need to be designed while taking into account actual behaviours and dispersal abilities, because landscape connectivity is both species- and landscape-specific (Tischendorf and Fahrig 2000; Baguette and Van Dyck 2007; Goswami and Vasudev 2017). Therefore, 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). Current conservation sciences are moving away from using non-dynamic land

bridges between habitually suitable patches, and landscape corridor design incorporates all available knowledge about species biology and ecology.

#### 1.1.1 Functional connectivity models

Functional connectivity models are often built on resistance surfaces: spatially-explicit probabilities of species movement considering environmental conditions, behavioural states and mortality risk (Beier et al. 2008; Zeller et al. 2012). A variety of methods and datasets have been used to model landscape resistance, including habitat suitability analysis and expert opinion (Keeley et al. 2016; Mui et al. 2017; Milanesi et al. 2017). However, connectivity models based on such data may not adequately reflect movement across the landscape and may have a tendency to underestimate connectivity potential (Mateo-Sánchez et al. 2015; Roffler et al. 2016; Ziółkowska et al. 2016). The datasets with the highest potential for landscape connectivity representation ideally should reflect animal dispersal abilities, behaviour states and the potential for maintaining viable populations. Wildlife data for such models can be obtained by capture-mark-recapture methods, radio-telemetry data, camera trapping or real-time behavioural observations (Larkin et al. 2004; Revilla et al. 2004; Baguette and Van Dyck 2007). Alternatively, genetic data can be used for estimating dispersal distance that produce meaningful population effects (realized dispersal; Cushman et al. 2006; Lester et al. 2007). A number of studies have revealed particularly high prediction accuracy of connectivity models based on animal movement data (GPS or VHF telemetry datasets) (Zeller et al. 2012; LaPoint et al. 2013; Ziółkowska et al. 2016).

#### 1.1.2 Functional models based on telemetry data

Global positioning system (GPS) spatio-temporal location data analysis is a relatively new approach in spatial and movement ecology, but is already widely used by ecologists and conservation biologists (Hebblewhite and Haydon 2010; Allen 2013). However, few studies have proposed relevant methods that would integrate animal movement GPS data into landscape connectivity models (Stevenson et al. 2013; LaPoint et al. 2013; Harju et al. 2013). At the same time, this approach is one of the most promising for wildlife corridor planning, because it provides information on fine-scale movement behaviour of animals within different landscapes, and therefore, it may significantly benefit functional landscape connectivity models. Integrating movement data into landscape connectivity modelling is facilitated by fast technological progress and the amount and variability of species movement data rapidly growing and becoming free publicly available resources (*e.g. movebank; https://www.movebank.org/*).

#### 1.1.3 Incorporating species-specific movement data

One way to incorporate individual movement data in functional landscape connectivity is using step-selection (SSF) or path-selection (PSF) functions for resistance surface

interpolation (Richard and Armstrong 2010; Zeller et al. 2012; Thurfjell et al. 2014; Carvalho et al. 2015). These two methods allow calculating the strength of species' habitat selection using steps of paths reflecting actual animal movements (Zeller et al. 2012, 2015; Keeley et al. 2016). Compared to other approaches, this method has unconditional advantages: it is based on real animal movement data and reflects animal knowledge of the environment, restricts resource selection by modelling realistic habitat availability around each step/path, and allows us to predict landscape resistance to movement rather than habitat suitability. Another advantage is a temporal component of the movement data enabling synchronizing analysis with environmental variables such as rainfall, seasonal vegetation and land use changes (Jeltsch et al. 2013). SSFs and PSFs 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).

#### 1.2 Challenges in the modelling process

Considering that SSFs and PSFs for functional connectivity modelling are relatively new to landscape ecology, these methods and their applications are still in a transitional phase. GPS movement data limit the temporal scale of analysis because it has fixed recording intervals, and subsequently, the functions are highly sensitive to the spatial scale (Thurfiell et al. 2014). An increasing number of multiscale studies reveal how the scale can significantly alter the final output (Zeller et al. 2017). Another problem is a comparatively small sample size of mostly single-species GPS datasets: high costs for operations and installations of the radio collars is a limiting factors for telemetry studies (Hebblewhite and Haydon 2010). There is no definite decision on what the best method is for measuring environmental variables (predictor covariates) for the functions: at the ending point of path/step (Roever et al. 2013), along the lines between the points (Fortin et al. 2005a), or within a buffer defined by a researcher (Coulon et al. 2008). Most connectivity studies disregard temporal component of the GPS movement data due to difficulties of methodological implementation and interpretation of the results. At the same time, few studies differentiated seasonal connectivity surfaces revealed substantial variances in results (Mui et al. 2017). Another issue of resistance-based connectivity models is a lack of methodological frameworks and independent datasets for validation of model predictions, and therefore, a lack of evidence of practical usefulness of these models (Wade et al. 2015).

### 1.3 Focal species for landscape connectivity models

#### 1.3.1 African elephant as a focal species

Since landscape connectivity is species-dependent, the focal species should potentially represent the wildlife of the study area based on their habitat preferences and management status (Margules and Pressey 2000). There are several reasons for selecting the African

elephant (*Loxodonta africana*) as a case study for modelling functional connectivity. As the most recognizable species of African megafauna, which has a high impact on vegetation and wildlife distribution, elephants possess a very high potential to accurately represent landscape connectivity (Western 1989; Epps et al. 2011). The African elephant is a keystone species that strongly affect savanna woody vegetation (Kerley and Landman 2006; Landman et al. 2008). Being a wide-ranging mammal with home ranges encompassing multiple habitats, elephants have been empirically shown to be a suitable focal species for connectivity planning (Epps et al. 2011; Caro and Riggio 2013).

Elephants increase movement connectivity for animals and genetic connectivity for trees, increase structural complexity and provide habitats for many species (Kerley and Landman 2006; Manning et al. 2006). At the same time, it was shown that the high elephant densities had a negative effect of woody vegetation (Cumming et al. 1997; Western and Maitumo 2004; Kerley and Landman 2006; Guldemond and Van Aarde 2008). When elephant densities exceed approximately 0.5 per km<sup>2</sup>, savanna woodlands are converted to shrublands or grasslands, and associated fauna may be negatively impacted (Cumming et al. 1997). However, extinction or decreasing number of the elephants could lead to elimination the habitat of smaller mammals (Western 1989). Therefore, elephants themselves are a driving force within the landscape.

Elephants are seasonal migrants and can cover large areas outside and inside protected areas searching for food or water sources. However, fencing protected areas and agriculture lands leads to the aggregation of elephants within relatively small areas, and prevents long migration, thereby increasing ecological pressure on sympatric species (Western 1989). Habitat suitability studies revealed that forage availability, distance to water and land cover have a significant effect on elephant local distribution (Pittiglio 2012). Elephants prefer heterogeneous landscapes over homogeneous (de Beer and van Aarde 2008). In some areas, the highly suitable patches are adjacent to increasing human population areas (Estes 2012).

#### 1.3.2 Seasonal and individual behaviour variability

Elephants respond quickly to changes in forage and water availability, even for shorterdistance migrations. They also change their topographical use depending on greenness availability and prefer lower elevations when foraging is available (Bohrer et al. 2014). However, individual strategies of movement towards foraging areas are not as straightforward as for a group of animals (Boettiger et al. 2011). Studies on artificial water sources and fences show different movements between wet and dry seasons (Redfern et al. 2003, 2005; Loarie et al. 2009). Artificial water sources allow elephants to remain at places where they could not persist historically; elephants "bunch-up" against fences during the wet season and it increase pressure on vegetation in certain regions (Loarie et al. 2009). Elephants turned less the further they were from a large permanent body of water and for males with increasing distance to the females (Duffy et al. 2011). Rapid and directional elephant movement patterns (goal-oriented movements) are associated with visiting perennial water (Polansky et al. 2015). Some specific elephant movement characteristics such as diel displacement and movement predictability have a strong correlation with resource availability. The frequency of the movements is higher when resources are available. Also, the behaviour patterns are correlated with an individual's social rank: lower ranked individuals use more energy and exhibit less behavioural movement autocorrelation than higher ranked individuals (Polansky et al. 2013). Such a strong individual behaviour variability in a complex with prominent seasonal preferences compile a good case study for integrating spatio-temporal variability into connectivity models.

#### 1.3.3 Human-elephant conflict

About 73% of African elephants move beyond protected areas and co-exist with the rural human population (Blanc 2008). Elephants are known as crop-raiders - resulting in elephants being killed near areas with extensive agriculture development (Graham et al. 2010). Although other grazing wildlife compete more for resources with livestock, elephants invariably lead to severe crop damage and people are afraid to fight back (Gadd 2005). Elephants have a long history of attacking and killing people in conflict areas (Western and Waithaka 2005). The number of people killed by elephants has changed throughout time, depending on the political situation and conservation policy of a country, but it regularly happens, and it makes the conflict even more acute (Western and Waithaka 2005). Intensive elephant and human population growth, and corresponding agricultural expansion may start a new round of the human-wildlife resource conflict (Blanc 2008; Estes 2012).

The co-existence of elephants with humans through the centuries makes the solution of human-wildlife conflict the number one problem for the conservation managers working within elephant range (Graham et al. 2009). Since elephants tend to make long-distance migratory movements and move out the protected areas on a regular basis, it is important to reveal primary corridors used for short and long-distance migrations, especially outside protected areas. Also, mapping migration paths used by the elephants between protected areas can help in estimating areas that need to be included in the protection and, as a result, help to keep the surrounding area safe from human-elephant conflict. Thus, understanding the factors that drive the species' movements, identifying attractions and threats that form these patterns is an urgent challenge for conservation managers.

#### **1.4 Dissertation structure**

In this dissertation, I extended and verified species-specific functional landscape connectivity models and demonstrated their implementation in conservation management using a case study. Specifically, I used remote sensing and GPS movement data from the Kenyan and Tanzanian Borderland African elephant population for modelling a resistance-based connectivity landscape using step-selection functions and graph theory methods for

movement corridors predictions. An effective framework was developed for integrating individual and seasonal variability in the landscape connectivity model. The framework was validated using simulations and field surveys, and I demonstrated that accounting for spatio-temporal connectivity variability is essential for accurate and applicable landscape connectivity models.

In **Chapter 2**, I developed a comprehensive up-to-date land cover map using Landsat datasets and Maximum Likelihood supervised classification method for the Borderland area between Kenya and Tanzania. Using these maps along with a set of available GIS datasets and GPS movement data from the elephants collared in the same area, I applied stepselection functions to predict seasonal landscape resistance surfaces. Based on seasonal metrics, we modelled movement corridors connecting major protected areas with circuit theory and least-cost path methods. Furthermore, we developed and validated a methodological approach for integrating inter-individual variability into resistance surface surface models for assessing how landscape connectivity changes across seasons, and for evaluating how seasonal connectivity differences affect predictions of movement corridors.

In **Chapter 3**, I applied a time series of connectivity models corresponding to fluctuating rainfall in African savannah for assessing a potential negative impact from a conservation fence installed in the study area. A quantitative framework was developed for predicting how a fence designed to mitigate human-elephant conflict locally can affect functional connectivity and movement corridors of the African elephants more broadly. I extended the approach from the Chapter 2 and modelled a time-series of connectivity surfaces reflecting gradual seasonal changes of the movement corridors in shapes, length and spatial attributes. The results led to a discussion on how and why such evaluation is crucial for environmental impact assessments, and if fencing is an appropriate solution for alleviating human-wildlife conflicts in the long-run.

**Chapter 4** is devoted to a thorough validation of the connectivity models built in Chapter 3 using independently collected wildlife datasets. I used data from long-term aerial count survey of elephants covering the entire study area for validating the predictive power of the connectivity landscape. To evaluate if the predicted corridors are intensively used by the elephants for movements, I conducted a field survey (72 km in total) in the research plots placed within and outside of the predicted corridors. The results provide statistical evidence that resistance-based connectivity models have strong predictive power, the corridors predicted from the models should be implemented, and that accounting for seasonal variability significantly improve the accuracy of the predictions. The final chapter summarizes the results and ties together the entire dissertation.

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# **Chapter 2**

Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons

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#### Abstract

Landscape connectivity is an important component of systematic conservation planning. Step-selection functions (SSFs) is a highly promising method for connectivity modelling. However, differences in movement behaviour across individuals and seasons are usually not considered in current SSF-based analyses, potentially leading to imprecise connectivity models.

Here, our objective was to use step-selection functions to build functional connectivity models for African elephants (*Loxodonta africana*) in a seasonal environment to illustrate the temporal variability of functional landscape connectivity. We provide a methodological framework for integrating detected inter-individual variability into resistance surface modelling, for assessing how landscape connectivity changes across seasons, and for evaluating how seasonal connectivity differences affect predictions of movement corridors. Using radio-tracking data from elephants in the Borderland area between Kenya and Tanzania, we applied SSFs to create seasonal landscape resistance surfaces. Based on seasonal models, we predicted movement corridors connecting major protected areas using circuit theory and least-cost path analysis.

Our findings demonstrate that individual variability and seasonality lead to substantial changes in landscape connectivity and predicted movement corridors. Specifically, we show that the models disregarding seasonal resource fluctuations underestimate connectivity for the wet and transitional seasons, and overestimate connectivity for the dry season. Based on our seasonal models, we predicted a connectivity network between large protected areas and highlight seasonal and consistent patterns that are most important for effective management planning. Our findings reveal that elephant movements in the borderland between Kenya and Tanzania are essential for maintaining connectivity in the dry season, and that existing corridors do not protect these movements in full extent.

#### **2.1 Introduction**

Developing effective management schemes for maintaining landscape connectivity in rapidly changing environments is one of the major tasks in systematic conservation planning (Margules & Pressey, 2000; Rudnick et al., 2012). The concept of landscape connectivity is often the basis for building corridors, which have been widely used in the field of conservation planning (Brooker, Brooker, & Cale, 1999; Pelletier et al., 2014). The corridors need to be designed while taking into account actual behaviours and dispersal abilities, because landscape connectivity is both species- and landscape-specific. In contrast to structural connectivity, functional connectivity comprises the response of individuals to landscape features (Brooks, 2003; Benz et al., 2016). For effective conservation planning,

models based on functional connectivity have a large potential as they reflect more than just species habitat preferences and can integrate spatial and temporal dynamics (Baguette & Van Dyck, 2007; Goswami & Vasudev, 2017).

Functional connectivity and conservation corridors modelling is commonly achieved using landscape resistance surfaces (Beier, Majka, & Spencer, 2008). The resistance surfaces represent spatially-explicit probabilities of species movement considering environmental conditions, behavioural states and mortality risk (Zeller, McGarigal, & Whiteley, 2012). A variety of datasets and methods can be used to model landscape resistance, including habitat suitability analysis or expert opinion (Keeley, Beier, & Gagnon, 2016; Milanesi et al., 2017; Mui et al., 2017). However, connectivity models based on such data may not adequately reflect movement across the landscape and may have a tendency to underestimate functional connectivity (Mateo-Sánchez et al., 2015; Roffler et al., 2016; Ziółkowska et al., 2016).

Hence, connectivity models and underlying landscape resistance surfaces should be based on empirical movement data (Zeller, McGarigal, & Whiteley, 2012). Step selection functions (SSFs) are a relatively recent but promising approach for analyzing such movement data to calculate resistance surfaces (Richard & Armstrong, 2010; Zeller, McGarigal, & Whiteley, 2012). SSFs allow estimating the strength of habitat selection by animals moving through a landscape using VHF or GPS data (Fortin, Morales, & Boyce, 2005; Thurfjell, Ciuti, & Boyce, 2014). Using actual movement steps or paths is more suitable for landscape resistance modelling as this reflects actual movements, rather than the simple presence of a species at a certain location (Zeller, McGarigal, & Whiteley, 2012; Zeller et al., 2015; Keeley, Beier, & Gagnon, 2016). Empirical movement steps or paths have successfully been applied to model functional connectivity and to predict movement corridors in a variety of species (Forester, Im, & Rathouz, 2009; Roever, van Aarde, & Leggett, 2013; Signer, Fieberg, & Avgar, 2017). Nevertheless, several analytical issues remain, particularly with respect to applying SSFs for resistance modeling.

First, it is a common practice in resource selection studies to use mixed effects models with individuals as random terms, or to average individual coefficients for obtaining population level coefficients (Duchesne, Fortin, & Courbin, 2010; Fieberg et al., 2010; Killeen et al., 2014). However, with very high individual-level differences and relatively small sample size, this approach could lead to overgeneralization and spatial biases. Observed inter-individual differences in resource selection could be due to individual life history, spatial memory and animal personality, all of which can strongly affect species dispersion and distribution within habitats (Wolf & Weissing, 2012). In theory, individual-based SSF models account for the animals' knowledge of the area because the selection procedure is always restricted to its home range. Randomly distributed individuals with highly overlapping home ranges and a large sample size will have a relatively equal input for a resistance surface modeling, and averaging of individual contributions is a suitable approach in such cases. However, it is

rarely the case in telemetry studies, considering equipment costs and employment efforts (Hebblewhite & Haydon, 2010). Small, unequal sample sizes with spatially unevenly distributed animals might impact resource selection functions, including SSFs. Specifically, averaging of SSF coefficients across all individuals may predict lower resistance values where sample size is larger, i.e., selection of well-presented areas for movement will appear stronger, only because more sampled individuals used an area. Indeed, inter-individual variability might also be detected simply because individuals find different environmental conditions to choose from within their home ranges, but would not actually show behavioural variability if they were exposed to the exact same conditions. Because of this, detecting inter-individual variability is particularly likely in cases when individuals were sampled across a large, heterogeneous study area, and when the sampling intensity varies across space. Hence, spatially inhomogeneous distribution of movement data requires a different way for interpolating SSF coefficients to avoid a spatial bias.

Second, disregarding seasonal variations of the environment can be another source of uncertainty when spatially interpolating results from SSFs to landscape resistance. For instance, resources availability is limited during dry seasons, especially in arid and semi-arid areas. Under these conditions, animal movement can be restricted compared to the wet season, simply because individuals only move among the few available resource patches. Consequently, landscape-wide resistance predicted from dry-season movement data will be higher compared to the wet season, and seasonal movement corridors might have different spatial arrangements and predicted intensity of use. Thus, understanding how connectivity changes across seasons and how these changes affect landscape connectivity may comprise vital information for effective conservation planning.

In this study, we used GPS movement data obtained from collared elephants from the Greater Amboseli Ecosystem in Eastern Africa to illustrate that accounting for seasonality can strongly impact our understanding of functional connectivity and alters predicted movement corridors. We chose the African elephant (*Loxodonta africana*) as the focal species for representing landscape connectivity in this region, as this species is a keystone megafauna that substantially impacts the vegetation and wildlife distributions in their environments and are likely a good umbrella species of connectivity across the landscape (Western, 1989; Epps et al., 2011).

In this chapter we aim to test a hypothesis that functional landscape connectivity is not a constant concept and it can significantly fluctuate over the seasons, especially in the areas prone to the droughts. We assumed that the model that is not accounting for seasonal changes overestimates overall landscape connectivity for the dry season and underestimates it for the wet season. Moreover, the model's predictions can be significantly affected by the sampling biases and individual variability of the collared individuals. Disregarding these

seasonal and individual fluctuations in functional connectivity models may negatively affect movement corridors predictions and consequently on-site management decisions.

#### 2.2 Methods

#### 2.2.1 Study area

The study area covers approximately 50,000 km2 and is located in the Borderland between Kenya and Tanzania. The Borderland encompasses the Greater Amboseli Ecosystem (GAE) and extends to the South Rift valley (Fig. 2.1). The region encloses 36 nationally protected lands and large segments of non-protected areas belong to group ranches that play an important role in local wildlife conservation initiatives (Ntiati, 2002; Browne-Nuñez, Jacobson, & Vaske, 2013). Intensive agricultural development, including fencing, in non-protected lands together with rapid human population growth increases the potential for fragmentation, connectivity loss and human-wildlife conflict (Western, 1975, 2007; Okello & D'amour, 2008).

#### 2.2.2 Telemetry data

We obtained GPS telemetry data from 14 elephants collared within the area of Amboseli-West Kilimanjaro and South-Rift-Magadi Ecosystems. Information on collars types and collaring operation is available in Ngene et al. (2014). Fix rates, sample sizes and collaring locations are presented in Supplement 1 in Supporting Material (Table S1). The movement data were regularized to 4 hours intervals. In cases where collars failed to receive the signal in more than 8 hours, the trajectories were burstified, and the bursts with less than 10 steps were excluded from further analysis.

#### 2.2.3 Environmental layers

Environmental data were collected from publicly available GIS datasets and derivatives from remote sensing data (Table S2, Supplement 1).

#### GIS layers

The GIS raster and vector data used in the analysis are presented in Table S2, Supplement 1. All vector layers were reprojected to the Cartesian coordinate system (UTM) and rasterized to a cell size of 250. The layers were transformed to continuous surfaces where each pixel represents the Euclidean distance to the nearest target features.

#### Remote-sensing analysis

We acquired satellite data from three global remote sensing missions: Terra, SRTM and Landsat (Table S2, Supplement 1). The normalized difference vegetation index (NDVI)

derived from MODIS has been shown in previous studies as a reliable proxy of forage quality for large mammals, including African elephant (Ryan et al., 2012; Wall, 2015). Using the NDVI time series allows reproduction of vegetation productivity dynamics corresponding to the real seasonal vegetation changes (Ngene, 2010; Bohrer et al., 2014). We created a time series on the monthly NDVI imagery corresponding to the entire time frame of available elephant GPS movement data (2007 - 2015).

We used multispectral Landsat 8 satellite imagery for land cover classification. The workflow of the supervised classification, post classification analysis and accuracy assessment are provided in the Supplement 2. We included in the model the proportional coverage of three major land cover classes (grassland, bushland and woodland). The proportion of each class was calculated by applying a circular buffer to each pixel of a raster surface with the radius of the average step length pooled over all elephants (1337 m).

#### 2.2.4 Resistance to movement modelling

#### Step-selection function

SSFs require information on habitat crossed by an animal during movement, i.e., habitat values are quantified along a line connecting two consecutive animal locations. This "used" habitat is then compared to "available" habitat, which means that habitat variables are collected along alternative steps where an animal could potentially have moved given the step lengths and angle distributions (Fortin, Morales, & Boyce, 2005; Forester, Im, & Rathouz, 2009). Each used step is compared to the set of available steps using conditional logistic regression (Manly et al., 2002; Johnson et al., 2006). SSFs take the form:

$$\widehat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_p x_p)$$

where  $\widehat{w}(x)$  is an exponential function given the sample of used and available habitat variables;  $\beta_1 \dots \beta_p$  are estimated regression coefficients; and  $x_1 \dots x_p$  are predictor covariates (Fortin et al. 2005b; Thurfjell et al. 2014).

We simulated 10 "control" (available) steps to each "case" (used) step and used step lengths drawn from a Gamma distribution with rate and shape parameters estimated from the empirical data (step lengths distribution for all collared elephants) using maximum likelihood (*rhr* R package) (Signer & Balkenhol, 2015). Turning angles for the control steps were drawn from a uniform distribution between  $-\pi$  and  $\pi$ . We collected environmental values crossed by a spatial line representing an animal's step. The average of these values characterizes the habitats choices (used and available). The methodological framework with data analysis steps is presented in Fig. 2.2.

For NDVI, we sampled movement data according to the exact date (year/month) in the time series and extracted NDVI values for each corresponding stratum. For the seasonal models,

we subset movement paths for the wet, dry and early dry seasons. Seasonality was estimated from the results of the long-term annual field monitoring based on vegetation productivity conducted by the African Conservation Center (see Table S3).

We tested environmental variables for collinearity by using pairwise scatterplots and Pearson correlation. Each pair had a correlation coefficient less than 0.7, so all variables were retained for further analysis (Zuur, Ieno, & Elphick, 2010).

Conditional multiple logistic regression models were built for each individual by including all possible permutations of explanatory variables including full (all environmental variables are included) and null (no environmental variables included) models. We applied both-way stepwise selection using Akaike information Criterion (AIC) and choose the model with the lowest AIC score (Akaike, 1974; Zar, 1996; Venables & Ripley, 2013).

To evaluate variability in individual step-selection, we compared the relative contribution of environmental covariates among seasons using Jaccard index of similarity. We assigned a value of 1 ("present") to a variable when its coefficient was included in the best model (lowest AIC score), and 0 when it was excluded from the best model ("absent").



Functional Landscape Connectivity Maps



Figure 2.1 Study area and functional connectivity maps for all-in-one and transitional seasonal models.



Figure 2.2 Workflow chart of the SSF modeling and functional connectivity assessment. *SSF*, step selection function; *MSPA*, morphological spatial patterns analysis; *PA*, protected areas; *AIC*, Akaike information criterion; *MCP*, minimum convex polygon.
#### Landscape resistance modelling

We spatially interpolated the results from SSFs by calculating the relative selection strength (Avgar et al., 2017) for each point of the raster image and then applying pixel-wise logit transformations for obtaining the 0-1 scaled probability values. The inverse values of these probabilities represent landscape resistance to movement surface. To adequately reflect all individuals with their potential variability in step-selection (due either to actual behavioural differences or due to sampling bias), we calculated a spatial weight matrix based on the inverse distance of each pixel to the individual' s home range center. For this, we estimated home ranges using 95% minimum convex polygon (MCP) (Anderson, 1982), and normalized distance values across all individuals so that the sum of inverse distances for each cell in the landscape ranged from 0 to 1 and summed to 1 across individuals for each cell. See Supplement 3 in Supporting Information for details and an example. We then applied a weighted overlay, where we summed the movement probability layers of all individuals after weighting them by the corresponding distance-to-home-range-center layer. The inverse of these movement probability surfaces represents landscape resistance surfaces, which we used for functional connectivity modelling (see next section). All analyses were performed using the raster package in R (Hijmans et al., 2016).

For validating the predictive power of the applied framework, we modelled resistance surfaces using two different methods: distance-to-home-range-center overlay (weighted overlay) and by averaging individual regression coefficients (averaging) (Fieberg et al., 2010). We followed a leave-one-out validation procedure, and excluded the movement data of each individual for constructing resistance surfaces using both approaches, so that we created 28 resistance surfaces in total (14 using weighted overlay, and 14 for using averaging). We then simulated movements for each left-out individual based on the respective resistance surfaces using the starting point and number of steps of the excluded individual (Quaglietta & Porto, 2017). In these simulations, the choice of steps of each individual was defined by the values of the underlying resistance surface: the lower the predicted resistance, the higher the probability that the next step will transit this area. Finally, we calculated utilization distributions (UD) for empirical and simulated movement data to compare actual movement patterns with those predicted from the two different methods (weighted overlay vs. simple averaging). Specifically, we used 90% kernel density estimators to quantify UDs reflecting individual movement behaviour and estimated the overlap between the UD derived from actual movement data and simulated tracks. The overlap index takes values from 0 to 1 with larger values indicating greater overlap between the two UDs (Fieberg & Kochanny, 2005). We repeated the movement simulations and overlapped calculations 100 times per individual. Finally, we compared the overlap between the weighted overlay versus averaging approach. We can expect a higher overlap between real and simulated movements for the approach that leads to resistance surfaces that better capture actual movements of individuals.

## 2.2.5 Functional landscape connectivity model

### MSPA

We compared landscape permeability (the proportion of landscape that most likely provides connectivity) of the all-in-one (the surface calculated for all dataset disregarding the seasons) and seasonal resistance maps through morphological spatial pattern analysis (MSPA) (Soille & Vogt, 2009). We used three descriptive categories: cores represent non-fragmented patches highly suitable for movements, islets represent fragmented smaller patches and connectors represent corridors connecting cores and islets (Vogt et al., 2006, 2007; Soille & Vogt, 2009).

We reclassified the resistance maps to Boolean images by applying a set of successive classification thresholds starting from 0.5 with increases of 0.02. The MSPA classification was conducted through Guidos Toolbox (Vogt et al., 2006) and iteratively applied to each set of binary images until increasing the threshold was equal to one. For estimating overall accuracy and potential pitfalls of the all-in-one model, we built a confusion matrix where the all-in-one model' s number of elements (cores, islets and connectors) was compared to the number of the same elements in seasonal models.

#### Least-cost path and circuit theory

We built seasonal functional connectivity networks among the core areas (largest national parks and conservancies) using circuit theory and least-cost path (LCP) methods (Fig. 2.1). The LCP approach estimates the shortest distance between target nodes (i.e. protected areas) while accounting for resistance to movement (Adriaensen et al., 2003). Circuittheoretic connectivity can be assessed using graph-theoretic metrics that can be directly interpreted in landscape connectivity terms (McRae et al., 2008). The amount of current running through the nodes reflects the likelihood of random walks along graph edges (Shah & McRae, 2008; Carroll, McRae, & Brookes, 2012). Estimated effective resistance values (connectivity measure within a least-cost corridor) enables the calculation of current flow centrality across the network (centrality score). The centrality score represents how important a link or core area is for overall network connectivity (McRae et al., 2008). We calculated, normalized and mosaicked the cost-weighted distance surfaces for building a single composite corridor map. We estimated current flow, effective resistances, cores and corridors centrality scores (Carroll, McRae, & Brookes, 2012). Finally, we predicted LCPs for each pair of the protected areas in the study area. The analysis was implemented in Linkage Mapper (ArcGIS 10.3.1) (McRae & Kavanagh, 2011).

# 2.3 Results

# 2.3.1 Step selection function models

The all-in-one SSF model revealed high inter-individual variability in habitat preferences (Table S3, Supplement 1). The number of explanatory variables selected in the final model ranged from 12 (1 individual) to 5 (2 individuals), with an average of 7.86±2.07 dependent variables affecting individual movement choices. NDVI and distance to protected area were significant explanatory variables for most individuals (11 and 9 individuals respectively). Anthropogenic factors, such as distance to developments area and distance to roads, were significant for 9 out of 14 individuals. Distance to large water surfaces and distances to towns were important only for half the individuals (7 out of 14).

Overall, seasonal models retained less dependent variables than the all-in-one model. The average number of habitat variables selected was  $6.14 \pm 2.0$ ,  $6.71 \pm 2.16$  and  $5.88 \pm 2.31$  for wet, dry and early dry seasons, respectively. NDVI was included in the models for almost all individuals in the wet season (12 out of 14), but was less important for the dry (10 out of 14) and early dry season (4 out of 8). Distance to protected areas in the seasonal models was less important than in the all-in-one model (6 out of 14 for the wet season, 7 out of 14 for dry seasons, and 3 out of 8 models for the early dry season; Table S3, Supplement 1). Jaccard indices calculated for coefficients across the seasons are less or equal to 0.5, which indicates low similarity between the data clusters (mean index values are below 0.5 for all compared pairs; Fig. 2.4).

# 2.3.2 Resistance to movement surface interpolation

## Accounting for individual variability

The results of our simulation-based validation confirmed that the weighted overlay produces more accurate predictions for animal movements compared to the averaging method. The surface modelled using averaging coefficients is sensitive to the spatial sampling distribution: it produced very low resistance values in the area where numerous individuals were collared, and high resistance values in the areas with a smaller sample size (Supplement 4). Tests with simulations confirmed the lower predictive power of the first method. All 14 resistance surfaces modelled with weighted overlay led to simulated UDs that have a higher overlap with the actual movement predictions based on weighted overlay surfaces were consistently better for all surfaces despite the spatial affiliation or home range size of tested individuals (Fig. 2.3, Supplement 4).

## Accounting for seasonal patterns

Seasonal resistance to movement surfaces reflect the differences in habitat preferences between the seasons (Supplement 5). In the all-in-one surface, the proportion of pixels with lower resistance values (less than 0.5) is 0.34, and the values increase to 0.5 in both the wet and early dry seasons. In the dry season, the proportion of lower resistance pixels is 0.27. The Pearson correlation coefficients for all pairs of resistance surfaces had values less than 0.7, except for all-in-one and dry season surfaces (r = 0.75).

# 2.3.3 Morphological spatial pattern analysis

The proportion of elements within the three morphological categories (cores, islets and connectors) for 23 classification thresholds changes (Fig.2.4). The overall accuracy of the seasonal models ranged from 0 to 30% across all classification thresholds (Table 2.1). The dry seasonal model tended to overestimate the number of elements (61%, 39% and 73% of elements are overestimated for the cores, islets and connectors accordingly); while for the wet season it tends to underestimate element numbers (70%, 57% and 83% are underestimated). The number of elements for islets and connectors are underestimated for the early dry season (61% and 57% accordingly), but the number of elements for cores are either underestimated or overestimated (48% of underestimates, and 52% of overestimates) (Table 2.1, Fig. 2.5).

# 2.3.4 Circuit-based and least-cost paths analysis

Using circuit-based analysis and LCP we modelled eight wide-ranging corridors maintaining overall functional connectivity between five large protected areas (Tables 2.3 – 2.4, Supplement 5). Connectivity parameters support the results of the morphological spatial pattern analysis. The five most prominent corridors modeled based on the all-in-one resistance surface have higher effective resistance values compared to the wet season, and lower resistance values for the dry season. The lowest resistance values and CWD/Path ratios were assigned to wet and early dry seasons, and the values decreased in the dry season (Table 2.3).

Amboseli NP, Enduimet and Shompole Conservancy have the highest current-flow centrality score and are always ranked among the top three despite seasonal differences (Table 2.2). The most important cumulative corridors were predicted for Amboseli and Enduimet; Amboseli and Tsavo West (including Chyulu Hills); Enduimet and Shompole. These three linkages are in the top 3 based on centrality ranking and have the lowest effective resistance values (Table 2.3, Supplement 5).

LCPs calculated for the wet season have a tendency to converge in the center of the study area connecting the west and east (Fig. S6 in Supplement 5). Wet and early dry seasons have a larger potential for providing connectivity in the north-western direction. Early dry season provides an alternative path between Chyulu Hills and Olkiramatian that does not exist for

other seasons. Furthermore, early dry and dry seasons demonstrate increasing permeability of the Tanzania's side (Supplement 5).



Figure 2.3 Overlap volumes calculated between utilization distributions (UD overlap volume) of collared elephants and simulated movement tracks (90% kernel density estimation). Each facet represents one individual excluded from resistance surface interpolation, and simulations (N = 100) based on this resistance surface. The data were simulated using two interpolation techniques: averaging regression coefficients (dark gray boxes) and weighted overlay using a distance to home-range center matrix (light gray boxes)



Figure 2.4 Jaccard index estimated for each pair of general and seasonal model. Gen, general model; Wet, wet season model; E.dry, early dry season model; Dry, dry season model.

# 2.4 Discussion and Conclusions

Using an empirical movement dataset of elephants, our study shows substantial variability in landscape connectivity and predicted movement corridors across seasons. Furthermore, our study also shows that accounting for observed inter-individual variability, which is either caused by actual behavioural differences in movement preferences, or by spatial sampling bias, significantly improves the ability to accurately predict movements from the modelled resistance surfaces. Hence, it is fundamental that corridor design accounts for seasonal differences and inter-individual variability. Indeed, integrating dynamic changes is among the most important factors for effective conservation applications, and one of the best approaches for conservation planning is to focus on preserving connectivity rather than large protected lands (Margules and Pressey 2000; Pressey et al. 2007).

Table 2.1 Confusion matrix						
	Cores (%)					
	Dry season	Wet season	Early dry season			
Accuracy	30.43	21.74	0.00			
Underestimates	8.70	69.57	47.83			
Overestimates	es 60.87 8.7		52.17			
	Islets (%)					
Accuracy	30.43	26.09	4.35			
Underestimates	30.43	56.52	60.87			
Overestimates	39.13	17.39	34.78			
	Connectors (bridges and loops) (%)					
Accuracy	21.74	17.39	8.70			
Underestimates	4.35	82.61	56.52			
Overestimates	73.91	0.00	34.78			

Table 2.1 Confusion matri

All-in-one model accuracy assessment using morphological spatial patterns analysis categories.

Accuracy: Proportion of cases with equal number of elements

(i.e. cores, islets, or connectors) predicted for all-in-one and seasonal model. Underestimates: Proportion of cases with smaller number of elements predicted for all-in-one compared to the seasonal model.

Overestimates: Proportion of cases with larger number of elements predicted for all-in-one compared to the seasonal model.

#### Accounting for individual variability

Individual differences and their effects on species ecology have been much debated (Bolnick et al. 2011; Maiorano et al. 2017). Individual variability is an influential factor for resistance surface modelling, particularly when collaring of individuals was unevenly distributed across the study area. Here, we suggest a framework using a weight matrix for modelling the overall resistance surface. Each resistance value obtained for an individual is weighted by the distance to the home range center and our validation confirmed that the typically used averaging method produces spatial biases caused by relatively small sample size and uneven distribution of collared animals. Simple coefficient averaging predicts an overly simplistic resistance surface with extremely low resistance values in the area with larger sample size, and high resistance where only few animals were collared (Supplement 4). In contrary, the weighted overlay produces a smoother distribution of resistance values and balance-out the data discrepancy. This problem is particularly apparent for the South Rift region in the study area, where only two individuals were collared (F4 and M10, Fig. 2.3). These animals' home ranges are relatively small and isolated from the rest of collared animals (Shompole and Olkiramatian Conservancies, Supplement 4). As expected, the simulation predictions are very poor for the averaged model, while weighted overlay produced a very strong prediction (e.g. F4 overlapping indices are 0.03±0.003 and 0.82±0.160 for first and second methods accordingly, Fig. 2.3).



Figure 2.5 Number of elements in each morphological class (cores, islets and connectors) calculated from the resistance surfaces and plotted against different classification thresholds.

We conclude that the weighted overlay method outperforms coefficient averaging for studies implemented on relatively small datasets of species that show strong individual variability. The offered approach allows to adjust the resistance interpolation according to the proximity to the sampling domains (each individual) and avoid spatial biases. Nevertheless, coefficient averaging might have an adequate predictive power for studies with a larger sample size, where study animals are evenly distributed within the area.

	All-in-One Model		Wet Season		Dry Season		Early dry season	
	Core		Core		Core		Core	
PA	centrality	rank	centrality	rank	centrality	rank	centrality	rank
Amboseli	6.20	2	6.56	3	6.50	3	7.26	1
Tsavo West and Chyulu								
Hills	5.02	4	4.19	4	4.23	4	4.96	4
Enduimet	6.09	3	6.56	2	6.54	2	4.91	5
Shompole	7.13	1	7.03	1	7.03	1	6.29	2
Olkiramatian	4.00	5	4.00	5	4.00	5	5.43	3

centrality value indicates greater importance of the PA for providing landscape-wide connectivity

Table 2.2. Protection Areas (PA) centrality and ranking estimated using circuit theory. A higher

A higher centrality value indicates greater importance of the PA for providing landscape-wide connectivity

## Comparing seasonal connectivity models

To compare the all-in-one connectivity model to the seasonal models, we applied two conceptually distinct methods: MSPA and circuit theory analysis. The first method allows the estimation of patch-based metrics and is based on a patch-corridor-matrix concept (Forman 1995; Zeller et al. 2017). The approach requires a binary classification and treats the area with low potential connectivity as a non-permeable matrix. However, a number of studies have shown that matrix quality can be heterogeneous and be responsible for different level of patches isolation (Vandermeer and Carvajal 2001; Revilla et al. 2004). In contrast, circuit analysis simulates random walkers across a continuous surface, and, therefore, uses the full permeability potential for predicting corridors.

The results of our research confirmed the assumption that the all-in-one model underestimated connectivity for the wet season and overestimated connectivity for the dry season. We used seasonal changes of NDVI values as a surrogate for resource availability, and large herbivores are known to travel with the seasonal "wave of green-up" to provide themselves enough food and water (Birkett et al. 2012; Merkle et al. 2016). We assume that these changes are captured by the seasonal connectivity models. Results of MSPA supported our conclusion of decreasing connectivity from wet to dry seasons. Overall, the accuracy of the all-in-one model was small compared to the seasonal models (less than 30%, Table 2.1).

The wet season provides the highest number of corridors and patches; while the dry season has a lower number of core areas, thus, the landscape is less variable and provides fewer possible connectors between habitat patches.

#### Identifying stable connectivity patterns across seasons

The seasonally stable connectivity patterns discovered in this research are particularly interesting as they complement hypotheses about population structure and distribution of elephants in the Greater Amboseli Ecosystem (Kikoti 2009; Moss et al. 2011). The results suggest that connectivity in the north-south direction via the Kenya-Tanzania border is higher than connectivity in the east-west direction for all seasons. This highlights the importance of Borderland movements for maintaining overall landscape connectivity. Previous studies suggested that the Amboseli elephant population extents only to the Chyulu Hills and Tsavo West (Moss et al. 2011). Indeed, the predicted corridor connecting Amboseli NP and Chyulu Hills was always ranked high in centrality score for all seasons. However, distinctive transboundary movements indicate that the elephants of southern Kenya and northern Tanzania are part of a single, contiguous population (Western 2007; Kikoti 2009). The Amboseli NP and the corridor between Amboseli and Enduimet PAs had the highest current-flow centrality scores and the lowest resistance for all seasonal connectivity models. A relatively short corridor connecting Kenya and Tanzania appears to be essential for elephant movements; aerial surveys confirm high concentrations of family groups within the same corridor in both the wet and dry seasons (KWS/TAWIRI report, unpublished data 2015).

Despite higher connectivity between the southern and northern ends of the study area, the high connectivity potential between the Amboseli Ecosystem and the South Rift Valley remains stable across all seasons (Table 2.3). Even though it is not certain whether elephant families from the South Rift and Amboseli form one single population, genetic studies showed independent colonization of the South Rift area between Amboseli and Maasai Mara NP (Ahlering et al. 2012a). Shompole Conservancy has slowly been recolonized by elephants over the past decade since the establishment of community conservancies in this area (Ahlering et al. 2012b). Elephant population growth, extensive agriculture developments and new electric fencing around Amboseli NP might push elephants out of the commonly used area to the safe conditions (Western 2007; Okello and D'amour 2008; Okello et al. 2015). Our results suggest that in addition to preserving the undoubtedly important Borderland corridor, special attention should be given to the corridors connecting Amboseli and the South Rift.

Nº		1	2	3	4	5	6	7	8
<u>CWD/Path</u> *	All-in-One	0.20	0.24	0.50	0.26	0.44	0.40	0.50	
	Model	0.29	0.34	0.50	0.26	0.44	0.42	0.53	-
	Wet Season	0.21	0.26	0.34	0.20	0.28	0.28	0.34	-
	Early Dry								
	Season	0.30	0.48	0.27	0.25	0.29	0.26	0.24	0.02
	Dry Season	0.30	0.47	0.61	0.26	0.48	0.48	0.63	-
	All-in-One								
	Model	22.20	7.44	75.00	24.84	87.13	-	68.44	-
Eff. Resist**	Wet Season	17.93	5.32	66.43	20.57	-	-	61.03	-
	Early Dry								
	Season	25.41	10.02	45.90	46.81	-	59.31	60.18	0.15
	Dry Season	45.45	9.61	257.76	49.57	-	-	152.97	-
<u>Centrality</u> ***	All-in-One								
	Model	2.41	3.82	2.18	1.96	1.68	-	2.40	-
	Wet Season	2.45	3.90	2.77	1.93	-	-	3.30	-
	Early Dry								
	Season	3.42	4.12	1.50	1.48	-	1.26	1.25	4.14
	Dry Season	2.40	3.78	2.82	2.07	-	-	3.24	-
<u>Rank</u>	All-in-One Mode	2	1	4	5	6	-	3	-
	Wet Season	2	1	4	5	-	-	3	-
	Early Dry								
	Season	3	2	4	5	-	6	7	1
	Drv Season	4	1	3	5	-	-	2	-

Table 2.3. Quantitative comparison of movement corridors predicted with least-cost and
circuit-theory models

\*CWD/Path: Ratio of cost-weighted distance to the unweighted length of the least-cost path (the distance traveled moving along the path)

**\*\*Eff. Resist**: Corridor's effective resistance, a measure of connectivity that complements least-cost path \*\*\*Centrality: Calculated using circuit analysis; the parameter explains a contribution of each link to overall landscape connectivity

#### Corridors as they appears in the table above:

(1) Amboseli/Tsavo West and Chyulu Hills	(5) Tsavo West and Chyulu Hills/
(2) Amboseli/Enduimet	(6) Tsavo West and Chyulu

- (3) Amboseli/Shompole

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(4) Tsavo West and Chyulu Hills/Enduimet
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Shompole (6) Tsavo West and Chyulu Hills/Olkiramatian (7) Enduimet/Shompole (8) Amboseli/Olkiramatian

# 2.5 Implications for conservation

Here, we modelled movement corridors connecting large protected areas and assessed their relative contribution in conserving landscape connectivity for the elephants. Preserving connectivity across non-protected lands is a critical issue for fragmented populations of African elephants as the protected areas are not large enough to maintain viable population sizes (Armbruster and Lande 1993).

Our study confirms that Amboseli NP is a stepping stone in preserving cross-border connectivity, while Shompole Conservancy is crucial for linking western and eastern parts of the research area. The wetlands adjacent to the eastern part of Shompole play a critical role in connectivity as all LCPs connect through this area.

Furthermore, we verified the importance of existing protected historical corridors for preserving functional landscape connectivity. The Greater Amboseli Ecosystem contains two historically protected areas, Kimana and Kitenden, established by signing a lease between conservation organizations (AWF and IFAW) and local communities (Supplement 6). Our analysis indicates that the Kimana corridor together with the Chyulu Hills PA play a crucial role in preserving connectivity in the eastern part of the study area, and its value is especially high in the dry season. The Kimana corridor encompasses a part of the swamps *en route* to the Chyulu Hills in an area suffering from rapid agricultural expansion (98% increase between 2010 and 2014; (Space For Giants Report 2015). The Kitenden corridor with the highest current-flow centrality score and lowest resistance predicted for all seasons was predicted to the west of Kitenden (Supplement 6). Aerial count data support the importance of this area (Amboseli/Enduimet corridor), so it is highly recommended for consideration in any prioritization scheme in management plans (KWS/TAWIR Report 2013).

We conclude that it is highly desirable to incorporate seasonal changes into functional connectivity models whenever it is feasible. This is especially relevant for systems with pronounced seasonal spatial variation of forage and water availability. Extreme environmental conditions, such as low rainfall or droughts, may significantly decrease landscape permeability and should be considered with special care in conservation prioritization and corridors planning.

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# **Chapter 3**

Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant

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# Abstract

Fencing is one of the most common methods of mitigating human-wildlife conflicts. At the same time, fencing is considered one of the most pressing threats emerging in conservation globally. Although fences act as barriers and can cause population isolation and fragmentation over time, it is difficult to quantitatively predict the consequences fences have for wildlife.

Here, we model how fencing designed to mitigate human-elephant conflict (HEC) on the Borderlands between Kenya and Tanzania will affect functional connectivity and movement corridors for African elephants. Specifically, we (1) model functional landscape connectivity integrating natural and anthropogenic factors; (2) predict seasonal movement corridors used by elephants in non-protected areas; and (3) evaluate whether fencing in one area can potentially intensify human-wildlife conflicts elsewhere.

We used GPS movement and remote sensing data to develop monthly step-selection functions to model functional connectivity. For future scenarios, we used an ongoing fencing project designed for HEC mitigation within the study area. We modelled movement corridors using least-cost path and circuit theory methods, evaluated their predictive power and quantified connectivity changes resulting from the planned fencing.

Our results suggest that fencing will not cause landscape fragmentation and will not change functional landscape connectivity dramatically within the study area. However, fencing will lead to a loss of connectivity locally and will increase the potential for HEC in new areas. We estimate that wetlands, important for movement corridors, will be more intensively used by the elephants, which may also cause problems of overgrazing. Seasonal analysis highlights an increasing usage of non-protected lands in the dry season and equal importance of the pinch point wetlands for preserving overall function connectivity.

*Synthesis and applications*. Fencing is a solution to small-scale human-elephant conflict problems but will not solve the issue at a broader scale. Moreover, our results highlight that it may intensify the conflicts and overuse of habitat patches in other areas, thereby negating conservation benefits. If fencing is employed on a broader scale, then it is imperative that corridors are integrated within protected area networks to ensure local connectivity of affected species.

# **3.1 Introduction**

Fencing has a long history in conservation management and has proven to be an effective tool for alleviating human-wildlife conflict by keeping wildlife out of certain zones, controlling animal movements and disease outbreaks (Hayward and Kerley 2009; Gadd

2012; Kesch et al. 2015; Durant et al. 2015). Conservation fencing involves separating biodiversity from the factors that threaten it, and a common application of fencing is to restrict animal movements to mitigate human-wildlife conflict (Hayward and Kerley 2009; Slotow 2012; Kesch et al. 2015). Fencing to relieve human-elephant conflict (HEC) is a specific focus of conservation managers because of the severity of the conflicts that ultimately lead to retributive persecution by people and death of animals, and because of the difficulties in applying other management schemes (Western and Waithaka 2005; Hoare 2012, 2015).

At the same time, fencing raises many concerns regarding its potential effect on wildlife and has recently been listed as one of the main emerging issues for global conservation and biodiversity (Sutherland et al. 2017). Among the possible impacts are constrained access to essential habitats, blocking of migration routes and pathways for escaping natural threats for the species (Mbaiwa and Mbaiwa 2006; Kowalczyk et al. 2012), loss of genetic exchange (Kowalczyk et al. 2012) and overgrazing and habitat degradation in fenced enclosures (Boone and Hobbs 2004). Simultaneously, fences can have negative impacts for humans by excluding local people from historically used areas, interrupting the seasonal movements of pastoralism and causing spatial division of communities (Lindsey et al. 2012).

Strategic planning for fences may reduce negative effects on species, but currently the only country in Africa that requires environmental impact assessment (EIA) for fencing is South Africa (Lindsey et al. 2012). EIA is a legal decision-making instrument recognized by international law designed at mitigating and assessing how human activities affect the environment (Morgan 2012). Even though fencing has a direct impact on the environment and may cause mass mortality events (Gadd 2012), very often it is not regulated and commonly used in many countries across the world. Recent political trends of broad-scale border fencing between countries bring new concerns how these changes will be affecting human and wildlife well-being (Linnell et al. 2016; Sutherland et al. 2017).

Given the impact of fencing on blocking of animal movements, mitigation measures should anticipate the effects of fences and should ideally consider species-specific landscape connectivity. One way to model landscape connectivity is to build a functional connectivity model that represents an animal's ability to traverse a variable and varying landscape (Cushman et al. 2009). Functional connectivity modelling is a suitable approach to assess impacts of fencing and it can be applied using a variety of different datasets and methods, including GPS movement data (Zeller et al. 2012; Thurfjell et al. 2014; Keeley et al. 2016; Milanesi et al. 2017). One of the many advantages of using continuous telemetry datasets is that it accounts for variable connectivity in different areas or across time (Hebblewhite and Haydon 2010; Pape and Löffler 2015). Various factors, including seasonality in resources distribution, may affect species mobility and need to be reflected in connectivity models (Mateo-Sánchez et al., 2016; Mui et al, 2017).

Elephants are bulk grazers and some families can use the same movement routes over decades (Moss et al. 2011). Movement corridors are essential for elephant population viability and genetic exchange (Douglas-Hamilton et al. 2005; Kioko and Seno 2011; Naidoo et al. 2018). Numerous studies on African elephants have focused on resistance-based landscape connectivity and corridor modelling using a variety of available methods and datasets (Cushman, Chase, & Griffin, 2010; Epps et al, 2013; Pittiglio et al., 2012; Roever, van Aarde, & Leggett, 2013). Even though the effect of fencing on elephant seasonal movements, vital corridors and landscape connectivity is a long-term concern for local conservation, we are unaware of any studies that have predicted the influence of fences on elephant movement corridors and connectivity.

Here, we chose the Borderland area between Kenya and Tanzania (Greater Amboseli Ecosystem, GAE) as a case study for predicting the potential impacts of fencing on elephant-specific landscape connectivity. The Amboseli Ecosystem has a history of HEC spanning 50 years (Kioko, Kiringe, & Omondi, 2006; Western & Waithaka, 2005) and the area has experienced rapid agricultural expansion – with the percentage of agricultural areas increasing from 925 km<sup>2</sup> (11.9 % of the ecosystem) in the 1970s to 3025 km<sup>2</sup> in the 2010s (38.9% of the ecosystem) (from Amboseli Conservation Program long-term aerial monitoring). At the same time, the elephant population has grown steadily since the 1970s (Moss et al. 2011) leading to increasing conflict with farmers (Kioko et al., 2006; Ngene et al., 2013; Okello, 2005; Western & Waithaka, 2005). The severity of the conflict is intensified by the loss in biomass available to elephants in the area due to competing livestock grazing pressure (Western et al., 2015).

Fencing for HEC mitigation has been applied in GAE since 1997, when two electrified fences were erected around agriculture fields at Kimana and Namelok (Okello and D'amour 2008). Because of rising HEC in the last few years, local NGOs and government organizations started constructing a new electrified fence on the upper slopes of Kilimanjaro (Big Life Foundation Report 2017).

In this research our goal is to test how fencing designed to mitigate human-elephant conflict will affect functional connectivity and movement corridors for African elephants. We hypothesise that incorporating a large electrified fence into the study area might change certain movement paths and potentially intensify human-wildlife conflicts in other areas. Additionally, we assumed that these effects will be specifically strong during the dry season which should be taken into consideration in lands management and preliminary environmental impact assessments.

# 3.2 Methods

# 3.2.1 Study area

The study area is located in the borderland between Kenya and Tanzania and part of the GAE. The rainfall in the area is highly variable, and is bimodal with a long rainy season from March – May, and shorter rains from October – December. The vast majority of the water sources are perennial and concentrated in the seasonal streams and minor rivers (Western 1975; Okello et al. 2016). The study area includes three large national parks (NPs), three community conservancies and two historically protected corridors: Kitenden and Kimana that are allocated and sustained through leasing programs by the International Fund for Animal Welfare (IFAW) and African Wildlife Foundation (AWF) (Fig. 3.1).

GAE currently contains two poorly maintained electrified fences erected for HEC mitigation in 1997 around agricultural fields in Kimana and Namelok regions (Fig. 3.1) (Okello and D'amour 2008). Construction work on a new 28 km electrified fence on the upper slopes of Kilimanjaro started in 2017 (Space For Giants Report 2015; Big Life Foundation Report 2017).

# 3.2.2 Telemetry data

GPS telemetry data were derived from twelve elephants immobilized and collared between 2013 and 2014 within the study area (details in Ngene et al. 2014; Ngene et al. 2017). Fix rates, sample sizes and collaring locations are presented in Table S1 of the Supporting Information. We explored individual movement data for spatial and temporal outliers, and excluded paths with irregular non-consistent GPS fixes. The data was resampled to constant 4-hour intervals. When the time gap between two consecutive points were more than 4 hours, all points before this gap have been saved as an independent data segment. The segments that included fewer than 10 consecutive points were eliminated from further analysis.



Figure 3.1. (a) Study area in the Borderland between Kenya and Tanzania; (b) Protected lands with the core areas estimated from the elephants' movement data using 50% threshold of kernel densities. Priority wetlands and flood plains defined as the pinch points by the circuit connectivity model; (c) Present and future fencing situation in the study area and protected historical corridors (Kitenden and Kimana corridors)

# 3.2.3 Functional landscape connectivity model

We calculated resistance to movement surfaces using a step-selection function (SSF) (Fortin et al. 2005b; Forester et al. 2009). SSF uses a case-control design where each habitat covariate used during the observed movement steps is contrasted to the habitats available to an animal using conditional logistic regression (Fortin et al., 2005; Johnson et al., 2006; Manly et al., 2007). In this study, we simulated 10 "available" to each "used" step. The step's lengths were simulated from the empirical movement data using Gamma distribution with a maximum likelihood. Turning angles for the available steps were drawn from a uniform distribution between  $-\pi$  and  $\pi$ . Besides habitat variables, we integrated step length as a predictor for excluding possible bias caused by a parametric distribution of step length

(Forester et al. 2009). We used publicly available GIS datasets and derivatives from remote sensing data for extracting the environmental covariates (Table S1). Land cover classification and post classification analysis were accomplished previously (Osipova et al. 2018)

We fitted penalized conditional logistic regression with least absolute shrinkage and selection operator (LASSO) (Reid and Tibshirani 2014). The advantage of this method over simple conditional logistic regression is that it calculates a penalized log-likelihood allowing us to perform parameter estimation and variable selection simultaneously (Reid and Tibshirani 2014). This approach avoids autocorrelation and biases in predictors, which is a common problem for telemetry data (Beyer et al. 2010; Street et al. 2016). We used the inverse of these movement probabilities to represent landscape resistance values. This is similar to other studies that have used the inverse of habitat suitabilities to reflect resistances, except that our resistances are based on actual movement data (i.e., step-selection), rather than on presence data (i.e., *point-selection*; Zeller et al. 2012).

Based on resistance surfaces, we modelled potential connectivity using circuit theory and least-cost path (LCP) methods. LCP allows for the estimation of cost-effective distances between the priority habitat patches, while circuit-theoretic connectivity estimates the current flows reflecting the likelihood of random walks and provides metrics that can be directly interpreted in terms of landscape connectivity (Adriaensen et al., 2003; Carroll, McRae, & Brookes, 2012; McRae et al., 2008; Shah & McRae, 2008). Both methods require an input layer with the core areas – the areas of high importance for the species (protected lands or major resources patches). The connectivity paths were calculated between these areas and their placement strongly affect the final connectivity maps (McRae and Kavanagh 2011). Here, we defined the core areas as the 50% threshold of the kernel density estimates calculated from the elephants' GPS fixes within the NPs and community conservancies. This approach helps to define the core area used by the elephants in protected lands and to avoid an effect of the artificial boundaries of the protected areas (Koen et al., 2010). The analysis was performed in Linkage Mapper (ArcGIS 10.5.1) (McRae and Kavanagh 2011) and *raster* package in R (Hijmans et al. 2016).

# 3.2.4 Accounting for seasonality

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 (Fig. S2 in the Supporting Information). We used a continuous time series of monthly normalized difference vegetation index (NDVI) derived from MODIS modelling forage availability fluctuation. We binned the two years of continuous movement data (2014 – 2015) into monthly subsets and used the corresponding NDVI layers for fitting SSF and modelling resistance surfaces. Finally, we modelled LCP and

circuit-based movement corridors connecting large protected areas for each consecutive month (24 surfaces overall).

We calculated mean current densities for each month and plotted the values as a time series for the whole study area, for protected and non-protected lands and for the priority wetlands within the movement corridors. A time series statistic was applied (i.e., Granger causality test; Granger, 1988) to test if seasonal changes in monthly average rainfall and NDVI can explain changes of monthly connectivity values.

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	Resis	tance	Current Density				
	2014	2015	2014	2015			
Jan	< 0.001	< 0.001	< 0.001	< 0.001			
Feb	< 0.001	< 0.001	< 0.001	< 0.001			
Mar	< 0.001	< 0.001	< 0.001	< 0.01			
Apr	< 0.001	< 0.001	< 0.001	< 0.001			
May	< 0.001	< 0.001	< 0.001	< 0.001			
Jun	< 0.01	< 0.001	< 0.001	< 0.001			
Jul	< 0.01	< 0.001	< 0.001	< 0.001			
Aug	n.s.*	< 0.01	< 0.001	< 0.001			
Sep	< 0.001	n.s.*	< 0.001	< 0.01			
Oct	n.s.*.	< 0.01	< 0.001	< 0.001			
Nov	< 0.001	n.s.*	< 0.001	< 0.001			
Dec	< 0.05	< 0.001	< 0.001	< 0.001			

Table 3.1. Results of the t-test (p-values) for predicted resistance and current density values within 1337 m buffers at GPS locations versus random points

\* p value was not significant

## 3.2.5 Model validations

To evaluate model performance, we retained 10% of the GPS fixes from the empirical data for each month. We buffered each GPS fix with a radius equal to an average step length of an elephant estimated from GPS data (1337 m), and recorded resistance and current flow values within the buffers for each resistance surface and cumulative current flows map, respectively. We repeated the same procedure with simulated random points and compared the final resistance and current density values using a t-test (Koen et al., 2014). If our monthly predictions of elephant movement have high predictive power, then the resistance values should be significantly smaller and the current flow values significantly larger at actual movement points compared to random points.

# 3.2.6 Assessing fencing effects

To reflect existing fencing conditions, we assigned resistance values of 1 (very high relative resistance value) to areas falling within Namelok and Kimana fences (Fig. 3.1). Since the resistance values range from 0 to 1, this step makes the fenced area highly resistant to movement, but still permeable as these fences are partly broken and occasionally raided by elephants (Okello and D'amour 2008). As for the future fencing scenario, we increased a resistance value to 100 in the area within the Kilimanjaro fence (future fencing scenario), as it is expected to be well maintained and completely impermeable. This approach was recommended by (McRae and Kavanagh 2011) for delineating the impermeable areas in Linkage Mapper (ArcGIS 10.5.1).

To highlight the areas most affected by fencing, we calculated the difference between existing and future connectivity values for each month. We subtracted the future from the existing connectivity raster modelled using LCP and circuit-theory. All cells of the resulting differences surfaces were standardized using z-scores, and we reclassified them to range between -1 and 1 (lowest to highest values), and summed all rasters. With this procedure, the lowest negative values highlight areas with the largest connectivity losses caused by the fence, while the highest positive values reflect areas with largest connectivity gains. To evaluate temporal connectivity changes, we computed a spatial correlation coefficient (Tjostheim's coefficient; Hubert et al. 1985) that summarizes the association between two spatial variables with values ranging from 0 (no spatial correlation) to 1 (perfect spatial correlation). We calculated the correlation coefficient for the whole study area and for the areas of high management priority (i.e., wetlands, historical corridors and potential humanconflict areas). Additionally, we compared changes in the ranks of the corridors and protected areas by estimating monthly highest centrality scores for the existing and future scenarios.

# 3.3 Results

# 3.3.1 Model results and validation

We modeled 24 resistance and connectivity maps (monthly sequence from January 2014 until December 2015) reflecting sequential seasonal changes for the study area. Most resistance (N = 20) and all cumulative current flow (N = 24) models revealed high potential for predicting movements (Table 3.1). Compared to predictions from random movements, empirically-derived movement predictions showed significantly lower resistance values ( $0.28 \pm 0.005$  and  $0.46 \pm 0.007$  for GPS fixes and random points, respectively; t-test, *p* < 0.05), and significantly higher cumulative current flows ( $0.12 \pm 0.003$  and  $0.02 \pm 0.001$ ; t-test, *p* < 0.05).


#### Connectivity Changes Caused by Fencing and Predicted Seasonal Corridors

Figure 3.2 (a) Predicted rates of connectivity changes caused by the fencing using least-cost path and circuit theory. Connectivity *loss/gain* are the areas that predicted to be less/more intensively used by the elephants after building the fence; (b) Illustration of the seasonal corridors for wet and dry months predicted for current and future fencing situation

#### 3.3.2 Seasonal patterns

Potential landscape connectivity has a seasonal character of gradually increasing in the wet months and decreasing in the dry months with the highest cumulative current flow values in the wettest months (March 2014 and May 2015;  $\mu = 0.19\pm0.091$  and  $\mu = 0.19\pm0.133$  accordingly); and lowest values in the first rainy months after the dry season (October 2014 and November 2015;  $\mu = 0.087\pm0.053$  and  $\mu = 0.092\pm0.049$ ) (Fig. 3.2). However, this pattern is reversed when protected areas are excluded from the analysis (Fig. 3.3 a-b). The difference in connectivity contribution of the non-protected wetlands and seasonal flood plains in wet and dry season revealed that they change their relative input simultaneously (Fig. 3.3a). The synchronous time series indicates that the elephants do not rely on specific wetlands and all

of them are similarly important for maintaining connectivity during the dry season. While Kimana and Borderland wetlands are natural sources of water, Esenlenkai and Chyulu Hills flood plains attracts elephants during the dry seasons because of the good protection and artificial water sources provided by the conservancy.

The results of Granger causality tests show that seasonal changes of the cumulative resistance values can be predicted to some degree by changes in the mean monthly rainfall, and especially by NDVI values (Granger causality test; p = 0.08 for monthly mean rainfall, p = 0.04 for monthly mean NDVI) (Fig. 3.4; Fig. S1).

### 3.3.3 Fencing effect

Spatial correlation analysis of the current flows for existing and future scenarios revealed that fencing will not cause significant changes in overall connectivity. Correlation coefficients between current and future current flow surfaces were higher than 0.5 for all months. Generally, correlation coefficients were slightly higher for the wet season (Fig. 3.4).

The number of corridors predicted for the future scenario is not significantly different from the existing scenario ( $14.37\pm2.45$  and  $14.12\pm2.35$  for existing and future scenarios). The centrality score assessment showed that the three corridors with the highest centrality scores stay equally important for the existing and future scenarios (corridors connecting Amboseli with Enduimet, Elerai and Kimana conservancies (22, 13 and 7 times ranked as  $1^{st}$ ,  $2^{nd}$  and  $3^{rd}$ ).

Major connectivity losses were predicted for the future fencing scenario around the corridors connecting Kimana and Elerai conservancies to Tsavo West NP and the corridors between Kenya and Tanzania. Conversely, non-protected lands among Kimana, Elerai and Amboseli NP will increase the cumulative current density values (Fig. 3.2). Therefore, fencing is not predicted to cause connectivity losses, because new restrictions to movement increase usage of other corridors.

## 3.3.4 High management priority and potential conflict area

The strongest input for maintaining overall connectivity in non-protected areas occurs in the corridors between eastern Amboseli and the Elerai Conservancy (21 out of 24 times ranked as 1<sup>st</sup>); Amboseli and Enduimet (12 times ranked as 2<sup>nd</sup>); Amboseli and Kimana Conservancy (7 times ranked as 3<sup>rd</sup>). Amboseli NP, Kimana and Elerai Conservancies had the highest centrality scores for most models (23, 12 and 8 models out of 24 scored these areas as 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> in ranking) (Table 3.2).



Figure 3.3. Mean current flow density values estimated and plotted for each month (2014–2015). (a) Mean current density for the entire area and for the wetlands selected as pinch points; (b) Mean current density plotted for the entire research area and excluding protected areas (PAs)

We identified four wetlands and flood plains most commonly highlighted by the model as pinch points within the corridors (Fig. 3.1b, Fig. 3.3a). Current flow analysis for these areas revealed that flow densities in Kimana and Borderland wetlands are constantly higher than the average current flows for the whole area, while Esenlenkai and Chyulu flood areas experience fewer currents. Cumulative flow of Kimana wetlands has the highest values compared to others and the magnitude increases in the dry months. All these areas tend to increase conductivity values in rainy months, and decrease them in dry months (Fig. 3.3a).

Only Kimana wetland and nearby Kimana historical corridor will be significantly affected by fencing (mean conductance values are  $0.3\pm0.18$  vs  $0.4\pm0.18$  for current and future scenarios; monthly spatial correlation values are less than 0.5, Fig. 3.4), while the Kitenden corridor did not change in current flow ( $0.2\pm0.08$  for current and future scenarios; monthly spatial correlation values are higher than 0.5). The same increase in conductance was detected for an agriculture field adjacent to Kimana wetland (Fig. 3.4). Another agriculture patch lying on the pinch point of the corridor connecting Kimana conservancy and Tsavo West NP did not reveal any significant changes in conductance potential ( $0.2\pm0.12$  and  $0.2\pm0.11$ ; monthly spatial correlation values are higher than 0.5).



Figure 3.4. Spatial correlation coefficients (Tjostheim's coefficient) calculated for monthly circuit connectivity surfaces modelled for current and future fencing scenarios. The plot includes values for the entire study area, for Kimana historical corridor and the adjacent agriculture area

## 3.4 Discussion and Conclusions

Crop raiding is the most prevalent type of HEC in Africa and Asia, and is increasing sharply with the spread of farms into elephant range areas such as Amboseli (Graham et al., 2010; Pozo et al., 2017). This conflict has led to an increase in human and elephant fatalities across much of Africa (Western and Waithaka 2005; Okello 2005; Gadd 2005; Lindsey et al. 2012). There is debate surrounding possible management schemes to mitigate this conflict, but fencing is still the most common tool as it gives an immediate, although not necessarily most effective, resolution to conflicts (Sitati and Walpole 2006; Hayward and Kerley 2009). Despite a broad application of fencing in HEC mitigation, it rarely has been a part of a preliminary EIA (Hayward and Kerley 2009). Our study illustrates how empirical movement data can be combined with connectivity modelling to predict the consequences of planned fencing on elephant movements across the landscape.

Protected Areas								
	Present	Future						
	Amboseli (upper core)	Amboseli (upper core)						
Rank 1	(23)	(22)						
Centrality								
score	17.5±1.87	17.7±1.74						
Rank 2	Kimana (12)	Kimana (14)						
Centrality								
score	14.5±1.60	14.8±1.65						
Rank 3	Elerai (8)	Amboseli (lower core) (9)						
Centrality								
score	13.5±1.33	13.5±1.42						
	Corridors							
Rank 1	Amboseli-Elerai (21)	Amboseli-Elerai (22)						
Centrality								
score	8.4±1.23	8.2±1.03						
Rank 2	Amboseli-Enduimet (16)	Amboseli-Enduimet (13)						
Centrality								
score	6.5±0.85	6.5±0.91						
Rank 3	Amboseli-Kimana (7)	Amboseli-Kimana (7)						
Centrality								
score	5.2±0.10	5.4±0.83						

Table 3.2. Top ranking protected areas and movement corridors based on centrality score values for present and future fencing scenarios

Corridors/protected areas were included in the table only when they were top ranked maximum number of times (the number of selected models are provided in parenthesis).

The Borderland elephants in GAE provide an example of how fencing may bring immediate, localized relief to HEC. Erecting the 28-km long fence around the agriculture fields on the upper slopes of Kilimanjaro is an example where construction of an electrified fence was considered the best and most urgent option by the local community (Space For Giants Report 2015). A number of challenges remain, including the maintenance responsibility and costs, but rapid installation of the fence has seen a large reduction in farm losses as well as human and elephant deaths (Big Life Foundation Report 2017).

The results of our study show that even though relatively large areas of elephant habitat will be isolated by the fence, it is unlikely to severely affect functional connectivity for the species across broad scales. The planned fence was intended to block areas between Enduimet and Elerai conservancies, yet the major connectivity routes occur in a north-south direction and pass through western Kilimanjaro's slopes (Enduimet Wildlife Management Area), and those in the east-west direction connecting Amboseli with Tsavo West NP through Kimana Wildlife Sanctuary (Ojwang et al. 2017). The deterrence of elephants from the farming areas will likely lead to increased use of the northern areas of the Amboseli ecosystem where rainfall is too low to support farming (Western and Lindsay 1984).

Even though fencing will not cause an overall decrease in landscape connectivity, it will create additional pressure on areas where conflict does not currently exist. Kimana wetland showed the highest conductance potential compared to other wetlands and flood plains, and, at the same time, it will be most affected by fencing. Increases in conductance are also significant in the Kimana historical corridor and in the agriculture fields nearby. These results suggest that building the fence on the upper slopes of Kilimanjaro for HEC mitigation will increase the probability of HEC elsewhere in the area. At the same time, an increasing presence of elephants in the protected historical corridor may come with harmful side effect such as fast habitat degradation caused by population concentration in safe protected areas (Western 1989).

In a highly seasonal environment where biodiversity depends on the amount of rainfall, time-series analysis provides important information to conservation decision making. Adding a seasonal component to our analysis helped to prioritize seasonal corridors, identify commonly used routes and to confirm the time of the year where elephant movements may cause HEC. As the importance of non-protected lands increased in the dry season and HEC occurs more often in the driest periods (King et al., 2017; Kioko et al., 2006), we suggest that the movement corridors with the highest ranks predicted for the dry period should receive special attention in local management planning and be considered for more formal protection within conservation estates.

Fence construction for human-wildlife conflict mitigation has two major disadvantages: they are expensive to maintain over the long term and may have unpredicted negative consequences for wildlife at larger spatial scales (Hayward and Kerley 2009). There are

extensive discussions on alternative management schemes that could be applied to mitigate HEC, including bee hives, capsicum-based products or buffer crops (Hoare, 2012; King et al., 2017; Osborn, 2002). Another tactic would be to change elephant behaviour in non-intrusive ways, for example via surface water manipulation (Chamaillé-Jammes et al. 2007). These methods are often less costly but still effective alternatives to fencing as they decrease the severity of the HEC, but keep the outfenced area partly permeable (Slotow 2012). Another advantage of these methods is direct involvement of the rural communities, which can change their attitude towards wildlife (Osborn & Parker, 2002). However, there are many uncertainties related to these approaches, and some of the long-term maintenance-related costs are comparable with those of electric fences (Grant et al., 2008).

While our results are specific to the Borderland elephants in GAE, the shifting of conflicts due to local mitigation measures is likely a general challenge for the management of humanwildlife conflicts. We therefore suggest managers to conduct an EIA before implementing actions to reduce human-wildlife conflicts, and to consider not only local but also broad-scale impacts. Assessing the costs and benefits of different mitigation measures is essential for finding optimal solutions (Lindsey et al., 2012; Ringma et al., 2017) and our study provides a framework for modelling and assessing connectivity for EIAs. Considering connectivity is crucial, because some local measures (e.g. fencing) might lead to immediate local successes, but shift the problem elsewhere by changing wildlife movement routes. This is essentially a 'cost' incurred by the measure which needs to be compared to its predicted benefits. While other mitigation measures (e.g., management of water resources) might show less pronounced reductions in local conflicts compared to fences, they might also not simply shift the problem to other sensitive areas, thus causing smaller costs at the landscape scale.

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# **Chapter 4**

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

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## Abstract

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.

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. 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.

The results of this study confirm that the resistance-based connectivity model is a valid approach for predicting movement corridors for the African elephant in the study area. 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.

## 4.1 Introduction

Resistance-based connectivity models are frequently used in conservation to tackle the global problem of habitat fragmentation and degradation (Bennett 2003; Noss 2006; Bennett and Saunders 2010b). Habitat fragmentation and 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 connectivity can dramatically affect many ecological processes, and therefore connectivity planning is a valuable complementary method to conventional conservation approaches (Bennett et al. 2006).

Movement corridors are the conservation tool directly derived from landscape connectivity models and are commonly applied by practitioners in species conservation and land-use planning. Despite some rational concerns regarding the usefulness of corridors and their overall performance (Hodgson et al. 2009b), numerous studies have shown that using connectivity models for corridor planning is successful and that these models have significant potential in conservation management (Gilbert-Norton et al. 2010; Doerr et al. 2010; Abrahms et al. 2016). At the same time, the variety of methods used for landscape resistance and connectivity modelling brings many uncertainties to the resulting corridors maps. These uncertainties are largely related to the adequate shape and dimensions of the planned corridors, and they need to be appropriately addressed to avoid false land planning decisions and financial losses (Wade et al. 2015).

Most landscape connectivity studies with an evaluation component address only internal validation (model uncertainty), which can readily be achieved through widely used statistical model validation, including cross-validation, area under a relative operating characteristic curve (ROC), bootstrapping or jackknifing (Pearce and Ferrier 2000; Bond et al. 2017). External validation is more challenging as it always requires an independent dataset. Moreover, the methodological framework for external validation has not yet been standardized or applied across a sufficient number of studies. Thus, Thurfjell et al. (2014) reviewed connectivity studies based on step-selection or path-selection functions (SSFs and PSFs), and emphasized that most of these studies neglected validation, and concluded that more research is required to ensure their successful realization in conservation practices.

Few researchers have attempted to externally evaluate the predictive performance of connectivity models and these attempts were mainly applied to evaluate structural corridors. These studies used species occurrence and GPS datasets for validating either already existing 'historical' 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 validate corridor performance (Mech and Hallett 2001) or validated habitat-based corridors using functional connectivity models, assuming that these models represent a species response to these habitats and therefore can be used for validation (Wang et al. 2008; Mateo-Sánchez et al. 2015; Naidoo et al. 2018). Functional connectivity models and corridors predicted from animal movement data have only 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 to this requirement and, when the sample size is large enough, the data can be split into predictions and validation subsets (Bond et al. 2017). However, considering that collecting telemetry data is logistically and financially demanding (Hebblewhite and Haydon 2010), the sample size is rarely sufficient for this approach. A good alternative to the telemetry data would be the population's repeatable counts collected in the same area where the predictions were made. The count data allows the derivation of the species' spatial preferences and fidelity to certain areas, if collected over a long period. Large mammals in open areas are often counted using aircrafts in aerial census

surveys (Jolly 1969; Western et al. 1976). This method provides high accuracy estimates in open areas with sparse vegetation because of good visibility of the animals and high level of accuracy in species recognition (Jachmann 2002; Ndaimani et al. 2016), and it is widely used in species population studies (Prins and Douglas-Hamilton 1990; Stoner et al. 2007; Singh and Milner-Gulland 2011; Okello et al. 2016). As this data type includes a spatial component, it has also been used to identify prominent migration corridors (Pittiglio et al. 2012; Mose et al. 2013). The specifications mentioned above make an aerial census highly informative in validating connectivity models.

In this study, we use independent aerial count data to validate a SSFs-derived functional connectivity model for the African elephant and report how predicted corridors perform compared to similar areas in the landscape outside of the corridors. We presumed that connectivity model has strong predictive power for observing elephants in areas with higher landscape connectivity values. We suggested that if the predicted higher density connectivity flows were 'working' corridors for the elephants, then elephant track density and abundance estimates would be the highest within predicted corridors.

## 4.2 Methods

#### 4.2.1 Study area

The 8300 km<sup>2</sup> study area is within the Greater Amboseli Ecosystem (Amboseli) in the borderland between Kenya and Tanzania (Fig. 4.1a). It is a semi-arid area with irregular rainfall with short rains from October to December, and a long rainy season from March to May. The area includes a number of large national parks and community conservancies, and is home to a relatively well-studied African elephant population of approximately 1200 individuals (Moss 2001; Moss et al. 2011). The population is currently recovering after heavy poaching in the 1970s, and existing protected areas alone cannot provide enough space and resources for the rapidly growing elephant numbers (Western 2007). As a result, elephants spend a large part of their time travelling and feeding in non-protected lands and very often this leads to human-elephant conflict (Western 2007; George et al. 2016). Considering the rapid agricultural development in Amboseli and the transition from nomadic to sedentary lifestyles amongst local communities (Okello and D'amour 2008), the frequency and severity of conflict is expected to increase. Thus, understanding connectivity in non-protected areas together with movement corridor predictions is necessary for effective landscape conservation.



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

Figure 4.1. (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.

### 4.2.2 Resistance surface and connectivity modelling

Osipova et al. (2018) developed a framework for modelling the seasonal resistance maps based on GPS telemetry data from 12 African elephants over two years using step-selection functions (SSFs) (Manly et al. 2002; Fortin et al. 2005b; Johnson et al. 2006). The resistance surface values estimated using this method 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 a least-cost path and circuit theory to model connectivity and delineate most likely movement corridors (McRae et al. 2008; Carroll et al. 2012a). We calculated circuit flows connecting the protected area patches regularly used by the elephants based on the movement data (Fig. 4.1b).

To evaluate the performance of the connectivity model, we used several resistance surfaces. For the validation scheme with aerial counts (see below), we modelled two resistance surfaces for wet and dry seasons. The seasons were estimated using remote sensing rainfall data (TRMM; TMPA/3B43 dataset). We subset corresponding movement data and the monthly NDVI layers (MODIS) for each season and fitted SSFs separately. For corridor validation using on ground counts, we used a connectivity model built on a subset of the GPS movement and NDVI data 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, see below).

## 4.2.3 Connectivity model validation methods

#### 1. 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 5x5 km size (Fig. 4.1a). 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. 4.1b).

We hypothesized that if the connectivity model performed well, the proportion of higher connectivity values in the grid cell would be a strong predictor of elephant presence. We expected grid cells with higher connectivity values to predict higher numbers of the elephants and *vice versa*. For testing this hypothesis, we fitted a generalized linear mixed

effect model (GLMM) with a set of environmental covariates and connectivity values per grid as fixed effects, and the years of observations as a random effect (Table 4.1). The environmental variables were chosen based on ecological relevance and tested for collinearity. 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 removed from the analysis 12 grid cells covering the core areas intensively used by the elephants within the protected lands. By doing that we assured that we are testing connectivity model only for non-protected areas (Fig. 4.1b). Animal count data are often overdispersed due to zero-inflation (high proportion of zeros in relation to the actual counts). The possible sources of zeros are discussed in Zuur et al. (2009). The recommended method of dealing with zero-inflated datasets is using a mixture model consisting of two parts. The binomial part is used for modelling the probability of observation of the zero values; and the count part 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 effect of connectivity may differ with seasonality.

We started with fitting the full model incorporating all explanatory variables, and then tested the importance of each variable 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<sup>2</sup>: marginal R<sup>2</sup><sub>m</sub> (variance explained by fixed terms) and conditional R<sup>2</sup><sub>c</sub> (variance explained by fixed and random terms) (Nakagawa and Schielzeth 2013). We verified the top selected model fit by plotting Pearson residuals against fitted values and each covariate, and the residuals were checked for spatial autocorrelation (Zuur et al. 2010).

#### 2. 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: four quadrats were positioned within the predicted corridors ('test quadrats'), and two quadrats were placed outside of the corridors ('control quadrats') (Fig. 4.1c). Each quadrat consists of 4 parallel transects 3 km long with a 1 km gap between them (72 km in total).

The survey area included mainly open savannah with a sparse vegetation or local-scale agriculture (Table 4.2). The data were collected with the help of an experienced tracker who identified footprints. Due to large size of the elephants' 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 days-14 days; more than two weeks ago). Using local knowledge for animal tracking has been successfully applied in the number of studies

on variety of species, including African elephants (Stander et al. 1997; Southgate et al. 2005; Norris et al. 2008; Southgate and Moseby 2008; Songhurst et al. 2016).

We placed test research quadrats in four predicted movement corridors connecting the protected areas (Fig. 4.1c). 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.4.1c). 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 estimated the track densities per quadrat by calculating a total number of sets of tracks recorded along the transects (the 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 two months. The higher the numbers, the more intensively the elephants moved through the research plot in the last two 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):

$$D = \frac{\pi}{2} \frac{x}{S\hat{M}}$$
 where:

- *D* animal density (abundance)
- *x* number of daily tracks crossing the survey transect;
- S survey transect length; and
- $\widehat{M}$  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 (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 iteration).

## 4.3 Results

#### 4.3.1 Connectivity model evaluation using aerial counts

A multicollinearity test revealed correlations between land cover variables (proportion of grasslands, bushlands and woodlands), so we retained only one land cover variable (proportion of grasslands) in the model. The pairwise Pearson correlation coefficients were less than 0.6 for the final set of explanatory variables (Supplement 1). Plotting Pearson residuals against original and fitted values, each explanatory variables and in spline correlogram did not indicate any problems with models fit (Supplement 1) (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 dataset from 2012 had a spline with a correlation larger than 0.5, but only at a distance of  $\sim 1$  km, which then rapidly decreased (Supplement 2). Considering the size of the grid cells (5 x 5 km) and results of spatial autocorrelation plots, we concluded that the dataset was not spatially correlated.

Table 4.1. Stepwise models' selection goodness-of-fit comparisons for zero-inflated GLMM fitted to the elephants counts data. Joint Akaike information criterion for the count and binary fitted models (AIC<sub>i</sub>), log likelihood (log lik), variance explained by fixed term only (marginal variance  $R^{2}_{m}$ ) and variance explained by fixed and random terms (conditional variance  $R^{2}_{c}$ ).

	AICj	log lik	Count part		Binary part	
Dropped fixed terms			$\mathbf{R}^{2}_{m}$	R <sup>2</sup> c	$\mathbf{R}^{2}$ m	R <sup>2</sup> c
None (full model)	3289.8	-1434.0	0.31	0.44	0.18	0.18
ConnectivityXSeasons	4471.9	-1815.5	0.17	0.31	0.08	0.08
Seasons (interaction term)	4055.5	-1818.9	0.21	0.33	0	0
All but						
ConnectivityXSeasons	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

**Full model**: Number of Elephants ~ Slope + NDVI + Proportion of Grasslands + Connectivity + (ConnectivityXSeasons) + (1/year)

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<sub>j</sub> = 3289.83,  $R^{2}_{c} = 0.44$ ). The model including only connectivity as an explanatory variable itself explained 23% of the data's variance (AIC<sub>j</sub> = 4146.83,  $R^{2}_{c} = 0.23$ ). 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<sub>j</sub> = 4471.94,  $R^{2}_{c} = 0.31$ ). The second and third most influential covariates were slope and seasonality as an interaction term (AIC<sub>j</sub> = 4073.61,  $R^{2}_{c} = 0.25$  for slope; AIC<sub>j</sub> = 4055.54,  $R^{2}_{c} = 0.33$  for seasonality) (Table 4.1). The full model predicted decreasing probability of zero observation and increasing probability of observing higher elephants number with higher connectivity values (Fig. 4.2).

### 4.3.2 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 4.2). 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 4.2).

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 4.2). We could not estimate abundance for the quadrat t3 because all counts in this quadrat were older than two 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 includes the highest track density recorded for the previous two months ( $4.25 \text{ tracks/km}^2$ , Table 4.2).

The highest track density/abundance ratio was for the corridor connecting Amboseli with Enduimet (quadrat t1, Fig. 4.1c); and the lowest values were for the corridor between Amboseli and Elerai (quadrat t3, Fig. 4.1c). The quadrat t4 in the high human disturbance area had track density values as high as the quadrats in the non-disturbed area (e.g. quadrat t2 has a track density 1.7 vs 1.3 for the quadrat t4).

		Low Human Distu	High Human Disturbance							
№ on map (Fig 1c)	c1	t1	t2	t3	c2	t4				
Dominant	open lands/	sparse bushland/	sparse	sparse	sparse	sparse				
vegetation type	sparse bushland	open lands	bushland	bushland	bushland	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				
	Elephants Density Estimates									
Number of										
inidivudal tracks	15	126	73	108	11	76				
Tracks Density*	0.5	3.7	1.7	4.25	0.5	1.3				
Abundance										
(Mean±SE)**	$0.04 \pm 0.0006$	$0.75 \pm 0.002$	$0.32 \pm 0.001$	N/A	$0.02 \pm 0.000$	$0.59 \pm 0.004$				

Table 4.2. 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).

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

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

# 4.4 Discussion and Conclusions

Our study demonstrates that connectivity values derived from landscape resistance model are the most significant predictor of spatially attributed elephant abundance estimated from the aerial census. 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 predict 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 the 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 H. 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 the 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. Stepwise excluding fixed terms shows that the goodness-of-fit of the model is most negatively affected when the connectivity predictor is excluded. At the same time, withdrawing all variables except connectivity leads to improved model fit compared to excluding just connectivity as a predictor. Connectivity with the season as an interaction term alone explains 23% of data variance (Table 4.1). Seasonality influence on the model's 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. 4.2). 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 is less than 50% per grid cell (Fig. 4.2). Predictions from the binary part 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 the elephants more frequently compared to those off the corridors. Track densities were two to four times higher in the corridors than off the corridors; and the number of individual tracks varied from 73 to 126 in the corridors, versus only 11 to 15 in the control quadrats. The corridor quadrats placed in the pristine lands adjacent to the large protected areas (PAs) revealed 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 as 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).



Figure 4.2 (a) Number of elephants (non-zero counts) estimated from the aerial census survey (2005 – 2016) plotted against the proportion of high connectivity values 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 versus, 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.
As the environmental conditions in the quadrats were similar, we assumed that the elephants use the corridors for movements despite human presence. This conclusion corresponds to some previous studies that have shown that small-scale agriculture attracts elephant for crop raiding and it regularly causes human-wildlife conflict (Graham et al. 2010). The study area has had long-term 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 could be beneficial to use more sample quadrats across the study area and possibly implement repeatable counts within and between different seasons. Long-term monitoring of the same predicted corridors can provide valuable information about the prediction accuracy and deliver more data for sensitivity analysis. Other sampling techniques can be considered, e.g. distance sampling (Buckland et al. 2001; Buckland 2004) or camera trapping methods (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. Using a case study, 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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# **Chapter 5** Conclusions

This dissertation aimed to explore the performance, advantages and potential pitfalls of resistance-based functional connectivity modelling in conservation science and management. Using the African elephant as a case study, I applied step-selection functions to the GPS tracking data and built functional landscape connectivity models. I integrated and evaluated the importance of seasonal and individual variation on model performance in systematic conservation planning and applied this methodological framework to a real-world conservation problem of fencing for human-wildlife conflict mitigation. The results of this work illustrated how connectivity predictions and their seasonal variability can be integrated in the environmental impact assessments. Finally, functional connectivity models and seasonal movement corridors were validated using independently collected datasets. The results of validation confirmed high predictive performance of such models for modeling the essential movement corridors.

# 5.1 Results overview

In **Chapter 2**, I presented a statistical framework for dealing with a relatively small dataset for a species with strong individual variability and validated it with individual simulations. Connectivity models accounting for seasonality were more precise; disregarding seasonal resource fluctuations underestimated connectivity for the wet and transitional seasons, and overestimate connectivity for the dry season. Therefore, it is highly desirable to incorporate seasonal changes into functional connectivity models whenever it is feasible. This is especially relevant for systems with pronounced seasonal spatial variation of forage and water availability. Extreme environmental conditions, such as low rainfall or droughts, may significantly decrease landscape permeability and should be considered with special care in conservation prioritization and corridor planning.

**Chapter 3** compiled a case study of fencing for a human-elephant conflict mitigation. I applied the quantitative research framework from Chapter 2, improved and extended, and used it for an impact assessment of fencing. The results revealed that fencing will not cause landscape fragmentation and will not change functional landscape connectivity dramatically. However, fencing will lead to a loss of connectivity locally and will increase the potential for human-elephant conflict in new areas. Using a seasonal component in the model revealed an increasing use of unprotected land in the dry season and equal importance of the core wetlands for preserving overall function connectivity in the study area. The discussion

touched upon the potential consequences of fencing for the elephants and how this policy can have unexpected outcomes in the future. Practical recommendations were given on using the functional connectivity modelling quantitative framework for environmental impact assessment and policy implementations.

The results of **Chapter 4** demonstrated that that the resistance-based connectivity model can be effectively used for predicting movement corridors for the focal species. I used independent aerial count dataset to validate a SSFs-derived functional connectivity model for the African elephant and conducted a field survey for estimating how predicted corridors perform compared to similar areas in the landscape outside of the corridors. The validation outcomes confirmed 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, and accounting for seasonality is an important factor for accurately predicting movements from connectivity models.

# 5.2 Synopsis

In the rapidly changing world where wildlife habitats are being converted into cultivated lands and human population size is constantly growing, the demand for methods allowing us to preserve connectivity in human-dominated landscapes is increasing. A working connectivity model should guarantee that a focal species will have enough connectivity for unrestricted movements and gene flow for maintaining a viable population. A variety of methods and biological datasets are applied for ensuring the best results for the corridor modelling, and models based on movement data are amongst the most popular. However, integrating functional connectivity models into conservation practice is a big challenge considering that this field of study is in its infancy, and methodologically and conceptually it is still filled with debates.

Functional connectivity is a response of individuals to landscape features and is unlikely be static in time and space. Despite the high potential of resistance-based connectivity models based on telemetry data to reflect temporal and seasonal variability of the landscape, only a few studies have attempted to incorporate spatio-temporal dynamics into modelling frameworks. It is a methodologically challenging task, but an essential step for providing biologically significant results in the hands of conservation managers. Another issue is a lack of evidence that the models' predictive potential is strong enough to reflect realistic landscape potential and dynamics for maintaining consistent metapopulations. It is a common problem when wildlife corridors offered by the land planners remain 'paper corridors', i.e. corridors that have been implemented as a policy tool but never been validated for effectiveness.

This dissertation aims to demonstrate how the resistance-based functional connectivity model can integrate seasonal and individual variability and how it can be used in a conservation management practice. I presented how incorporating seasonal variability can make a distinct difference in final outcomes and how disregarding these differences can negatively affect management decisions on the ground. I emphasize that accounting for individual variability is essential for a relatively small sample size and spatially biased datasets, and accounting for seasonality is crucial for the areas prone to droughts.

The case of using fencing for human-wildlife conflict mitigation described in Chapter 2 is a perfect illustration of how such a dynamic connectivity model can be useful in environmental impact assessment and decision-making policy. It demonstrated that one of the most widely used wildlife management tools – fencing – can bring unpredicted consequences for elephant connectivity without proper preliminary assessment. The results of this case study endorse using functional connectivity model as an evaluation instrument prior to building fences or other linear landscape features that can potentially affect animal movement and gene flow.

The final part of this dissertation is devoted to evaluation of the previously built connectivity model and predicted movement corridors. I used annual aerial counts to evaluate the connectivity model, and a field survey to assess the performance of predicted corridors. The results revealed that higher connectivity values predict high number of elephants registered from an aircraft over 11 years, and that prediction was even more precise when connectivity values were tested separately for different seasons. This research was complemented with a field survey by counting elephant tracks within and outside of the predicted corridors. The results confirmed two initial hypotheses: (1) the corridors predicted using functional connectivity models are intensively used by the elephants for movements; and (2) accounting for seasonality significantly improves model's performance.

Even though functional connectivity modelling in conservation science is progressing very fast, the number of challenges remains, including terminological confusions, difficulties in data gathering and complexity and inconsistency in methodological approaches. Developing connectivity models with high predictive power will stay in high demand in conservation management because habitat fragmentation will be intensified by environmental changes. Unique capacity of the movement data to capture spatio-temporal relationship of an organism with an environment have a potential to incorporate these changes in conservation decision-making. In this research, I successfully simulated gradual fluctuations in connectivity over time using monthly subsets of movement data over two years, and this approach can be developed further into time series analysis of the variations over extended period. Such complex models would allow to predict how connectivity can be affected by the droughts, anthropogenic factors and by the climate change in the long run.

Another valuable development would be applying multi-species connectivity models instead of single-species approach. Some attempts have been made to model corridors based on ecological communities' parameters, but very often these corridors are less effective for the specific focal species. To find a trade-off between single and multiple species models would be another important development for the future studies. Complex movement models potentially can be integrated with genetic data-based models and individual-based simulations for assessing the effect of connectivity at the metapopulation level.

From the practical management perspective, new reproducible quantitative frameworks should be developed so they can be relatively easily applied by the practitioners. These frameworks have to be simple enough for implementation, yet they need to be based on solid scientific knowledge and be flexible for constant improvements. It can be standalone software or toolboxes for commonly used GIS applications with a simple interface and descriptive manuals.

Finally, functional connectivity models can be strengthened with a suitable *a posteriori* evaluation using independent datasets. Only few case studies have been focused on validation of management strategies and it is unclear how much functional the conservation corridors designed based on connectivity predictions. Resistance and connectivity surfaces should be validated for assuring that they accurately predict the corridors. Planned corridors, in its turn, can be evaluated on-site with the monitoring programs. Long-term monitoring of conservation corridors would help to refine the corridors' width and length, their locations and adjust them to changing environment and species demands.

The results of this research demonstrate a case study with a strong evidence that functional landscape connectivity models have a strong predictive power. The most accurate and fruitful conservation applications should take into consideration individual and seasonal variability, as well as human-introduced barriers such as fencing, railroads or highways. Considering high functional connectivity model performance, verified predictive power and flexibility, we strongly encourage wildlife conservation manager to integrate these models in the environmental impact assessments projects, land use plans and policy developments for highly fragmented or human-dominated landscapes.

# Supplementary material to Chapter 2

			Date	Date	Sample Size	Regularized	Mean Fix	Regularized	Data
ID	Sex	Collaring	(Begin)	(End)	(Initial)	Sample Size	Rates (h)	Fix Rates (h)	owner
M1	male	Elerai	Apr/14	Dec/15	3285	3280	44	4.0	IFAW, SES*
		Elangata		Dec/15	5205	5200		1.0	IFAW
M2	male	Wuas	Dec/13	May/15	2587	2584	5.0	4.0	SFS*
M3	male	Elangata	Dec/13		2550	2550	4.0	4.0	IFAW,
_		Wuas		Dec/15	3778	3770	4.8	4.0	SFS*
M4	male	Eselenkei	Feb/13	Fab/15	3778	3763	4.6	4.0	IFAW, SES*
				1,60/12	5778	5705	4.0	4.0	IFAW
M5	male	Kimana	Feb/13	Dec/15	5764	5754	4.3	4.0	SFS*
		***	G (1.4						IFAW,
M6	male	Kitirua	Sep/14	Dec/15	2421	2418	4.6	4.0	SFS*
F1	famala	Kuku	Mar/13						IFAW,
11	lemate	KuKu	wiai/15	Dec/15	5529	5512	4.4	4.0	SFS*
F2	female	Mailua	Dec/13						IFAW,
12	Ternule	Wallau	Dec, 15	Jul/14	1241	1241	4.6	4.0	SFS*
M7	male	Mailua	Dec/13	D /15	2750	27.42	4.0	1.0	IFAW,
				Dec/15	3750	3743	4.8	4.0	SFS*
M8	male	Mbirikani	Mar/13	L.1/15	4077	4250	47	4.0	IFAW,
				Jul/13	4277	4239	4.7	4.0	SFS* IEAW
M9	male	Osewan	Feb/13	Ju1/15	1616	4624	4.5	4.0	IFAW, SES*
				Jul/15	4040	4024	4.5	4.0	IFAW
F3	female	Rombo	Mar/13	Dec/15	4961	4945	4.9	4.0	SFS*
F4	female	Olkiramatian	Jan/07	Aug/09	20805	5679	1.1	4.0	ACC**
M10	male	Olkiramatian	Feb/10	Dec/10	7335	1863	1.0	4.0	ACC**

Supplementary 1. Telemetry data and seasonality specifications

Table S1. GPS movement data specification

\* International Fund of Animal Welfare

\*\* African Conservation Centre

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2007	wet	wet	early dry	early dry	dry	dry	dry	dry	dry	dry	dry	dry
2008	dry	wet	early dry	early dry	dry	dry	dry	dry	dry	dry	dry	wet
2009	dry	dry	dry	dry	dry	dry	dry	dry	dry	dry	wet	wet
2010	wet	wet	wet	wet	wet	early dry	early dry	early dry	dry	dry	dry	wet
2013	wet	wet	wet	wet	wet	early dry	early dry	early dry	dry	dry	wet	wet
2014	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	wet
2015	wet	wet	wet	dry	wet	dry	dry	dry	dry	dry	dry	wet

Table S2. Seasonality in the study area, defined according to the African Conservation Center field studies

	Environmental data layers					Number of times (M) and ratio (Ratio) of environmental variables included in the individual models							
	Name Data Source		Initial Data Resolution	All-in-One Model		Wet Season		Early Dry Season		Dry Season			
				№	Ratio	No	Ratio	N₫	Ratio	N₂	Ratio		
	Slope Distance to water	SRTM* Digital Chart of the	30 m	8	0.6	9	0.6	5	0.6	9	0.6		
	bodies	World	Vector data	7	0.5	6	0.4	5	0.6	7	0.5		
F	Distance to wetlands	WRI**	Vector data	8	0.6	5	0.4	2	0.3	8	0.6		
turi	Distance to rivers	WRI	Vector data	7	0.5	6	0.4	4	0.5	4	0.3		
Na	NDVI	MODIS***	250 m	11	0.8	12	0.9	4	0.5	10	0.7		
	Proportion of Bushland	Landsat 7, Landsat 8	30 m	9	0.6	7	0.5	6	0.8	6	0.4		
	Proportion of Woodland	Landsat 7, Landsat 8	30 m	7	0.5	6	0.4	5	0.6	6	0.4		
	Proportion of Grassland	Landsat 7, Landsat 8	30 m	9	0.6	6	0.4	3	0.4	9	0.6		
. <u>.</u>	Distance to major roads	WRI	Vector data	9	0.6	5	0.4	3	0.4	10	0.7		
geni	Distance to railways	WRI	Vector data	9	0.6	6	0.4	2	0.3	7	0.5		
hropo	Distance to towns Distance to protected	WRI	Vector data	7	0.5	5	0.4	3	0.4	4	0.3		
Ant	areas	WDPA****	Vector data	10	0.7	6	0.4	3	0.4	7	0.5		
•	Distance to agriculture	Google Earth Satellite	2.5 m - 30 m	9	0.6	7	0.5	2	0.3	7	0.5		

### Table S3. Environmental variables and their relative contribution in individual SSF models

### **Supplementary 2**

### **Remote sensing analytical workflow**

Land cover supervised classification

Eastern part of the research area was previously classified and validated by the NASA DEVELOP National Program in collaboration with the African Conservation Centre (Voelker et al. 2013). We used spectral bands from Landsat 8 and performed land cover supervised classification relying on the NASA product as a reference layer. The workflow charts of the analytical steps implemented for classification and post classification analysis represented in workflow charts 1 & 2. We classified two congruent tiles with the same spatial extent for filling the major gaps caused by large non-transparent clouds. We used land cover classes adapted after NASA DEVELOP program (5 general classes). For building the classification training sites we used previously existed land cover maps along with the false color composites, high resolution Google Earth satellite imageries, and NDVI layers. Each spectral signature was tested for separability using Jeffries-Matusita distance (Ifarraguerri and Prairie 2004) and Bray-Curtis similarity index (Bray and Curtis 1957). Approved spectral signature was applied for the Landsat band sets using the Maximum Likelihood supervised classification method. We performed an accuracy assessment by using a random points method. Overall accuracy values for the classified images are 92% and 99.6% (0.88 and 0.99 kappa values). An image with higher accuracy was used as a base layer for post classification routine.

As the scene were partly clouded, we developed a methodological framework for filling missing pixels from another tile with the same path/row numbers, and then applying object-based algorithm developed by Zhu & Woodcock (2012). We applied majority filter for filling small patches with missing values with the values of their contiguous neighboring cells and smoothed out the classes' boundaries. Finally, we mosaicked the clouds-free classified map with the land cover maps produced by NASA DEVELOP and cropped the final map to study area (workflow chart 1).

For avoiding misclassification of the natural land covers we included additional classes to the final land cover map: agriculture area, wetlands and open waters. We subset three major land cover classes (grassland, bushland and woodland) into single layers, and calculated the proportional coverage of each class within a circular buffer with the radius of the average step length estimated from the telemetry data (workflow chart 2).

Development areas were not incorporated in the classification scheme due to the failure to distinguish the spectral signature for them from those of other classes (Voelker et al. 2013). Hence, for plotting development areas, we used Google Earth Satellite imagery. We designed a grid of the cell size 15 x 15 km with a unique identification number. Using the Open Layers plug-in for QGIS 2.14.1, we zoomed in each quadrant to the scale 1:10,000 and digitized all visible human development areas in each quadrant. After inspection of all quadrants within the area we selected only the plots with an area larger than 0.5 km<sup>2</sup> to avoid incoherence between the tiles with different resolutions. The final product was reprojected, rasterized and transformed to the continuous surface representing the distance to development areas.



Fig. S1: Workflow chart for remote sensing classification analysis



Fig. S2: Workflow chart for remote sensing post classification analysis

# Supplementary 3. Probability surfaces weighted overlay based on the proximity to the home range center

## <u>Workflow</u>

1. Create an individual movement probability surface for each individual (14 layers). For this, first multiply habitat layers by the corresponding regression coefficient and add them up. Calculate log odd ratio for each point and apply pixelwise logit transformation. Resulting layers range from 0 to 1. Save the 14 maps in a raster stack

2. Calculate the (seasonal) home range (HR) for each individual, and calculate distance to the HR. Inverse the distances values so the larger the value, the closer animal was to its' HR center.

3. Stack the individual rasters of inverse distances (again 14 layers). In this stack we need to normalize each pixel from 0 to 1, so later we can use it as a weight matrix. We normalize each corresponding pixel (i.e. pixel with the same coordinate) in a raster stack. Therefore, each pixel has a weight (from 0 to 1) based on how far each individual was to this pixel (see example below). The closer the pixel to the individual home range center, the more weight it has (value is closer to 1). Now we have a stack of individual weighted matrices

4. Multiply these weight matrices with the corresponding individual probability surface (from step 1). Then sum across individuals. We will have a final movement probability map where each pixel is weighted and all values range from 0 to 1.

Example of the calculation for one pixel:

Assume we are considering a single pixel with the same coordinate, but for different individuals (in this example 3 individuals):

1. Inverse distances to the home range center are: 5, 500, 20 meters. The distances are inverse values, meaning that the larger the distance, the closer the animal actually was to its' HR center.

Normalize these distance from 0 to 1: 5/(5+500+20) = 0.0095; 500/(5+500+20) = 0.95; 20/(5+500+20) = 0.038. Here we can see that the sum of all pixels values is equal to 1 (0.95+0.0095+0.038 = 1).

2. Individual probability of use during movement values for the pixel with the same coordinates are: 0.9, 0.2, 0.5 for the three individual. Now we adjust these values by multiplying them with the weight layers calculated above:

0.9\*0.0095 = 0.0086

0.2\*0.95 = 0.19

0.5\*0.038 = 0.019

Here we can see how the weighted overly adjust the probability values. E.g., an individual with a very high predicted probability (0.9) has a home range quite far from the pixel, and the raw

probability value would be an overestimation of the probability that the individual would use the pixel during movement. This is because the raw probability is calculated based purely on the environmental resources combination, irrespective of the spatial proximity of the individual. At the same time we can see that if the selection strength is not very high (0.2), but an animal was relatively close to the HR center, the value remain almost the same (0.19).

# Supplementary 4. Resistance to movement models estimated using averaging coefficients and weighted overlay methods



Fig S3. Resistance to movement models estimated using averaging coefficients and weighted overlay methods. Home ranges of the individual elephants are calculated using 90% kernel density utilization distribution.



Fig S4. Resistance values distribution for two resistance to movement models estimated using averaging coefficients and weighted overlay methods.



Supplementary 5. Functional landscape connectivity models

Functional Landscape Connectivity Maps

Fig. S5: Functional landscape connectivity model (SSF, least-cost path and Circuit analysis) based on data subset for the all season (All-in-One Model)



Functional Landscape Connectivity Maps Wet Season

Fig. S6: Functional landscape connectivity model (SSF, least-cost path and Circuit analysis) based on data subset for the wet season (Wet Season Model)



#### Functional Landscape Connectivity Maps Early Dry Season

Fig. S7: Functional landscape connectivity model (SSF, least-cost path and Circuit analysis) based on data subset for the early dry season (Early Dry Season Model)

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#### Functional Landscape Connectivity Maps Dry Season

Fig. S8: Functional landscape connectivity model (SSF, least-cost path and Circuit analysis) based on data subset for the dry season (Dry Season Model)

### Supplement 6. Historical corridors performance



## Functional Landscape Connectivity and Historical Corridors Wet Season

Fig. S9: Current flow within historical corridors (Kimana and Kitenden corridors) based on data subset for the wet season (Wet Season Model)



Functional Landscape Connectivity and Historical Corridors Dry Season

Fig. S10: Current flow within historical corridors (Kimana and Kitenden corridors) based on data subset for the dry season (Dry Season Model)

# Supplementary material to Chapter 3

ID	Collaring	Sex	Sample Size	Data owner		
M1	Elerai	male	3280	IFAW		
M2	Elangata Wuas	male	2584	IFAW		
M3	Elangata Wuas	male	3770	IFAW		
M4	Eselenkei	male	3763	IFAW		
M5	Kimana	male	5754	IFAW		
M6	Kitirua	male	2418	IFAW		
M7	Mailua	male	3743	IFAW		
M8	Mbirikani	male	4259	IFAW		
M9	Osewan	male	4624	IFAW		
F1	Kuku	female	5512	IFAW		
F2	Mailua	female	1241	IFAW		
F3	Rombo	female	4945	IFAW		
(b) Environmental data						

### Table S1. Telemetry and environmental data specifications

	Name	Format	Initial Data Resolution	Data Source
	Slope	Raster data	30 m	SRTM
	Distance to wetlands	Vector data	-	WWF
al	Distance to rivers	Vector data	-	WRI
ıtur	NDVI	Raster data	250 m	MODIS
Na	Proportion of bushland	Raster data	30 m	Landsat 7, Landsat 8
	Proportion of woodland	Raster data	30 m	Landsat 7, Landsat 8
	Proportion of grassland	Raster data	30 m	Landsat 7, Landsat 8
nic	Human population density	Raster data	100 m	WorldPop
hropogeı	Distance to major roads	Vector data	-	WRI
	Distance to protected areas	Vector data	-	WDPA
Ant	Distance to agriculture	Raster data	2.5 m - 30 m	Google Earth Satellite

#### (a) GPS movement data

IFAW - International Fund of Animal Welfare

SRTM - Shuttle Radar Topography Mission

WWF-World Wide Fund for Nature

WRI - World Resource Institute

MODIS - Moderate Resolution Imaging Spectroradiometer

WDPA - World Database on Protected Areas



**Fig. S1.** Mean monthly rainfall and NDVI data averaged for the study area extent. Rainfall data is requested from the Tropical Rainfall Measuring Mission (TRMM; TMPA/3B43); NDVI data is requested from the Moderate Resolution Imaging Spectroradiometer (MODIS; MOD13Q1).

**Media S1**. Animation of the monthly connectivity models (2014-2015) representing changes in connectivity caused by building of a new fence (Current and Future scenarios). The monthly precipitation data is requested from the Tropical Rainfall Measuring Mission (TRMM; TMPA/3B43)

Data available from the Dryad Digital Repository: <u>https://doi.org/10.5061/dryad.n1804pf</u>

# Supplementary material to Chapter 4

# Supplement 1

### Data fitting assessment plots



Pairwise Pearson correlation coefficients plot for the explainatory variables used for fitting GLMM model



Actual vs Predicted Values





Spline correlogram with 95% bootstrap confidence interval of Pearson residuals with all explainatory variables fitted to the GLMM model



Residuals vs Connectivity Values

Pearson's Residuals

## **Residuals vs Proportion of Grasslands**



Pearson's Residuals



Residuals vs NDVI Values

Pearson's Residuals

## Residuals vs Slope Values



Pearson's Residuals
# Supplement 2

Spline correlogram with 95% bootstrap confidence interval of elephants presents datasets collected using aerial survey method in 2005 – 2016. Each plot represents one sampling year.



















## **Curriculum Vitae**

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#### **EDUCATION**

10/14 - 02/19	<b>Ph.D</b> . Dual degree from University of Göttingen, Germany and Bangor University, UK	
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08/02 - 07/09	B.S. and M.S., Biology, St Petersburg University, Russia	
GRANTS AND FELLOWSHIPS		

- Endeavor Research Fellowship, Australia
- Erasmus Mundus Joint Doctorate Scholarship, Forest and Nature for Society (FONASO), EU
- Fulbright Scholarship, Fulbright Graduate Students Program. Two years Master's program scholarships, USA.

### **RESEARCH EXPERIENCE**

10/14 – 12/17	Researcher in University of Göttingen, Germany
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PURI ICATIONS	

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