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Spatial determinants of habitat use, mortality and connectivity for elephant populations across southern Africa

by

Carrie Lynn Roever

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Spatial determinants of habitat use, mortality and connectivity for elephant populations across southern Africa

Student:	**Carrie Lynn Roever**
Supervisor:	**Professor Rudi J. van Aarde** Conservation Ecology Research Unit Department of Zoology & Entomology University of Pretoria Hatfield, South Africa 0083 rjvaarde@zoology.up.ac.za
Department:	Department of Zoology & Entomology
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Dedication

I dedicate this thesis to my dad, Jerry Roever.

Abstract

Southern Africa contains 58% of the world's savannah elephant population, yet 72% of their range occurs outside of protected areas. It is, therefore, important to develop management guidelines that satisfy the needs of both elephants and people while maintaining environmental heterogeneity and ecosystem processes. Managing elephants as a metapopulation may provide the solution. The goal of this thesis was then to use a habitat-based approach to identify landscape characteristics which could contribute to the functionality of a metapopulation for elephants.

Using resource selection function models, I identified habitat suitability for elephants across southern Africa and used these models to evaluate whether current habitat configurations allow for the assumptions of connectivity and asynchronous population dynamics required by a metapopulation. I found that water, tree cover, slope, and human presence were important predictors of elephant habitat selection. Furthermore, functional responses in habitat selection were present across space and time for water and tree cover, showing the adaptability of this generalist species to resource heterogeneity.

Using habitat selection along with circuit theory current flow maps, I then found a high likelihood of connectivity in the central portion of our study area (i.e. between the Chobe, Kafue, Luangwa, and Zambezi cluster). Main factors limiting connectivity were the high human density in the east and a lack of surface water in the west. These factors effectively isolate elephants in the Etosha cluster in Namibia and Niassa clusters in Mozambique from the central region. Models further identified two clusters where elephants might benefit from being managed as part of a conservation network, 1) northern Zambia and Malawi and 2) northern Mozambique.

Incorporating information on elephant mortalities in northern Botswana into habitat selection estimations, I found that source habitats for elephants occurred within the central Okavango Delta region and sink habitats were associated with periphery of the study area where human use was highest. Eighty percent of elephant mortalities occurred within 25 km of people. The protected designation of an area had less influence on elephant mortality than did the locations of the area in relation to human development. To exacerbate human-elephant conflicts, people tended to settle in areas of high-quality elephant habitats, creating resource competition between elephants and people. Consequently, elephant mortality near humans increased as a function of habitat suitability, and elephants responded by using less suitable habitats. While humans occupied only 0.7% of the study area, mortality and behavioural effects impacted 43%.

Based on the habitat factors examined here, elephants in southern Africa could be managed as a metapopulation if (1) connectivity is maintained and encouraged and (2) spatial heterogeneity in resources and risks serves to stabilize elephant demography. This habitat-based system of management could serve to alleviate unstable elephant populations in southern Africa and create more natural, self-sustaining regulatory mechanisms.

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I would also like to thank all of the funders that contributed to the elephant program over the last 15 years. Without you, the massive amounts of elephant telemetry data, aerial survey data, and GIS layers that went into this thesis would not have been possible. I am also thankful for the personal funding generously provided by Conservation International's Africa Wilderness Programme, the International Fund for Animal Welfare, the Peace Park Foundation, the University of Pretoria, and the US Fish and Wildlife Service.

Finally, I would like to thank my family. Even though they were sad to see me travel so far from home, their unwavering support and occasional care-packages containing reminders of home were always with me.

Disclaimer

This thesis contains four manuscripts (Chapters 2-5), prepared for submission to different peer-reviewed journals. Chapter 2 has been published in *Ecography* (2012; 35, 972-982), and Chapter 3 has been published in *Biological Conservation* (2013; 157, 128-135). For consistency, styles and formatting for all Chapters follow the requirements for the journal *Biological Conservation*. I hereby declare all the work to be my own and that I have acknowledged all those that helped me and contributed in producing this thesis.

Carrie L. Roever

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Chapter 1. General Introduction

Wildlife population management is often a central component of both theoretical and applied ecological research. Ecologists are confronted with problems of augmenting small, isolated populations (e.g. Hedrick and Fredrickson 2010; Meretsky et al. 2000) and of reducing large populations that are damaging their resource base (e.g. Fortin et al. 2005; McCullough et al. 1997). With African savannah elephants (*Loxodonta africana*), both of these problems occur; populations that are exposed to poaching can quickly become diminished (Barnes 1999; Barnes and Kapela 1991; Ntumi et al. 2009); whereas, those in protected parks that are given supplemental water can boom and alter woodland structure (Asner et al. 2012; Dunham 1988; Skarpe et al. 2004). Managing elephant population demography then becomes costly and time consuming for managers and can place stress on the animals through culling, relocation, and immunocontraception (i.e. Kerley and Shrader 2007; Pimm and van Aarde 2001; van Aarde et al. 2006).

To alleviate some of these management issues, the idea of managing elephants as a metapopulation was first introduced by van Aarde and Jackson (2007). The metapopulation theory was first developed for small, discrete, and isolated populations (Hanski 2004), but has since grown into a potential management scheme to regulate populations and maintain connectivity. For large mammals, the metapopulation concept relies on having discrete local breeding populations with asynchrony in demography and dispersal between populations (Driscoll 2007; Olivier et al. 2009). Source populations supplement the mortality in sink areas, resulting in a net stable population (Pulliam 1988; van Aarde and Jackson 2007). Managing large mammals in this manner is rare due to their large spatial requirements (Olivier et al. 2009), but in southern

Africa, the spatial location of parks and the large roaming distances of elephants make this idea feasible (van Aarde and Jackson 2007). However, Armstrong (2005) noted that managing wildlife populations based on metapopulation theory alone could result in a failure to identify positive management strategies and potentially make erroneous management recommendations. For instance, ignoring the quality of habitat patches might cause patches of poor quality to be incorrectly included in the metapopulation network (Armstrong 2005; Battin 2004). Armstrong (2005) therefore recommends a metapopulation concept be integrated with a habitat-based approach, to ensure appropriate management of species across broad spatial scales.

Integrating the metapopulation concept with a habitat-based approach first requires a basic understanding of habitat utilization by elephants. While much research has been done to describe the resource requirements of elephants, these studies have generally focused on selection at a single location (e.g. de Knegt et al. 2011; Vanleeuwe 2010) or for a single habitat feature (e.g. Loarie et al. 2009; Smit and Ferreira 2010; Young et al. 2009). However elephants are habitat generalists, whose wide ecological tolerances make them well suited to survive in a variety of habitat conditions. Across southern Africa, elephants occur in the deserts of northern Namibia to the mesic forests of Mozambique (van Aarde et al. 2008). Under these varying conditions, habitat selection is expected to change as a function of local resource availability. Selection for water, for example, may be an important predictor of elephant habitat selection in arid environments or in the dry season when water is limited, but as water increases on the landscape, it may become a poor predictor of habitat selection patterns. When habitat selection changes as a function of the availability of a resource, this is known as a functional response (Boyce and McDonald 1999; Mysterud and Ims 1998). While functional responses in habitat selection can be a hindrance to the applicability of these models at the local scale, they provide insights into limiting and key resources at large spatial scales when selection is examined across a gradient of resource availabilities (Boyce and McDonald 1999; Gillies et al. 2006; McLoughlin et al. 2010). Using the information gained from habitat selection estimations, habitats can then serve as a foundation to answer a variety of ecological questions pertaining to the feasibility of the metapopulation concept for elephants across southern Africa.

A key criterion for the existence of a metapopulation is dispersal between sub-populations (Driscoll 2007; Olivier et al. 2009). Yet dispersal is often difficult to quantify for wildlife, largely because long-distance dispersal events are rare (Hoffman et al. 2006; Sutherland et al. 2000). Generally only a few individuals within a population carry telemetry collars, further decreasing the odds of observation. Yet using information gained for habitat selection models, we can identify areas of potential connectivity based on habitat requirements. If, for example, we know that elephants need to be close to water and far from people, we can use this information to create a probabilistic model of habitat use, called a resource selection function (Manly et al. 2002). This probability surface can then be used to analyzed landscape connectivity to identify the path of least resistance between two inhabited areas using least cost path analysis (Chetkiewicz and Boyce 2009) or, going further, to identify the permeability of habitats across the entire study area using circuit theory (McRae et al. 2008). Habitats then become the foundation for connectivity in a spatially-structured metapopulation, identifying important corridors or barriers to dispersal. Areas of high connectivity can be given priority for future research, and considerations can be made to manage these areas collectively.

While habitat selection is an important predictor of elephant distribution across the landscape, mortality also plays a vital role in both the habitat and metapopulation concepts. Habitat selection alone does not yield increased survival and fitness. If the habitat is an ecological trap, for example, animals may be attracted to a habitat which ultimately increases their mortality risk (Battin 2004). Invariably, habitat selection studies try to identify high-quality habitats; those that are used by the species, enhance their lifetime survival and recruitment, contribute to demographic performance, and incur limited mortality risk. However, habitat selection studies often fall short on all but the first objective, unless critical life history parameters are also incorporated (Nielsen et al. 2006). This integration is necessary in linking the habitat-based approach to a second criterion of metapopulations, asynchronous population dynamics. Heterogeneity in habitat quality and mortality risk across the landscape creates population sources (high use, low mortality), sinks (high use, high mortality), and non-habitat (low use). The interplay between these habitat classes is ultimately what leads to population stability in a metapopulation. While this asynchrony in dynamics has been observed in elephant populations in different parks and protected areas (Olivier 2009), the next step is to link these demographic observations to the habitat components that regulate population processes. Then, habitat heterogeneity becomes a central component promoting net stable population growth within a metapopulation.

Using a habitat-based approach, critical assumptions of the metapopulation theory can be tested, but in reality the landscape is also inhabited by humans. For many large mammal species, including elephants, humans play an integral role in species distribution (Morrison et al. 2007), and our tolerance or intolerance of a species ultimately plays a large role in species persistence (Woodroffe 2000; Woodroffe et al. 2005). Humans contribute to direct changes in habitat suitability (Hoffman and O'Riain 2012), fragmentation (Crooks 2002), mortality (Nielsen et al. 2004), and indirect changes in animal behaviour (Harju et al. 2011). Humans and wildlife may also be in direct competition for resources or for space, which could result in increased human-wildlife conflict. These cumulative pressures imposed by humans will likely play an integral role in the success or failure of the metapopulation concept for elephants in southern Africa. Understanding how human distribution on the landscape influences elephant habitat use and mortality is necessary to insure effective elephant management, particularly if human populations continue to increase.

Management of any wildlife species is ultimately complex and requires inputs from a variety of information sources. In the past, managers often relied on expert opinion and common sense to design population targets and conservation plans, but as our knowledge of wildlife systems increase, these methods are proving insufficient. Worldwide, wildlife is encountering threats from many sides; habitats are being fragmented, human populations are increasing, and global climate change is creating unknown future environments. Consequently, ecologists are increasingly using advanced modelling techniques to inform management actions. This thesis attempts to inform one such management plan for elephants.

In this study, I will use habitat selection theory to test the feasibility of managing elephants as a spatially-structured metapopulation in southern Africa. Following this general introduction, chapters in this thesis are organized into independent papers, two of which have been published (Chapter 2 and 3). I begin by describing elephant habitat selection across southern African and examine functional response to resource availability (Chapter 2). I use these models as a foundation to next examine connectivity between elephant populations (Chapter 3). Mortality also plays a role in the functionality of habitat, so I then examine the habitat associations of elephant mortalities in northern Botswana using elephant carcass data (Chapter 4). Finally, I then explore the consequences of human-elephant competition for resources (Chapter 5). Taken together, this works forms the first steps towards creating a habitat-based management plan for elephants in southern Africa using metapopulation theory.

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Chapter 2. Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant

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Abstract

Resource selection function (RSF) models are commonly used to quantify species/ habitat associations and predict species occurrence on the landscape. However, these models are sensitive to changes in resource availability and can result in a functional response to resource abundance, where preferences change as a function of availability. For generalist species, which utilize a wide range of habitats and resources, quantifying habitat selection is particularly challenging. Spatial and temporal changes in resource abundance can result in changes in selection preference affecting the robustness of habitat selection models. We examined selection preference across a wide range of ecological conditions for a generalist mega-herbivore, the savannah elephant (*Loxodonta africana*), to quantify general patterns in selection and to illustrate the importance of functional responses in elephant habitat selection. We found a functional response in habitat selection across both space and time for tree cover, with tree cover being unimportant to habitat selection in the mesic, eastern populations during the wet season. A temporal functional response for water was also evident, with greater variability in selection

during the wet season. Selection for low slopes, high tree cover, and far distance from people was consistent across populations; however, variability in selection coefficients changed as a function of the abundance of a given resource within the home range. This variability of selection coefficients could be used to improve confidence estimations for inferences drawn from habitat selection models. Quantifying functional responses in habitat selection is one way to better predict how wildlife will respond to an ever-changing environment, and they provide promising insights into the habitat selection of generalist species.

Introduction

Understanding the complex, dynamic interaction between species occurrence and habitat is essential to predict and manage responses of species to natural or anthropogenic environmental changes. Some ecologists therefore rely on resource selection function (RSF) models to quantify these species/habitat interactions. RSF models compare samples of used and available resource units to estimate the relative probably of occurrence based on resource characteristics (Boyce et al. 2002; Manly et al. 2002). This multivariate approach is becoming progressively more flexible and can incorporate cumulative effects for human development (Houle et al. 2010), intraspecific competition (McLoughlin et al. 2010), and predation (Hebblewhite et al. 2005). RSF models can also be used to inform conservation management decisions because they offer spatially explicit and predictive models of species occurrence (e.g. Aldridge and Boyce 2007; Johnson et al. 2004). Knowledge of habitat selection is integral for habitat protection and augmentation (Aldridge and Boyce 2007; Johnson et al. 2004), the reestablishment of species to previously unoccupied habitat (Merrill et al. 1999), and the identification of dispersal corridors (Chetkiewicz and Boyce 2009) as well as attractive sinks (Nielsen et al. 2006). Such knowledge may aid in conservation planning that aims to ensure the viability of a population, the connectivity among sub-populations in a metapopulation, or restore the spatial structuring of populations (e.g. van Aarde and Jackson 2007).

One of the main limitations of RSF models, however, is that the estimate of selection is contingent upon the sample of availability (Beyer et al. 2010). For example, if use of a resource remains constant but local availability decreases, then the parameter estimate will change from avoidance to selection. In a habitat selection framework, this is known as a functional response (Mysterud and Ims 1998). Functional responses in habitat selection can be an artifact of sampling intensity (see Beyer et al. 2010), however they can also be driven by behavioural changes is selection. As a resource becomes more scares on the landscape, an animal needing to meet some daily requirement, be it nutritional, physiological, or social, must spend a disproportionate amount of time utilizing that resource. Consequently, selection for a resource changes as a function of its availability. The presence of a functional response severely limits the application of an RSF model created for one location to a different area where availability is not equivalent (Beyer et al. 2010; Boyce et al. 2002; Manly et al. 2002). Under natural conditions resources are seldom equally available across the distributional range of a species. RSF models therefore are typically not applied beyond the bounds of a study area unless independent validation data exists and, when they are, caveats are stipulated. Models that are accurate outside of the study area are hailed as robust (Boyce et al. 2002; Wiens et al. 2008). Spatially robust models most often occur for habitat specialists, where species/habitat associations are simple and resilient to changes in availability (Boyce et al. 2002).

Temporal variation in resource availability can also limit the predictive ability of habitat selection models (Wiens et al. 2008). Seasonality in resource abundance, even within the same region, can alter the selection patterns of a species as food preferences change (Boyce et al. 2002). Habitat specialists may be less sensitive to seasonal changes as they are often tied to a single food source or habitat type. For example, northern spotted owls in California are always closely associated with mature forest (Meyer et al. 1998), and wolverines are closely associated with high-elevation subalpine habitats (Copeland et al. 2007). Conversely, a generalist species like grizzly bears have vast shifts in diet (Munro et al. 2006), and consequently habitat selection preferences change as seasons change (Nielsen et al. 2002).

So what do ecologists do when confronted with a generalist species where habitat associations are more complex? Boyce et al. (2002) suggest that selection by generalist species be analyzed across a range of environmental conditions, to quantify how selection changes as a function of availability. Instead of being viewed as problems to be overcome, functional responses can instead be used to predict selection in different regions where resources abundance varies (Boyce et al. 2002; Matthiopoulos et al. 2011). To incorporate a functional response into an RSF model, a random coefficient in a mixed-effects model can be used (Gillies et al. 2006; McLoughlin et al. 2010); however, a random coefficient can only be applied to one habitat covariate within a model. For many generalist species, a functional response is present for more than one habitat covariate; therefore, separate models are required for each sub-population (Boyce et al. 2002; Nielsen et al. 2002). The use of separate models also allows one to use the information theoretic approach to determine whether different habitat covariates are important in different regions or seasons (Burnham and Anderson 2002).

Despite the call to study multiple populations of generalist species to better understand patterns in habitat selection, this advice is rarely followed, largely due to the data requirements for such an analysis. In this paper, we examine habitat selection of a generalist herbivore species, the African savannah elephant (*Loxodonta africana*), among seven populations in eight countries across southern Africa. Elephants are ideally suited for a study on functional responses in habitat selection because they are widely distributed across southern Africa where they occupy landscapes ranging from the deserts of Namibia to the dense, wet forests of Mozambique. Their diets also vary seasonally; individuals shift from mainly grazing on tender grasses in the wet season to mainly browsing on the leaves, twigs, branches, and bark of trees in the dry season (Codron et al. 2011).

Here, we develop habitat selection models at the scale of the home range that includes factors elephants are known to respond to: water (de Beer et al. 2006; Harris et al. 2008), slope (Wall et al. 2006), vegetation structure (Harris et al. 2008; Loarie et al. 2009; Young et al. 2009), and human presence (Harris et al. 2008; Hoare and du Toit 1999; Jackson et al. 2008). We test for differences in male and female selection in the wet and dry seasons using the information theoretic approach to first quantify support for competing models. Then using the full model, we examine how the selection coefficients changed as a function of availability within an individual's home range (Hebblewhite and Merrill 2008; Houle et al. 2010). Our main objective was to quantify spatial functional responses, examining temporal functional responses only at a course, two-season scale. Specifically, in the more arid, western portion of the study area, we expect water and tree cover to be important covariates in habitat use in response to the limited availability of water (Leggett 2006) and the shortage of trees that provide shade (Kinahan et al. 2007) and offer some forage for elephants (Loarie et al. 2009). In the more mesic, eastern portion of the study area, we expect elephant's selection of tree cover to be unimportant for selection because trees are more plentiful and should, consequently, not limit elephant selection (Illius 2006; Mysterud and Ims 1998). We further expect a functional response to human presence, as elephants often come into conflict with people (Hoare 1999; Jackson et al. 2008). Thus, elephants in more remote areas would show greater indifference to human presence.

Methods

Study Area

The study area comprised a large portion of the distributional range of elephants in southern Africa and included portions of Angola, Botswana, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe (Figure 2-1). The region included a desert/grassland mosaic in the west, dry woodlands in the central region, and mesic forest in the east. Seasonal rainfall patterns drive vegetation structure (Sankaran et al. 2005). Mesic regions to the east had greater rainfall and hence greater tree cover compared to western portion of the study area (Table 2-1). Topographic conditions also varied, with more dramatic changes in elevation near the western and eastern coasts and relatively flat, unvarying terrain in the central region. Human density was low over much of the study area, with pockets of increased human densities near major waterways and roadways.

Elephant Data

Elephants (n=102) were captured and collared with Africa Wildlife Tracking GPS collars (model SM 2000E; Africa Wildlife Tracking, Pretoria, South Africa) between December 2002 and September 2010. Collars were programmed to relocate individuals at varying intervals, ranging from 1 to 24 hours, with most elephants having multiple interval settings during the collaring period. Telemetry locations were divided into two seasons and combined across years. Core wet season was defined as December through March inclusive, and core dry season was defined as June through September (Young et al. 2009). Locations in the transition months of April, May, October, and November were omitted from the analysis. Only individuals with more than 100 locations per season were retained for the analysis, resulting in 35,167 locations among 86 individuals for the dry season and 43,141 locations among 88 individuals for the wet season analysis.

Home ranges were generated separately for the core wet and dry season for each individual using the local convex hull (LoCoH) nonparametric kernel method (Getz et al. 2007). The adaptive sphere of influence (*a*-LoCoH) algorithm was used to construct kernels, with *a* equal to the furthest distance between any two locations (Getz et al. 2007). LoCoH home ranges, which ranged in area from 50 to 9,000 km^2, fit tightly around telemetry locations often leaving holes, which we believed were unrealistic. To reduce these holes, home ranges were further buffered by 3 km, the mean distance elephants within our study traveled during a 12 hour period. Home ranges were created using R software (R Development Core Team 2011), along with the packages “adehabitat” (Calenge 2006) and “NNCH” (Getz and Wilmers 2004).

The majority of elephants within this study roamed freely and were not confined to parks, countries, or other intangible human boundaries (van Aarde and Ferreira 2009). However, fences were present along the borders of Etosha National Park and along international boundaries in Khaudum Game Reserve and Kruger National Park. For analytical purposes elephants were grouped by study site, hereby referred to as populations, resulting in seven populations: Etosha, Chobe, Kafue, Zambezi, Luangwa, Niassa, and Limpopo (ordered from west to northeast, with the most distant population, Limpopo, last; Figure 2-1). Population names were often based on the nearest major protected area for convenience.

Habitat Covariates

Habitat covariates were chosen based on their known or suspected influence on elephant space use. In order to ensure that direct comparisons could be made among models, habitat was described using covariates that could be applied to all populations, thereby avoiding site-specific variables such as categorical land cover descriptors. The structure (Harris et al. 2008; Kinahan et al. 2007) and greenness (Loarie et al. 2009; Young et al. 2009) of vegetation is known to be an important predictor of elephant space use because it provides both food and shade. Vegetation structure was characterized using the Moderate Resolution Imaging Spectrometer (MODIS) Vegetation Continuous Fields product (Hansen et al. 2006), from which we estimate the proportions of tree cover at a resolution of 0.25 km^2, defined as woody vegetation greater than 5 m in height (Hansen et al. 2002). An enhanced vegetation index (EVI) was used to quantify greenness (Pettorelli 2006). For the core wet and dry seasons, EVI layers for the 8 years of this study were obtained and used to calculate mean EVI within a season at a resolution of 0.64 km^2.

Water was located using geospatial data from Tracks4Africa (2010) and man-made watering point data supplied by conservation authorities. Water body locations were then validated against Landsat imagery, and missing water bodies were hand-digitized. Separate water layers were made for each season, with the core wet season including all water categories and the core dry season including only main rivers, river deltas, lakes, dams, and man-made watering holes. Distance to water was then calculated for telemetry locations within each season.

Elephants typically avoid humans and human disturbance (Harris et al. 2008; Hoare and du Toit 1999), particularly during daylight hours when humans are more active (Jackson et al. 2008). We included several covariates that reflect the land-use patterns of people. Human density was estimated with LandScan (2008) human population data at a resolution of 1 km^2. Hoare and du Toit (1999) found that elephants avoided areas with greater than 15.6 people/ km^2; therefore, we identified areas with greater than 16 people/ km^2 (rounding up) and calculated the distance from each elephant location to these pixels. Road data were obtained from Tracks4Africa (2010). Studies of other large mammals have shown an avoidance of high-traffic volume roads but neutral or positive selection for low-traffic volume roads which potentially facilitate movement (Chruszcz et al. 2003; Dickson et al. 2005); therefore, roads were categorized based on size. We determined distances of locations to main roads (freeway, national, or main roads) and secondary roads (all other road categories).

Finally, elephants avoid steep slopes due to their large body size (Wall et al. 2006), so we included slope derived from a 90 x 90 m resolution digital elevation model (Jarvis et al. 2006) in our analyses. All geospatial analysis was completed using the Spatial Analyst extension of ArcGIS 9.3.1 (ESRI 2009) and Geospatial Modelling Environment (Beyer 2011).

Habitat Selection Models

Habitat selection was modelled separately for the seven elephant populations and for males and females, with one collared female actually representing a breeding herd with several adult females and their offspring. Elephant locations (1) were compared to randomly generated locations (0) using a mixed effect logistic regression model for location *i* and individual *j*, taking the form:

$$w(x_{ij}) = \exp(\beta + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_j), \tag{1}$$

where $w(x_{ij})$ is the resource selection function, β_n is the coefficient for the *n*-th predictor variable x_n , and γ is the random intercept for animal *j* (Gillies et al. 2006; Manly et al. 2002). The random intercept was used to control for the lack of independence of points within individuals and differences in sample size among individuals (Gillies et al. 2006). We implemented a design III approach (Manly et al. 2002; Thomas and Taylor 1990), whereby random locations were generated within the home range of each elephant at a density of 3 points/km^2. At this density, contamination (i.e. use and available locations occurring within the same raster pixel) was less than 15% for the habitat covariate mapped at the coarsest resolution (800 x 800 m), and was therefore negligible (Johnson et al. 2006).

We used model selection (Burnham and Anderson 2002) to determine which habitat covariates had the greatest influence on resource selection for each of the seven populations. Seven a priori candidate models were ranked using Bayesian Information Criterion (BIC; Table 2-

2). BIC was used as it favours more parsimonious models compared to Akaike's Information Criterion (AIC), which favours complex models when sample sizes are large (Burnham and Anderson 2002; Grueber et al. 2011). Variables that were highly correlated (Pearson's $r > 0.6$) were not included in the same model. Correlations occurred between tree cover and mean EVI (Pearson's $r = 0.68$). Because tree cover is an indicator of both food resources and thermoregulatory needs (i.e. shade cover; Kinahan et al. 2007), tree cover was used in subsequent models. All continuous variables were tested for the potential presence of a nonlinear relationship with the inclusion of a quadratic term in a univariate analysis and by examining histograms. Model fit of the top-ranked model for each population was evaluated using k-fold cross validation ($k = 5$) and the Spearman rank correlation coefficient (Boyce et al. 2002). Analyses were conducted in R software (R Development Core Team 2011) using the lme4 package (Bates and Maechler 2010).

To test the presence of functional responses, we used a two-step approach (Hebblewhite and Merrill 2008; Houle et al. 2010). First we model habitat selection for each individual, so that all covariates could vary in slope and intercept, using the full model (model 7, Table 2-2). We then assessed how the selection coefficient of a given covariate changed as a function of the mean value of that covariate within the individual's home range (log transformed). Significance was evaluated using a linear regression. Where models displayed heterogeneity of variance, generalized least squares were used instead of a simple linear regression (Zuur et al. 2010). This procedure could only be applied to covariates with linear selection coefficients (i.e. slope, proportion tree, distance to people, and distance to main roads).

Results

Dry Season RSF Models

The top-ranked model was the full model (model 7) for all female and most male (4 of 6) populations during the dry season (Table 2-3). The top models provided good fit to the data using k-fold cross validation expect for Niassa females (Spearman rank $r_s = 0.48$, and $p > 0.05$) and Chobe males ($r_s = 0.62$, and $p > 0.05$; Table 2-3). The inclusion of all variables in most top-ranked models was counter to our expectations that selection for some covariates would be less important as availability changed. This indicated that all variables examined in this study were important to elephant habitat selection irrespective of availability during the dry season. The strength and direction of covariates was consistent across most populations in the top-ranked models. Elephants from most populations selected areas of low slope (female (f) = 5 of 7, male (m) = 4 of 6), high tree cover (f = 7 of 7, m = 3 of 6), far distances from people (f = 4 of 7, m = 4 of 6), and close proximity to main road (f = 3 of 7, m = 5 of 6; Table 2-4). Populations varied in the maximum distance elephants traveled from water, ranging from 6 km in the Zambezi to 79 km in the Chobe population. Despite this, elephants in most populations (f = 4 of 7, m = 5 of 6) selected areas near and far from water at greater frequencies than random (Table 2-4; Figure 2-2). This U-shaped pattern is what I expected as animals select areas near water for drinking and temperature regulation and far from water in search of forage. Only Niassa females selected areas of intermediate distances from water during the dry season (i.e. the selection coefficient had a hump-shaped curve). Selection for secondary roads was less consistent across populations. Males and females in Niassa and Limpopo along with Etosha females and Chobe males selected areas of intermediate distance from secondary roads; whereas, the elephants from the remaining populations selected areas near to secondary roads or areas both near and far from these roads.

Wet Season RSF Models

In the wet season, Etosha, Chobe, Kafue, and Zambezi populations continued to have the full model (model 7) as the top-ranked model for both sexes (Table 2-3). However, among the more easterly populations, Luangwa, Niassa, and Limpopo, the top-ranked model was the limiting factors model (model 6) for those females and for Limpopo males. Of these eastern populations, only Luangwa males had a top-ranked model that included tree cover, indicating that during the wet season tree cover was not an important predictor of elephant habitat selection in these populations. This was concurrent with our expectations that tree cover would be less influential for elephants in more mesic environments. The top models provided good fit for most populations during the wet season; however, model fit was poor for Niassa females and males ($r_s = 0.61$ and 0.03, respectively, and $p > 0.05$; Table 2-3). Selection for water during the wet season was more variable across populations than it was in the dry season. Luangwa and Limpopo females selected areas both near and far from water, Zambezi and Chobe females selected intermediate distance from water, Kafue and Niassa females selected areas close to water, and Etosha females selected areas far from water. Half of the male populations (3 of 6) selected areas both near and far from water, while the remaining three were variable in selection (Figure 2-2). This variability in selection indicated a functional response to water seasonally. Selection for low slopes (f = 5 of 7, m = 3 of 6), high tree cover (f = 4 of 7, m = 3 of 6), and far from people (f = 4 of 7, m = 3 of 6) was similar to the dry season. However, selection for main roads was counter to dry season selection, with nearly equal numbers avoiding (f = 3 of 7, m = 3 of 6) and selecting (f = 4 of 7, m = 3 of 6) main roads. In the wet season, selection for secondary roads continued to be as variable as it was in the dry season.

Functional Responses

When comparing the selection coefficient for a given covariate to the mean value of that covariate within an individual's home range, we found a significant functional response for proximity to humans during the dry season (R^2 adjusted=0.04, *P* = 0.03; Figure 2-3). As the mean distance from humans increased (i.e. as there were fewer people within the home range) selection for proximity to people decreased. We expected selection for proximity to human to be less significant when elephants were far from human development; however, we did not find this pattern. Instead, we found a general pattern of avoidance when they were far from people and high heterogeneity in the selection coefficient when elephants were close to people.

While the functional responses tested were not significant within a linear regression model for all other covariates examined, the variability of selection coefficients at varying levels of resource abundance indicated similar patterns as observed with the proximity to humans covariate. Because of heterogeneity of variance in the slope and tree cover models, generalized least squares techniques were used. While most elephants selected areas of low slope, when the home range of an individual was located in a relatively flat area, the selection coefficient was more variable (Figure 3). A similar pattern occurred with tree cover. When the proportion of tree cover within an individual's home range was low, the variability in the selection coefficient increased with some individuals having relatively strong selection for trees. Functional responses for distance to main road were not significant during either season and displayed no variance in heterogeneity.

Discussion

Although elephants are generalist mega-herbivores with wide ecological tolerances, we found consistency in their habitat selection patterns, lending insight into the biology of the species.

Elephants in most populations and both seasons had the full model (model 7) as the top-ranked BIC model. This is not unexpected given that for inclusion in BIC models, we considered covariates which relate to some biological process or limiting factor for elephants (e.g. food, water, terrain, and human presence). We did, however, find that in the wetter, eastern populations (Luangwa, Niassa, and Limpopo) tree cover was not an important predictor of elephant use in the wet season, as expected. The decline in the importance of the vegetation covariate suggested a functional response for vegetation, where its importance declines both temporally (within these populations as increased rainfall makes food more readily available) and spatially (across populations as vegetative cover increases). This functional response was not supported when we examined the abundance of tree cover within each individual's home range. However, when we further excluded non-significant selection coefficients from the analysis to reflect their lack of importance in those models, the function response was significant in the dry season ($P = 0.02$).

Our results also revealed evidence of a temporal functional response for water. Water is a limiting factor for elephants, as demonstrated by their close association with watering holes in the dry season (de Beer et al. 2006; Harris et al. 2008; Shannon et al. 2009; Young et al. 2009) and their population increases when supplemental water is provided (Owen-Smith et al. 2006). In the dry season, elephants in most populations (f = 4 of 7, m = 5 of 6) selected areas near and far water; whereas, in the wet season, selection for water was highly variable, with individuals selecting areas near, far, and at intermediate distance from water (Figure 2-2). The change in selection for water as a function of season suggests a functional response, as higher rainfall during the wet season results in greater abundance and wider distribution of water throughout the study area. However, we did not find a spatial functional response for water as expected. The more mesic, eastern populations had similar selection patterns for water in the dry season, indicating that water was a limiting factor, even in these wetter regions.

Selection for low slopes, high tree cover, and far distance from people was consistent across populations and seasons and was similar to previous studies of elephant selection patterns (see Harris et al. 2008; Hoare and du Toit 1999; Kinahan et al. 2007; Loarie et al. 2009; Wall et al. 2006). The real ecological insight gained from studying elephant selection across a large spatial scale, however, comes from the heterogeneity of variance displayed in the functional responses. Previous research into function responses of habitat selection has not reported such heterogeneity in variance. This could be an artifact of low sample size, as most studies have few individuals along the continuum of available abundance (see Hebblewhite and Merrill 2008; Houle et al. 2010). However, heterogeneity of variance in habitat selection should be expected for some habitat covariates. Slope, for example, does not limit elephant movement when the home range is situated in a relatively flat area. As a result, we found high variability in the selection coefficients in these locations. When elephant home ranges occur in regions of high topographic variation, slope became a limiting factor and, consequently, the selection coefficients were consistently negative (i.e. elephants selected flat areas; Figure 2-3).

One of the main criticisms of RSF models is that they are limited in their ability to make predictions in different areas or at different times (Garshelis 2000; Manly et al. 2002). Some authors contend that using information gained about functional responses in selection could help remedy this problem (Boyce et al. 2002; Matthiopoulos et al. 2011; McLoughlin et al. 2010). For elephants, selection at the scale measured in this study was relatively consistent and the measured functional responses were not significant; consequently, we do not believe that the function responses discovered here could be used towards those ends. However, researchers could use information about heterogeneity of variance to better estimate the confidence around habitat selection models applied to new regions, especially when no data on animal use is available. If, for example, an area was relatively flat in slope or was in close proximity to human development, one would expect much more variable selection patterns and less accurate estimates of habitat selection for elephants based on the functional responses observed in this study.

Among the covariates examined, the human presence covariates were least consistence across populations. While elephants generally avoided humans, variability in selection increased as individual home ranges were in closer proximity to people (Figure 2-3). Selection for road covariates was also variable between populations (Table 2-4a,b). This variability in elephant selection was counter to our expectations that humans would have little influence on selection when elephants were far from people. However, the variability in selection for human-use features is not an uncommon pattern in selection by generalist species where humans are both a source of food and a potential threat, and likely indicates that individual elephants were using different strategies when near human development. In grizzly bears, for instance, some individuals become habituated to human food sources or use human settlements as a refuge from more dominant individuals (Mattson et al. 1992; McLellan and Shackleton 1988), while others avoid humans due to the increased mortality risk (Gibeau et al. 2002; Wielgus and Vernier 2003). Human-use features may also co-occur with areas preferred by wildlife, such as near rivers and the more fertile floodplains (Roever et al. 2008). Roads within protected areas, for example, are often established along the best game viewing routes, such as near rivers and watering holes. The threats posed to elephants by roads within protected areas should be minimal (see Blake et al. 2008) and could confound inferences drawn about selection of roads located outside of protected areas. Spatial scale is also likely influencing the patterns observed for human use features. Avoidance of humans is likely occurring at a broader spatial scale; whereby, the elephant home range was already situated in a low human-density area (Hoare and du Toit 1999), thus within-home range selection patterns were more variable.

Other variables also display variability, even within the same population. Selection for tree cover, for example, was positive for females in Etosha in both seasons, yet negative for males in both seasons. This variability is selection patterns is likely an artifact of a collaring bias for the Etosha cluster. In the bounds of Etosha NP only females were collared (n = 9 females), and outside of the park boundaries, mostly males (8 of 9) were collared. This shows the sensitivity of RSF models to local resources availability, and that even within close, yet non-overlapping, proximity changes in availability can produce opposing habitat selection patterns. It also further underscores the need to quantify how selection changes and a function of resource availability.

This study represents an amalgamation of habitat selection theory for elephants across southern Africa; however, a study area of this magnitude, particularly in the developing world, creates unique challenges. To make comparisons across regions, the habitat covariates chosen had to be consistent across the study area. Unfortunately, GIS data quality often varies from one country to the next, so while detailed geospatial data were available for South Africa, Namibia, and Mozambique, information was often lacking for Malawi, Zambia, and Zimbabwe. Consequently, we used global datasets which, while excellent in quality, use larger spatial resolution (the smallest being 90 x 90 m for slope but increasing to 500 x 500 m for tree cover). This larger resolution could help explain the poor model fit for Niassa females and Chobe males in the dry season and Niassa females and males in the wet season. Prediction of elephant habitat selection could be improved if fine scale information on vegetation characteristics and the presence of standing water across the seasons were available. As some of the world's most diverse and valuable wildlife resources are in the developing world, efforts should be made to increase the quality of geospatial data in these regions for the betterment of wildlife management.

Studying a generalist species over a wide spatial scale can lend insight into the biology of that species (Boyce et al. 2002), which could be particularly important in predicting changes in animal space-use in this ever-changing world. Our analysis confirms expectations that a generalist mega-herbivore showed a functional response, particularly when the relevant resource was uncommon or limiting (Illius 2006; Mysterud and Ims 1998). We also found that selection by this generalist species is more variable when at different levels of resource abundance, which can be used to better estimate confidence around model predictions. In southern Africa, elephant management strategies are moving towards reinstating a more natural, self-sustaining spatial dynamic through the development of transfrontier conservation areas (see Hanks 2001; van Aarde and Jackson 2007; Western 2003). Current initiatives strive to remove fences around parks, reduce artificial water sources, and promote cooperation between countries, allowing wildlife access to greater and more natural roaming areas. However, information on how elephants will respond to these changes is lacking because experimentation on many large mammal species, particularly those of management concern, is not feasible. Consequently, researchers must work within the context of present-day landscapes, and these conservation initiatives can benefit from relying on our illustrated functional responses to better predict elephant selection within these changing landscapes.

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Table 2-1. General description of some local conditions within each study site (population). The presence of water was calculated independently for the dry and wet seasons. High human use was defined as a human density of > 16 people/km^2 using LandScan (2008) human population data.

Population	Mean slope (degrees)	Mean proximity to water (km)		Mean percent tree cover	Percent area of high human use	Density of roads (km/km^2)	Mean elephant home range (km^2)
		Dry season	Wet season				
Etosha	4.6	10.6	6.2	8.9	0.1	0.07	573
Chobe	0.6	18.5	18.9	10.8	0.8	0.04	1,431
Kafue	1.0	5.6	9.1	18.7	0.5	0.06	482
Zambezi	3.8	2.0	2.3	17.9	21.9	0.20	143
Luangwa	2.3	6.0	5.4	21.0	12.8	0.12	378
Niassa	2.0	19.6	19.0	30.1	27.3	0.02	543
Limpopo	1.9	4.6	4.5	17.5	1.0	0.16	845

Table 2-2. Candidate models considered when assessing habitat selection by elephants across southern Africa. The number of fixed and random parameters (K) is presented.

Model	Model Structure	K
1. Null		2
2. Landscape	Slope + Distance to water + (Distance to water)^2	5
3. Water and Food	Distance to water + (Distance to water)^2 + Proportion tree	5
4. Slope, Water, and Food	Slope + Distance to water + (Distance to water)^2 + Proportion tree	6
5. Human Density	Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	6
6. Limiting Factors	Slope + Distance to water + (Distance to water)^2 + Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	9
7. Full	Slope + Distance to water + (Distance to water)^2 + Proportion tree + Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	10

Table 2-3. The top ranking model using Bayesian information criterion (BIC) for female and male elephant habitat selection in the dry and wet season. Top model weight (w) is presented along with Spearman rank correlation coefficient (r_s) and significance for model fit (*).

	Females				Males			
	Top Model	w	r_s		Top Model	w	r_s	
Dry Season								
Etosha	7. Full	1.00	0.96	*	7. Full	1.00	0.96	*
Chobe	7. Full	1.00	0.96	*	7. Full	1.00	0.62	
Kafue	7. Full	1.00	0.98	*	7. Full	1.00	0.96	*
Zambezi	7. Full	1.00	0.96	*				
Luangwa	7. Full	0.73	0.95	*	5. Human Density	0.95	0.79	*
Niassa	7. Full	0.97	0.48		7. Full	1.00	1.00	*
Limpopo	7. Full	0.82	0.95	*	6. Limiting Factors	0.88	1.00	*
Wet Season								
Etosha	7. Full	0.62	0.98	*	7. Full	1.00	0.84	*
Chobe	7. Full	1.00	0.89	*	7. Full	1.00	0.99	*
Kafue	7. Full	1.00	1.00	*	7. Full	0.95	0.87	*
Zambezi	7. Full	1.00	0.83	*				
Luangwa	6. Limiting Factors	0.99	0.73	*	7. Full	1.00	0.95	*
Niassa	6. Limiting Factors	0.88	0.61		5. Human Density	1.00	0.03	
Limpopo	6. Limiting Factors	0.98	0.89	*	6. Limiting Factors	0.73	0.99	*

Table 2-4. Parameter estimates of the top-ranked BIC model for each population in the dry (a) and wet (b) season. Estimates for which confidence intervals do not cross zero are indicated by *. Missing values (-) occur when a given parameter was not included in the top model.

(a)

	Females						
	Etosha	Chobe	Kafue	Zambezi	Luangwa	Niassa	Limpopo
Slope	-0.12 *	0.39 *	0.24 *	-0.15 *	-0.05 *	-0.03 *	-0.06 *
Distance to water†	-4.10 *	-0.54 *	-0.24	-0.73	-1.41 *	3.18 *	-4.64 *
(Distance to water†)^2	1.10 *	0.12 *	-1.64 *	-4.71 *	0.37 *	-0.70 *	3.58 *
Proportion tree	27.67 *	4.31 *	3.72 *	1.81 *	0.77 *	1.55 *	1.07 *
Distance to humans	0.24 *	0.04	-1.08 *	1.37 *	0.41 *	-0.18	-0.45 *
Distance to main road†	-0.16 *	0.06 *	0.76 *	0.29 *	-0.05	1.27 *	-0.54 *
Distance to secondary road†	1.83 *	-0.20 *	-0.81 *	-7.67 *	-1.58 *	3.88 *	0.86 *
(Distance to secondary road†)^2	-1.28 *	-0.04	0.33 *	8.62 *	0.80 *	-0.73 *	-0.55

	Males					
	Etosha	Chobe	Kafue	Luangwa	Niassa	Limpopo
Slope	-0.12 *	0.15 *	-0.03	-	-0.21 *	-0.20 *
Distance to water†	-0.56 *	-1.08 *	-1.09 *	-	-1.59 *	-2.73 *
(Distance to water†)^2	0.09 *	0.13 *	0.20	-	0.36 *	1.03 *
Proportion tree	-22.74 *	3.72 *	3.42 *	-	2.44 *	-
Distance to humans	0.06 *	0.05	-0.34 *	1.26 *	1.23 *	-0.61 *
Distance to main road†	-0.12 *	-0.12 *	0.04	-0.10	-0.41 *	-0.66 *
Distance to secondary road†	-2.50 *	0.71 *	-2.25 *	-0.16	1.71 *	0.47 *
(Distance to secondary road†)^2	0.58 *	-0.05 *	0.62 *	-0.53	-0.96 *	-0.41 *

† distance measures were in km and multiplied by 0.1 to facilitate model convergence.

(b)

	Females						
	Etosha	Chobe	Kafue	Zambezi	Luangwa	Niassa	Limpopo
Slope	-0.15 *	0.24 *	0.03	-0.17 *	-0.10 *	-0.07 *	-0.10 *
Distance to water†	0.64 *	0.11	-0.51	0.93	-0.39 *	-0.22 *	-0.55
(Distance to water†)^2	0.15 *	-0.04 *	-1.48 *	-1.17	0.16 *	0.01	0.71 *
Proportion tree	7.52 *	2.44 *	2.83 *	1.66 *	-	-	-
Distance to humans	-0.09 *	0.10 *	-0.85 *	1.18 *	0.37 *	-0.52 *	0.15
Distance to main road†	0.03	-0.04 *	0.25 *	-0.11 *	0.07 *	0.69 *	-0.40 *
Distance to secondary road†	-1.00 *	0.34 *	-2.26 *	-5.12 *	-0.67 *	1.08 *	2.98 *
(Distance to secondary road†)^2	0.23 *	-0.04 *	0.67 *	6.04 *	0.21 *	-0.05	-2.11 *

	Males					
	Etosha	Chobe	Kafue	Luangwa	Niassa	Limpopo
Slope	-0.07 *	0.08	0.05	-0.13 *	-	-0.35 *
Distance to water†	-0.29 *	-0.21 *	-0.63 *	-2.77 *	-	0.56
(Distance to water†)^2	0.15 *	0.09 *	0.01	1.51 *	-	-0.34
Proportion tree	-14.80 *	3.39 *	3.11 *	2.25 *	-	-
Distance to humans	0.31 *	-0.13 *	0.15	2.06 *	-0.57 *	-0.03
Distance to main road†	-0.02	0.13 *	-0.32 *	0.22 *	0.01	-0.21 *
Distance to secondary road†	-1.37 *	-0.33 *	-0.20	-2.11 *	1.05 *	0.17
(Distance to secondary road†)^2	0.30 *	0.00	0.05	0.97 *	-0.60 *	-0.41 *

† Distance measures were in km and multiplied by 0.1 to facilitate model convergence.

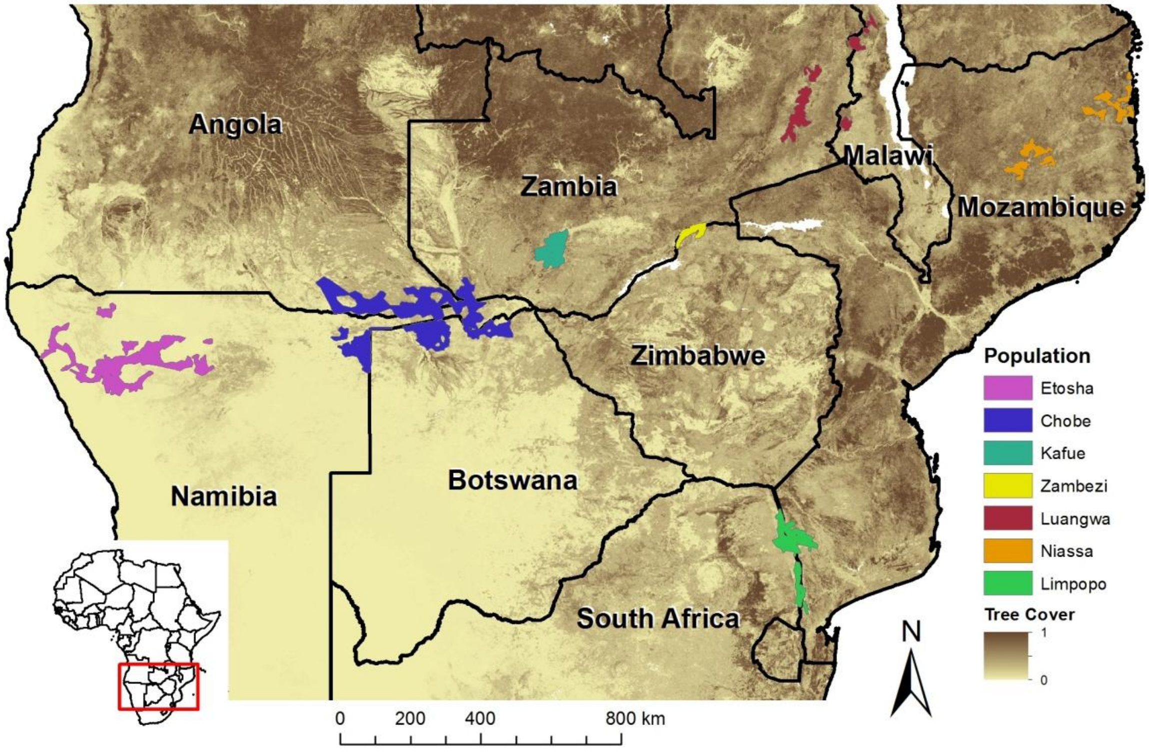

Figure 2-1. Map of the study area located in eight countries in southern Africa. Elephant local convex hull home ranges were grouped into seven populations (Etosha, Chobe, Kafue, Zambezi, Luangwa, Niassa, and Limpopo) based on study site. Proportion of tree cover from no tree cover (0) to complete coverage (1) is presented.

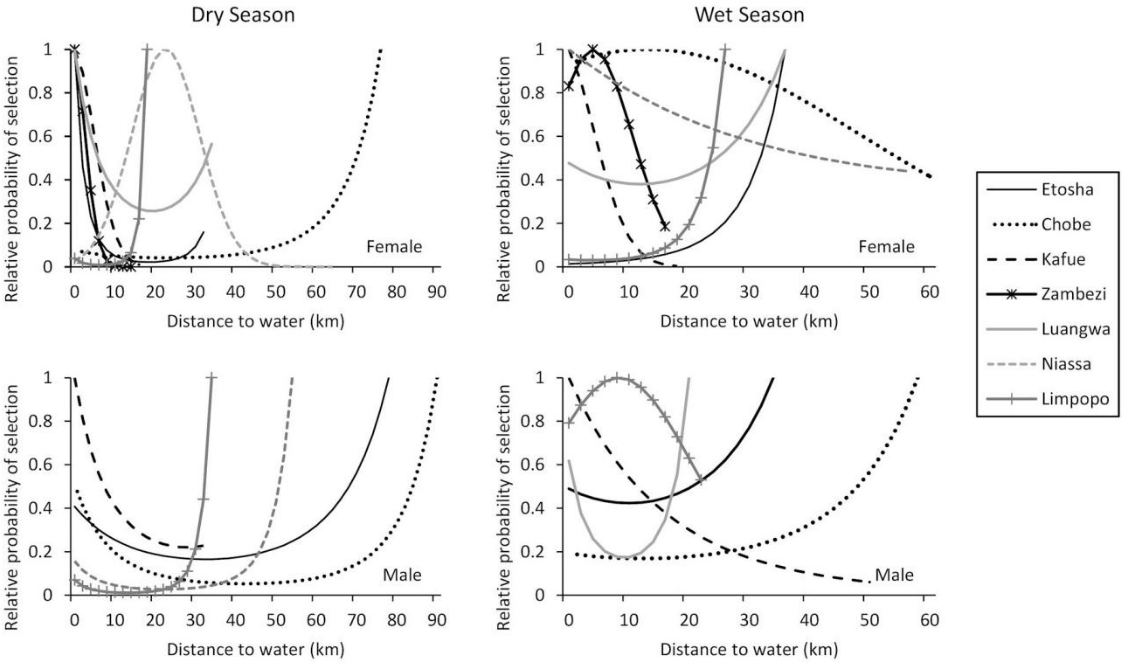

Figure 2-2. Relative probability of selection of water for females and males in the dry and wet seasons as a function of the distance to water. Values for each population are displayed only across the range of distances observed within that population. In the dry season, both male and female elephants had a U-shaped selection, where they selected areas both near and far from water. In the wet season, selection for water showed greater variability across populations for both sexes.

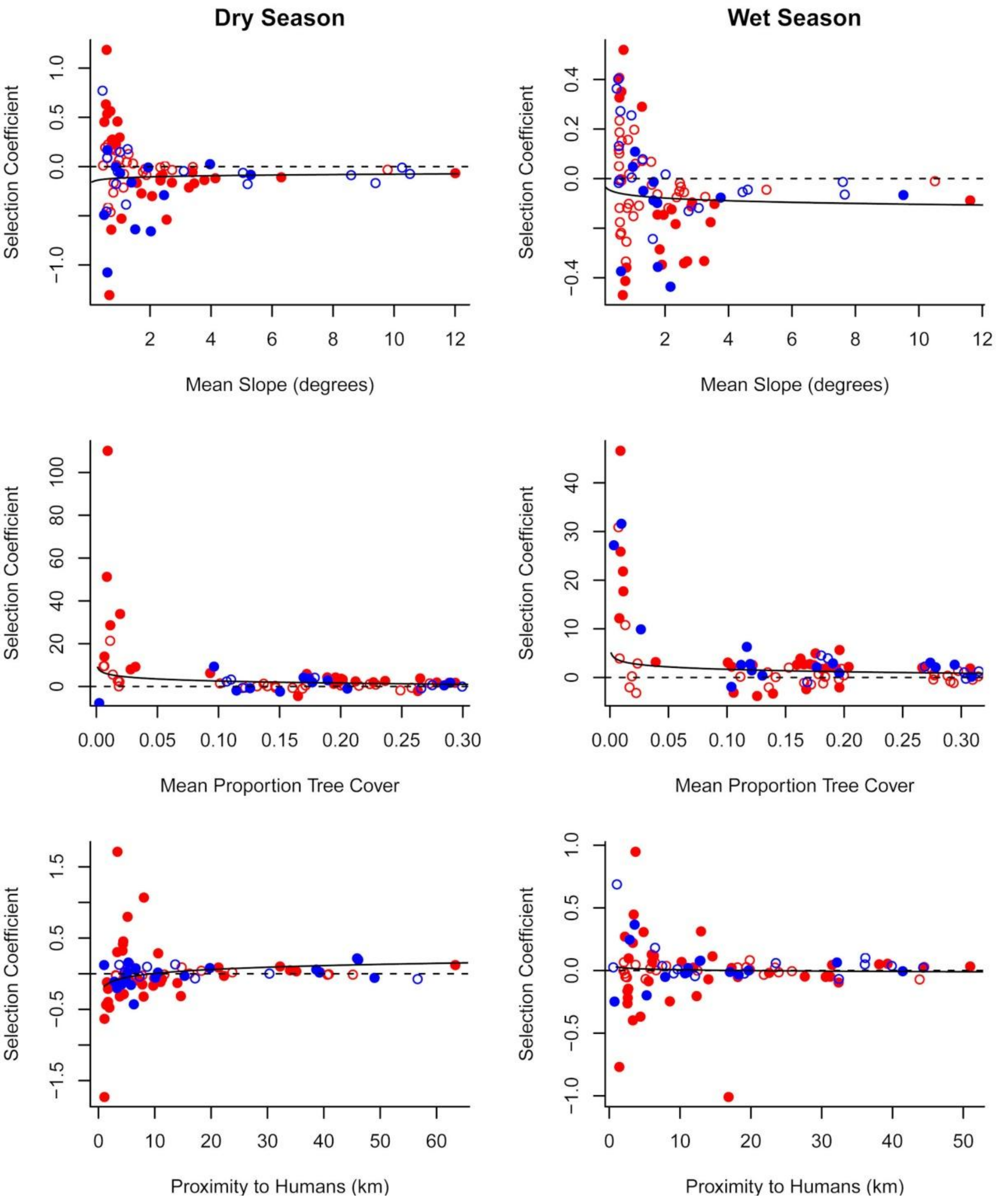

Figure 2-3. Functional responses in habitat selection for female (red) and male (blue) elephants. Selection coefficients were estimated for each individual using a resource selection function model and were modelled as a function of the mean slope, tree cover, or proximity to humans within each home range. Both significant (filled circle) and non-significant (open circle) selection coefficients were modelled. Only the regression for proximity to humans during the dry season was significant (*P* = 0.03).

Chapter 3. Functional connectivity within conservation networks: Delineating corridors for African elephants

Publication Details

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Abstract

Managing multiple parks, reserves, and conservation areas collectively as conservation networks is a recent, yet growing trend. But in order for these networks to be ecologically viable, the functional connectivity of the landscape must be ensured. We assessed the connectivity between six African savannah elephant populations in southern Africa to test whether existing conservation networks were functioning and to identify other areas that could benefit from being included in conservation networks. We used resource selection function models to create an index of habitat selection by males and female elephants. We employed this habitat use index as a resistance surface, and applied circuit theory to assess connectivity between adjacent elephant populations within six clusters of protected areas across southern Africa. Circuit theory current flow maps predicted a high likelihood of connectivity in the central portion of our study area (i.e. between the Chobe, Kafue, Luangwa, and Zambezi cluster). Main factors limiting connectivity across the study area were high human density in the east and a lack of surface water in the west. These

factors effectively isolate elephants in the Etosha cluster in Namibia and Niassa clusters in Mozambique from the central region. Our models further identified two clusters where elephants might benefit from being managed as part of a conservation network, 1) northern Zambia and Malawi and 2) northern Mozambique. We conclude that using habitat selection and circuit theory models to identify conservation networks is a data-based method that can be applied to other focal species to identify and conserve functional connectivity.

Introduction

As the human world becomes more connected, wildlife and wild lands become increasingly fragmented (Crooks and Sanjayan 2006). Historically, the world's biodiversity was preserved through the establishment of parks and protected areas, but current initiatives are moving towards increasing connectivity between these wildlife islands (Hanks 2001; van Aarde and Jackson 2007). The establishment of transfrontier conservation areas (TFCA) and corridors interconnecting multiple protected areas, such as the Kavango-Zambezi TFCA in southern Africa and the Yellowstone to Yukon Corridor in the North America, are an increasing trend. The objectives of these conservation networks differ, but most generally include increasing connectivity or promoting dispersal and migration. Thus once a conservation network has been established, the first step to achieve these objectives is to identify, maintain, and where necessary increase functional connectivity on the landscape (Hanks 2001).

Large mammals are of particular interest for conservation networks because these species operate at broad spatial scales and consequently their populations are more likely to be fragmented (Crooks 2002). Large mammals are also often in direct competition with humans; predators compete with human-hunters for game (e.g. Brown and Conover 2011; Herfindal et al. 2005), ungulates and ruminants harbour diseases which infect domestic animals (e.g. Corner

2006), and herbivores damage gardens and crops (e.g. Conover and Kania 1995; Madhusudan 2003). Consequently, many large mammal species are restricted to protected areas or areas with low human density (Morrison et al. 2007). Functional conservation network that will address the landscape needs of large mammals must promote dispersal between parks, particularly through the establishment of corridors (Hanks 2001). Corridors are defined as continuous strips of land that facilitate animal movement across the landscape (Beier and Noss 1998; Puth and Wilson 2001). They reduce the effects of habitat loss and fragmentation and may increase genetic mixing (Crooks and Sanjayan 2006).

Corridors that increase functional connectivity for large mammals may also restore essential ecological processes. Large herbivores, in particular, aid in long-distance seed dispersal (Janzen 1984), effectively reducing the isolation of some plant species in small reserves (Couvreur et al. 2004). Some large herbivores are also ecosystem engineers that can transform plant communities (see Hobbs 1996; Manier and Hobbs 2006; Pringle et al. 2007). Occasionally such transformation is undesirable, and this has become a particular management concern for African savannah elephants (*Loxodonta africana*). In southern and East Africa, elephants at high densities have the ability to transform woodlands to shrublands or grasslands (Dublin et al. 1990; Scholes and Mennell 2008; Western and Maitumo 2004). Their confinement and compression into anomalously small areas likely accentuates their transformative influences (Loarie et al. 2009b; van Aarde et al. 2006). Historical long-distance movements was believed to limit local overgrazing (Coughenour 2008), but today long-distance migration among terrestrial vertebrates is one of the world’s most endangered biological phenomenon (Bartlam-Brooks et al. 2011; Berger 2004).

Restoring elephant movements between protected areas and managing elephants as spatially-structured metapopulations has been proposed by van Aarde and Jackson (2007) as a means to reduce local impact, reduce the need for elephant culling, and stabilize elephant numbers regionally. This study will test whether corridors currently exist between protected areas and if already established conservation networks are functionally connected for elephants. Opportunities for dispersal may exist in southern Africa because protected areas are within close proximity of each other and are embedded in a matrix of mostly untransformed habitats with few people (Cushman et al. 2010; Mittermeier et al. 2003). Furthermore, elephants are ideal candidates for designing corridors because they are an umbrella species, often co-occurring with other species of conservation concern (Epps et al. 2007). In this paper, we will assess the potential for connectivity between existing elephant populations in southern Africa using circuit theory and resource selection function (RSF) models.

Circuit theory is based on a random walk, with connectivity between habitat patches increasing with the number of alternative routes and decreasing with distance (McRae et al. 2008). Circuit theory uses the principles of an electric circuit, where a current (animal) flows through nodes and resistors (habitat patches and matrix) with voltage (probability of animal travel) and resistance (permeability of habitat types; McRae et al. 2008). The resulting product is a prediction of 'current density' or a probability of movement across each pixel of the landscape. Among the benefits of circuit theory is that it does not assume perfect knowledge of the landscape (McRae et al. 2008). To identify habitats with the greatest flow and least resistance to movements, we will use a RSF model. An RSF model compares used and available resource units to estimate the probability of occurrence (Boyce et al. 2002; Manly et al. 2002). We assume that habitat types that are avoided provide greater resistance to movement (Chetkiewicz et al. 2006; McRae et al. 2008). While our objective was to determine the likelihood of connectivity between known elephant populations in southern Africa, our approach could also help managers enhance or promote potential corridors for other species.

Methods

Study Area

Located in southern Africa, our study area extended from the western to the eastern coast and encompassed portions of Angola, Botswana, Malawi, Mozambique, Namibia, Zambia, and Zimbabwe (Figure 3-1). Within the study area, we identified six clusters of protected areas within which elephant populations were known or suspected to be interconnected (see van Aarde and Ferreira 2009). Habitats varied across clusters from predominantly arid grassland in Namibia to mesic woodlands in Mozambique. Terrain was relatively flat across most of the study area, except near the Etendeka Mountains in western Namibia and the Muchinga Mountains in Zambia. The distance between neighbouring clusters varied from 180 to 430 km (Table 3-1). Two conservation networks occurred within the study area, the Kavango-Zambezi TFCA which included the Chobe and Kafue cluster and the Niassa-Selous corridor located north of the Niassa cluster (Figure 3-1). Human presence was relatively low across the region, with pockets of increased human densities near major waterways and roadways. Elephants were generally free roaming, except where fences existed, either along the borders of protected areas (Etosha National Park) or along international boundaries (between Namibia and Botswana).

Elephant Data

Between December 2002 and September 2010, 93 elephants[1] were captured and collared with Africa Wildlife Tracking GPS collars (model SM 2000E). Collars were programmed to locate individuals at varying intervals, ranging from 1 to 24 hours, with most animals having multiple interval settings during the tracking period. Elephants are less mobile during the dry season and more faithful to dry season home ranges across years (Young et al. 2009); consequently, we

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[1] Sample size differs from Chapter 2 because elephants in Kruger were not included in this analysis, and were only used for model validation.

assumed that during the wet season elephants were more likely to make exploratory forays or use corridors. Using only locations recorded during the core wet season (December through March, inclusive), individuals with more than 100 locations during this period were retained for the analysis, resulting in 79 individuals (53 females, each representing a breeding herd, and 26 males). An additional nine elephants (6 females and 3 males) were collared in the Limpopo region (Figure 3-1) and used to test model fit.

The local convex hull (LoCoH) nonparametric kernel method was used to generate a home range for each individual (Getz and Wilmers 2004). The adaptive sphere of influence (*a*-LoCoH) algorithm was used to construct kernels, with *a* equal to the furthest distance between any two locations (Getz et al. 2007). The resulting home ranges fit tightly to the animal locations, often leaving holes which we believed were unrealistic; therefore, we further buffered home ranges by 10 km. This had the added advantage of further identifying areas which elephants presumably had access to but did not use. Home ranges were created using R software (R Development Core Team 2011), along with the packages “adehabitat” (Calenge 2006) and “NNCH” (Wayne Getz Lab 2005).

Habitat Covariates

Habitat covariates known to influence elephant habitat selection and home range placement were used in the analysis. These included surface water (de Beer et al. 2006; Harris et al. 2008), slope (Wall et al. 2006), vegetation cover (Harris et al. 2008; Loarie et al. 2009a), and human presence (Harris et al. 2008; Hoare and du Toit 1999; Jackson et al. 2008). Wet season surface water was located using data from Tracks4Africa (2010) and man-made watering point data provided by conservation authorities. These data were manually validated against Landsat imagery and missing water bodies were hand-digitized. Distance to water (km) was then calculated for each location. It should be noted that small water bodies, such as mud holes, could not be identified with this method. Using a 90 m^2 digital elevation model, slope was derived in degrees (Jarvis et al. 2006). Vegetative structure was characterized using MODIS Vegetation Continuous Fields (Hansen et al. 2006), which estimates the proportion of tree and herbaceous cover at a 500 m^2 resolution. Owing to collinearity between tree and herbaceous cover within clusters, only proportion of tree cover was included in the analysis. Finally, human presence was represented using two variables. Landscan (2008) human population data estimated daily human density at a resolution of 1 km^2, and road infrastructure data (Tracks4Africa 2010) was used to determine distance (km) of locations from main and secondary roads. Distance to main roads was calculated using roads categorized as freeway, national road, or main road. All other road categories were included in the secondary road classification. All geospatial analysis was completed using the Spatial Analyst extension of ArcGIS 10.0 (ESRI 2010) and Geospatial Modelling Environment (Beyer 2011).

Habitat Selection Models

Habitat selection was modelled separately for males and females and combined across the six clusters. Elephant locations (1) were compared to randomly generated locations (0) using a mixed-effects logistic regression model. The random intercept was used to control for the lack of independence of points within individuals and unbalanced sample sizes (Gillies et al. 2006). We used a design III RSF approach (Manly et al. 2002), where random locations were generated within the 10 km buffered home range of each elephant at a density of 3 points/km^2. Since the scale of the largest habitat covariate was 1 km^2, we were aware that contamination could be an issue (Keating and Cherry 2004). Contamination occurs when the use and random locations occur within the same pixel. Therefore, the density of random points was chosen to reduce contamination to less than 20% based on Johnson et al. (2006).

All habitat variables were used to assess elephant habitat selection, as they are all known to influence elephant habitat selection (Roever et al. 2012). No variables were highly correlated when examined using Pearson's correlation coefficient ($r > 0.6$). Each continuous variable was tested for the presence of a nonlinear relationship using a quadratic term. Model fit was evaluated using k-fold cross validation ($k = 5$) and the Spearman rank correlation coefficient (Boyce et al. 2002). Model fit was further evaluated using the independent elephant data from Limpopo following a similar method to k-fold cross validation, whereby the predicted RSF scores are placed in equal-area bins. The number of elephant locations falling into each bin is then tallied. Bins of higher RSF scores are expected to have higher frequencies of observations, and significance is tested using the Spearman rank correlation coefficient (Boyce et al. 2002).

Using the RSF model results, we created a habitat use index for males and females. We applied this model to the entire study area. To maintain predictive integrity, model predictions were limited to habitats observed in the model. For instance, the maximum distance to water observed in the use and available data was 58 km, consequently, any area further than 58 km from water was not assessed[2]. Analyses were done using R software (R Development Core Team 2011) and the lme4 package (Bates and Maechler 2010).

Connectivity Models

Connectivity between clusters was evaluated using circuit theory (McRae et al. 2008) and the program Circuitscape (McRae and Shah 2009). Home ranges were used as the source and end nodes of the circuit. Home ranges were combined into a single node if they were within 20km of each other, unless they were separated by a fence. We used the one-to-many criterion, whereby one source was connected to all end nodes in an iterative fashion. The habitat use index created from the RSF model was used as the resistance surface. Areas with a high probability of use were assumed to allow a greater current flow (or less resistance) than those with a low probability of

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[2] Maximum distance to water differs from Chapter 2, which was 79km, because only the wet season data were analysed here.

use. Owing to the processing limitations of the Circuitscape program, the study area was segmented into five sections and the habitat use index was generalized to 500 m^2 pixels. We began by using only the habitat use index as the resistance surface, but then further limited movement by adding absolute barriers. Based on known elephant habitat use, we hypothesized that distance to water, slope, and human population density had maximum values which posed a complete barrier to movement. We defined absolute barriers as any value greater than values observed in 99 percent of the elephant telemetry locations of these covariates. Consequently, areas further than 48 km from water, with a slope greater than 11.4 degrees, or containing more than 45 people/km^2 were classified as absolute barriers.

Results

Habitat Selection

Both male and female wet season habitat selection models provided good fit using k-fold cross validation (Spearman rank $r_s = 0.782$, p = 0.01 for females and $r_s = 0.952$, $p < 0.01$ for males). Relative to availability, female elephants selected areas with low slopes, high tree cover, and low human population density (Table 3-2, Figure 3-2). They preferred to be further from main roads and had a nonlinear relationship with secondary roads, showing slight selection for areas near these roads but mostly avoiding them. Selection for water also had a nonlinear relationship, with females selecting areas both near and far from water relative to availability. Male elephants selected low slopes and low human population density, and they preferred areas of intermediate tree cover. Males avoided main roads but selected secondary roads. A nonlinear relationship with water also was present for males; however, they were less inclined to be close to water as compared with females. Model validation using the independent Limpopo data was significant for males ($r_s = 0.6364$, $p = 0.05$) but not for females ($r_s = -0.6969$, $p = 0.03$), indicating the female model was a poor predictor of elephant use in regions beyond the study area.

Connectivity

Adding absolute barriers to the circuit theory current flow maps did not alter connectivity between clusters, however barriers did restrict the width and alter the location of potential corridors. For both maps, current flow was high between Chobe and Kafue for male and female elephants (Figure 3-3 & 3-4). The high flow can be attributed to wide areas of suitable habitat allowing for multiple routes of travel. Potential corridors between the Zambezi cluster and its neighbouring clusters, Kafue and Luangwa, were less straightforward. When examining the current flow map without absolute barriers, it appeared that a corridor could exist between the Zambezi and Kafue clusters (Figure 3-3). However, the steep terrain between the two clusters added several absolute barriers, narrowing the corridor and shifting flow to the southwest (Figure 3-4). In the easterly direction, the connection between the Zambezi and Luangwa had some support in both current flow maps (Figure 3-3 & 3-4). This corridor was long (320 km) and narrow, which could limit its utility. Flow also decreased for females in some areas between the Zambezi and Luangwa, further reducing its functionality as a potential corridor.

The current flow maps further showed low flow for males or females between Etosha and Chobe and between Luangwa and Niassa (Figure 3-3 & 3-4). The distance between Etosha and Chobe was large (300 km) and the area contained few water sources. In the Namibian portion of our study area, some regions were up to 70 km from water, and in Angola, this distance rose to greater than 100 km. The furthest any elephant occurred from water was 58 km, with a mean distance of 10 km. The greatest barrier for dispersal between Luangwa and Niassa was the high human density in Malawi. In addition, Lake Malawi created a bottleneck, limiting potential flow to one 11 km wide area.

Discussion

In general, the wet season habitat selection patterns of male and female elephants were similar and supported the relevance of previously reported habitat covariates (see Harris et al. 2008; Hoare and du Toit 1999; Loarie et al. 2009a; Roever et al. 2012; Wall et al. 2006). Both sexes had a nonlinear relationship with water, selecting for areas both near and far from water relative to availability (Table 3-2). This agrees with what we know about elephant behaviour, as elephants regularly go to water to drink and then travel far afield in search of food (Leggett 2006). Our elephants also avoided steep terrain, possibly due to due to physiological and energetic constraints (see Wall et al. 2006). Females had a sharper decline in the use of higher slopes with the inclusion of the quadratic term, suggesting that they selected more for flat terrain than males. Both sexes also avoided areas of high human density as well as areas near main roads. Males, however, remained closer to secondary roads, while females avoided them.

Our circuit theory current maps identified potential corridors among several clusters of protected areas in the central portion of the study area (Figures 3-3 & 3-4). Between the Chobe and Kafue clusters, we identified a wide area suitable for potential animal movement, supporting the functionality of the Kavango-Zambezi TFCA. Our maps further indicate that the Zambezi cluster may be connected to the Kavango-Zambezi TFCA via Kafue and an additional corridor through Zimbabwe. The Zambezi cluster was only 67 km from the Zimbabwe portion of the Kavango-Zambezi TFCA, and although we had no data from elephant populations in Zimbabwe, a potential corridor to the TFCA was identified by both female and male current flow maps. In addition to highlighting connectivity around the Kavango-Zambezi TFCA, the current flow maps also identified a potential corridor between the Zambezi and Luangwa cluster. The steep terrain of the Muchinga Mountains, north of the Zambezi cluster, restricted potential animal movements between Luangwa and Zambezi; however, this mountain range also restricted human development. Elephants are capable of living in such habitats, as seen with elephants in the Etosha cluster which occur within the Etendeka Mountains; therefore, the viability of this corridor should not be discounted. It is estimated that 58 percent of African elephants occur within southern Africa, and of those approximately 85 percent are located in the Chobe, Kafue, Luangwa and Zambezi clusters (see Blanc et al. 2007). Consequently, the provision of these corridors linking Chobe, Kafue, Luangwa, and Zambezi will unite most of southern Africa's elephants into a single entity that could function as a metapopulation.

The main factors limiting connectivity across the study area where access to surface water in the west and a high human density in the east. Elephants in the Etosha cluster are effectively isolated by the lack of water in areas east of the cluster. Blanc et al. (2007) suggested that elephants' range possibly extended east of Etosha and north into Angola. While elephants have been recolonizing south eastern Angola after the civil war ended in 2002 (Chase and Griffin 2011), our results indicate that it is unlikely that elephants will cross the arid regions of north-central Namibia and south-central Angola. In the east, the potential corridor between Luangwa and Niassa was not limited by water, but instead, the high human density present in Malawi. Hoare and du Toit (1999) found the elephants in Zimbabwe did not coexist with humans when the latter reached a density of 15.6 persons/km^2. Within our data, only 4.8 percent of elephant telemetry locations (1,919 of 39,900) exceeded Hoare and du Toit's threshold. Elephants occurred in areas with a maximum human density of 1,512 persons/km^2, showing that elephants can and do penetrate areas of higher human density. Whether they could exist in these areas for very long, though, is questionable, particularly without a nearby refuge. Unfortunately, Malawi has few areas outside of parks and game reserves with human densities below 15.6 persons/km^2, so the potential for connectivity between Luangwa and Niassa is unlikely. Our results therefore suggest that the Etosha and Niassa clusters have limited potential to be managed as a spatially-structured metapopulation within the conservation areas examined in this study and, importantly, connectivity along an east-west axis may be limited.

Despite the lack of connectivity between Niassa and the other clusters examined in this study, the Niassa cluster still might benefit from inclusion with other conservation areas in northern Mozambique and southern Tanzania. Current flow maps showed connectivity not only between elephant data within the Niassa Cluster but also a potential corridor to Niassa Game Reserve. The Niassa Game Reserve is connected by the Selous-Niassa Corridor to Selous Game Reserve in southern Tanzania (Hofer et al. 2004; Figure 3-1), and elephants in this region could benefit from being connected to and managed collectively with those in the Niassa and Selous Game Reserves (see Baldus et al. 2003).

Here, we used habitat selection models to identify corridors for elephants, making the assumption that habitat use reflects landscape resistance. However, other behavioural factors not identified in the model may also influence dispersal (Belisle 2005; Lima and Zollner 1996). One limitation we observed was the inability to incorporate the periodic nature of elephants moving near and far from water. The region highlighted as a potential corridor for males between the Zambezi and Luangwa had a 240 km expanse without crossing water. It is unrealistic to assume that this route would be a viable corridor for elephants; however it should not be completely discounted. The female current flow maps for the same region identified portions of the Luangwa River, located 45 km to the northwest, as a viable corridor. Consequently, incorporating the width of the valley into the corridor design may make this potential route more viable for both sexes.

Using RSF models to make predictions about elephant use in areas other than the study area can be problematic (Boyce et al. 2002), as seen in our independent testing data from

Limpopo. The female model had poor fit; consequently, models should be used with caution and corridors should be further validated with field data. In our analysis, we attempted to limit unrealistic predictions by bounding all variables to values only seen within the model; however, this does not compensate for changes in the proportion of each variable (Aarts et al. 2008; Matthiopoulos et al. 2011). For the current flow maps, we suspect that adding absolute barriers using the 99th percentile of elephant locations produced more realistic predictions. While elephants used extreme areas of slope, human density, and distance to water, these forays were rare and the animal did not generally penetrate far into these less hospitable habitats. Therefore, it is plausible to assume that corridors based on these extreme values will have limited utility; however, this deduction also requires further validation.

Speculation has it that elephants were once wide-spread across Africa, but current populations have become fragmented and compressed into isolated protected areas (see Blanc et al. 2007). Interrupting natural movement patterns in elephants intensifies the damage that these ecosystem engineers cause to vegetation (Loarie et al. 2009b; van Aarde et al. 2006). Increasing connectivity between elephant populations is expected to alleviate problems caused by confinement and induce a dynamic that stabilizes populations regionally and removes the concern of local “hyper-abundance” (van Aarde and Jackson 2007). Based on the results of this study, elephant dispersal along the east-west gradient is plausible across much of our study area; therefore, if corridors are projected and enhanced, the foundations for a metapopulation as suggested in van Aarde and Jackson (2007) could be implemented. However, connectivity alone does not constitute a metapopulation (Driscoll 2007), and the presence of a corridor does not guarantee dispersal. The functionality of corridors must be monitored and, where necessary, promoted to ensure the continued flow between populations. Without active management efforts to maintain connectivity between protected areas along the east-west axis, it is likely that human development and encroachment will continue to isolate wildlife in southern Africa.

This study represents the largest effort to identity connectivity for a species to which we are aware, crossing seven countries. Yet these techniques are universally applicable at a variety of spatial scales and provide quantitative measures of habitat selection and animal flow rates (McRae et al. 2008). They require limited data input, they rely on realized habitat use by the animal, and they need little inferences by the authors or other sources of expert opinion (Chetkiewicz and Boyce 2009). Ultimately, habitat fragmentation is a global problem, and conservation and management efforts need tools to quickly identify and focus research efforts in areas where we have the highest probability to successfully restore connectivity.

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Table 3-1. Euclidian distance between neighboring clusters of elephant data arranged from west to east.

Cluster	Distance between neighboring clusters (km)
Etosha and Chobe	300
Chobe and Kafue	180
Kafue and Zambezi	300
Zambezi and Luangwa	320
Luangwa and Niassa	430

Table 3-2. Coefficient estimates and standard errors for habitat selection models. Significance to $p = 0.001$ is indicated (***), and quadratic terms not included in the final model are denoted (-).

	Females			Males		
	Estimate	SE		Estimate	SE	
Distance to water	-0.227	0.025	***	-0.426	0.033	***
(Distance to water)^2	0.055	0.006	***	0.128	0.008	***
Slope	-0.175	0.010	***	-0.085	0.004	***
(Slope)^2	0.002	0.001	***	-	-	
Proportion tree cover	0.541	0.097	***	7.452	0.418	***
(Proportion tree cover)^2	-	-		-8.126	0.762	***
Human population density	-0.010	0.001	***	-0.002	0.001	***
Distance to main road	0.092	0.006	***	0.074	0.008	***
Distance to secondary road	-0.073	0.022	***	-0.530	0.028	***
(Distance to secondary road)^2	0.018	0.004	***	0.025	0.005	***

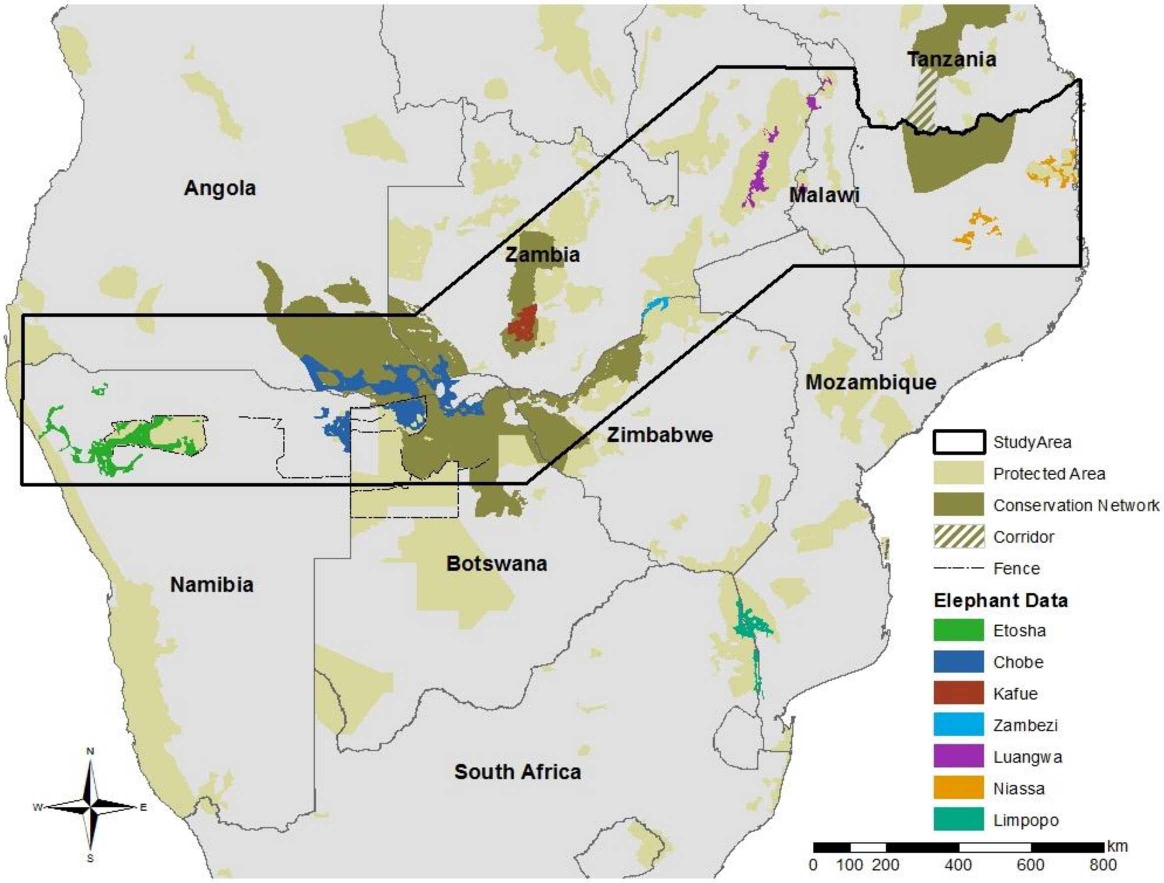

Figure 3-1. Map of the study area in southern Africa incorporating seven countries. Areas with elephant telemetry data were grouped into clusters based on location and following the designation proposed by van Aarde and Ferreira (2009). Data from the Limpopo cluster were used for out-of-sample model testing.

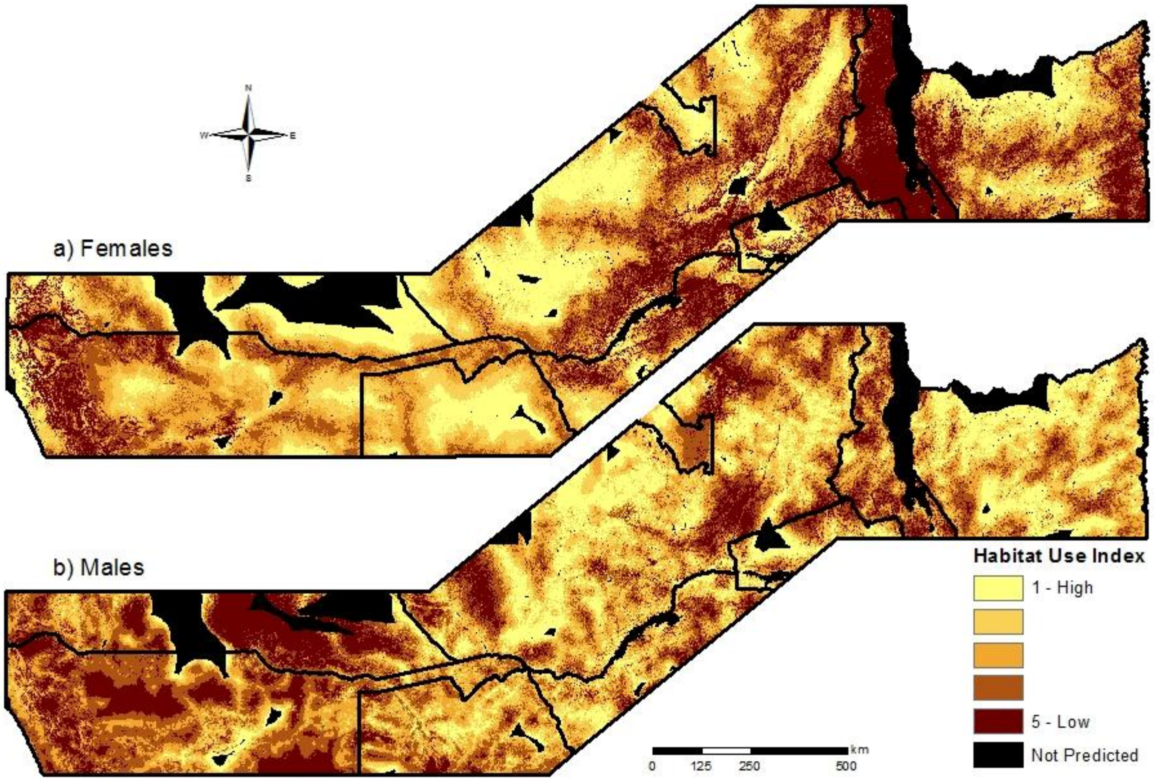

Figure 3-2. Relative index of habitat use for female (a) and male (b) elephants. Black regions represent areas that were not predicted because the variable values were outside of the range observed within the habitat selection model.

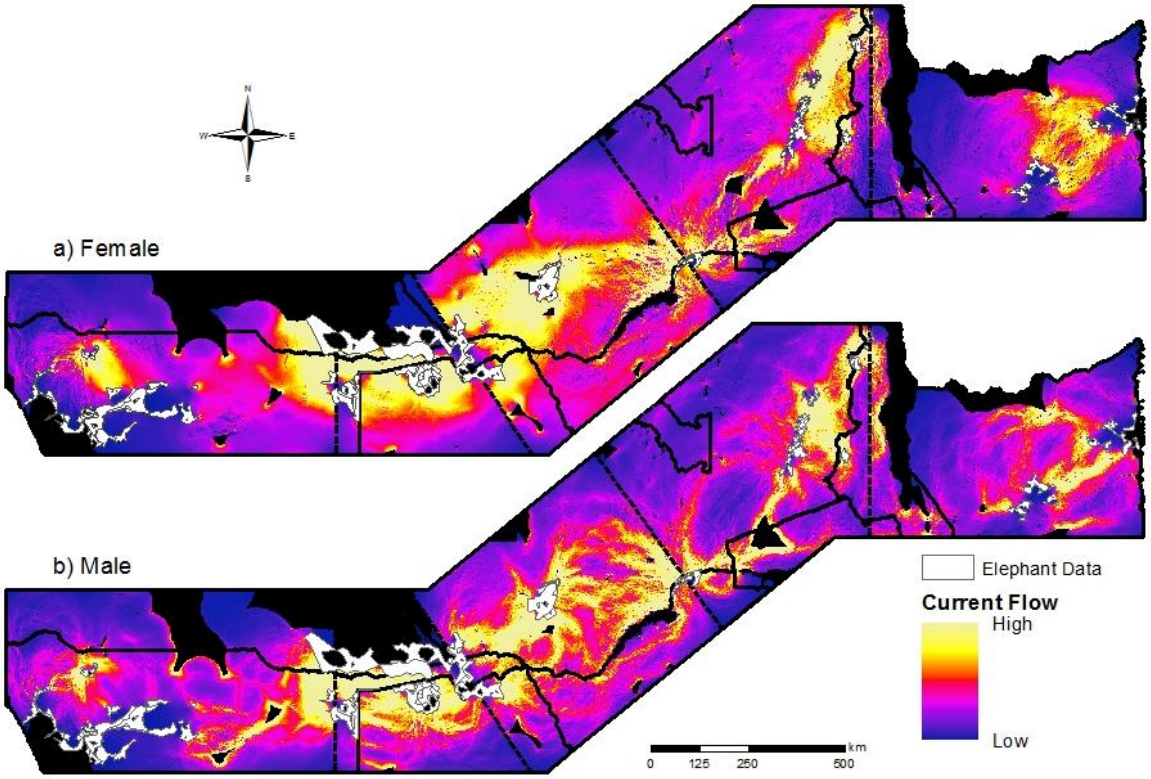

Figure 3-3. Current flow using the habitat selection index as the resistance. Owing to the computing limitations of the program Circuitscape, the study area was divided into five sections (dashed black line). Black regions indicate areas of zero flow.

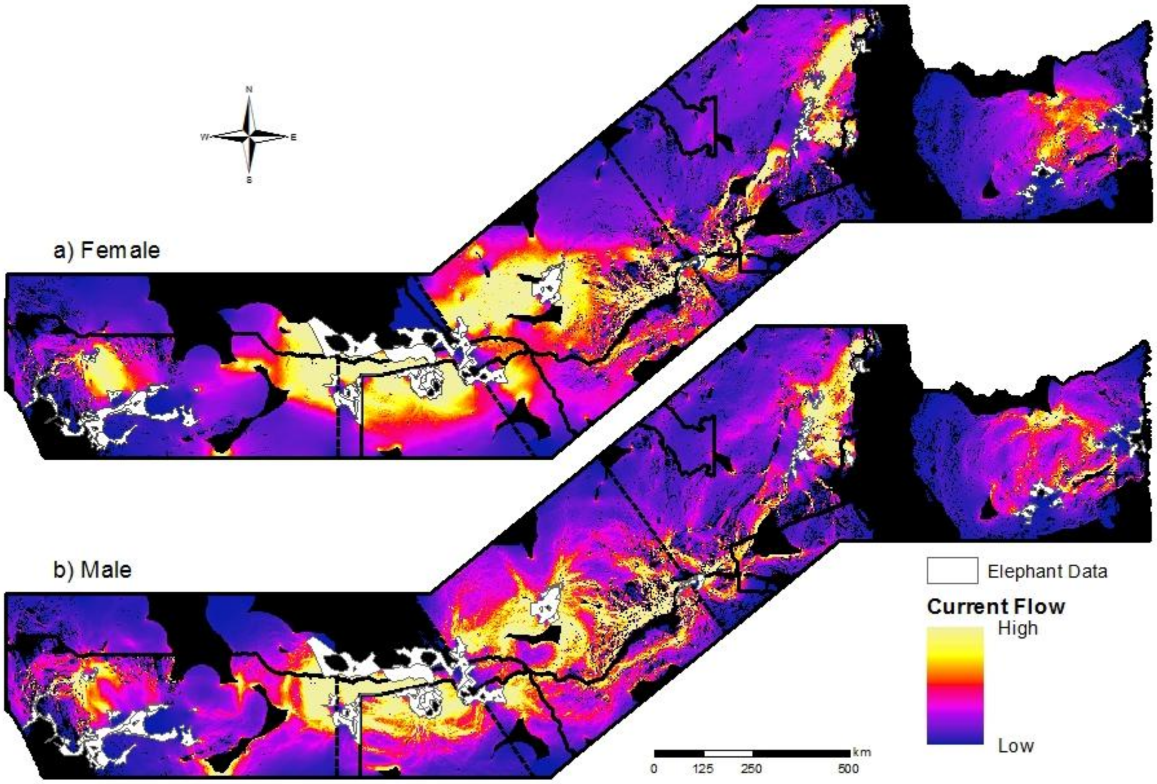

Figure 3-4. Current flow using the habitat selection index as the resistance, along with absolute barriers. Absolute barriers were defined as values greater than those observed within 99 percent of the elephant location data for distance to water, human population density, and slope. Black regions indicate areas of zero flow.

Chapter 4. Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants

Publication Details

Roever, C.L., van Aarde, R.J., Chase, M.J. Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. Biological Conservation, *in review*. R.J. van Aarde supervised the study, and M.J. Chase provided all of the aerial survey data.

Abstract

Empirical models of habitat selection are increasingly used to guide and inform habitat-based management plans for wildlife species. However, habitat selection does not necessarily equate to habitat quality particularly if selection is maladaptive, so incorporating measures of fitness into estimations of occurrence is necessary to increase model robustness. Here, we incorporated spatially explicit mortality events with the habitat selection of elephants to predict secure and risky habitats in northern Botswana. Following a two-step approach, we first predict the relative probability of use and the relative probability of mortality based on landscape features using logistic regression models. Combining these two indices, we then identified low mortality and high use (primary habitat) and areas of high mortality and high use (primary risk). We found that mortalities of adult elephants were closely associated with anthropogenic features, with 80% of mortalities occurring within 25 km of people. Conversely, elephant habitat selection was highest at distances of 30 to 50 km from people. Primary habitat for elephants occurred in the central portion of the study area and within the Okavango Delta; whereas risky areas occurred along the

periphery near humans. The protected designation of an area had less influence on the proportion of prime habitat therein than did the locations of the area in relation to human development. Elephant management in southern Africa is moving towards a more self-sustaining, habitat-based approach, and information on selection and mortality could serve as a baseline to help identify demographic sources and sinks to stabilize elephant demography.

Introduction

Using telemetry data to predict habitat utilization is a common practice in ecology, and the results are often used as a guide to protect and preserve habitats important to wildlife species (e.g. Johnson et al., 2004; Meyer et al., 1998). However, habitat utilization is only one aspect within a complex set of factors that ultimately relate to individual fitness. Selection, for example, could be maladaptive, whereby individuals select areas that ultimately increase their mortality risk or decrease their reproductive success (Battin, 2004; Delibes et al., 2001). To avoid the misclassification of highly used habitats as high-quality habitats, it is necessary to temper estimations of habitat selection with some indication of fitness or risk, particularly when habitat selection appraisals are to be used as an impetus for conservation action.

The main limitation of incorporating indices of fitness into animal occurrence models is that spatially-explicit fitness data is often difficult to obtain (Nielsen et al., 2006). Studies that incorporate offspring survival are most common for avian species, where fledging success at the nest site can readily be established (Aldridge and Boyce, 2007; Donovan and Thompson, 2001). However, with mammalian species the estimation of recruitment and survival are generally less straightforward. Changes in the demographic parameters of large mammals in particular occur over relatively long timescales because of their multi-year or multi-decade life spans and their low reproductive and mortality rates. Most large mammals are also highly mobile with large ranging patterns, making it difficult to relocate individuals to monitor survival and fecundity. Studies linking reproductive success to habitats have been most successful in ungulates on islands and other closed systems (McLoughlin et al., 2007, 2008). Given limitations in time, resources, study species, and study area, researchers resort to data that are more readily available, such as mortality location data (Dzialak et al., 2011; Falcucci et al., 2009; Nielsen et al., 2006).

Just as live animals inform habitat selection estimations, carcass locations provide spatially explicit information on where animals die and can be used to inform the riskiness of habitats (Nielsen et al., 2006). However, mortality location data is often underutilized in the literature. African elephants, for example, have carcasses that are easily visible from the air for several years after death (Douglas-Hamilton and Hillman, 1981), and while carcasses have been used to inform local mortality rates (e.g. Dudley et al., 2001; Dunham, 2008) and CITES status (e.g. Wittemyer et al., 2013), we found no peer-reviewed study exploiting the spatial location of carcasses. Knowing where animals die can provide valuable insight into risky landscapes, which is helpful information to guide conservation and management plans. Grizzly bears mortalities in Alberta, for example, were concentrated around roads or hiking trails (Benn and Herrero, 2002), prompting calls to regulate human access in grizzly bear habitats (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). Relating mortality locations to habitat selection models has also been used to better inform habitat-based management plans (i.e. Nielsen et al., 2006).

Habitat heterogeneity contributes to the spatial pattern of use and mortalities of elephants, and describing those patterns in particularly important in Africa, where the management of savannah elephants is a continuing concern (van Aarde and Jackson, 2007). Hunting and poaching in the late 19th and early to mid 20th century reduced some populations to near extinction (Roth and Douglas-Hamilton, 1991; Whyte et al., 2003), but actions taken to decrease poaching in the mid to late-20th century were largely successful in southern Africa (Whyte et al., 2003). The decline and subsequent recovery of elephant populations also may explain changes in woodland habitat (Guldemond and van Aarde, 2008; Nasseri et al., 2011), prompting concern for elephant-related tree damage (van Aarde et al., 2008). Their role as ecosystem engineers and the susceptibility to population decline from legal and illegal hunting makes it particularly important to quantify how habitats contribute to elephant habitat selection and mortality risk.

Using the information theoretic approach, we modelled habitat selection from elephant occurrence data obtained during aerial surveys. We then created an index of habitat use by elephants. Following a similar procedure, we next modelled the relative probability of elephant mortality using the locations of elephant carcasses. Combining the relative probability of use and mortality indexes, we then defined areas of high use and low mortality as secure habitats, and areas of high use and high mortality as risky areas. By interrelating conditions where elephants live with where they die, we can begin to establish a habitat-based approach to elephant management and work towards understanding and maintaining natural regulatory processes where needed, as proposed by van Aarde and Jackson(2007) and supported by others (Chamaillé-Jammes et al., 2008). These indices, while not a direct measure of demographic sources and sinks, do provide insights for the prioritization of conservation actions and can serve as a baseline to direct future studies into elephant demography.

Methods

Study Area

The study area in northern Botswana incorporated an area of 74 355 km^2. Study area boundaries to the north and east coincide with national borders for Namibia, Zambia, and Zimbabwe, respectively (Figure 4-1). Twenty percent of the study area was protected within the confines of Chobe National Park (NP), Makgadikgadi NP, Moremi Game Reserve (GR), and Nxai Pan NP, while an additional 65% occurred within Wildlife Management Areas (WMAs; Chase, 2011). WMAs were designated with a two letter code and number and, for the purpose of this study, were grouped into study regions (Figure 4-1). Legal trophy hunting of elephant males was permitted in WMAs between the months of April and September, with a quota of 400 males in 2010 and 306 taken. Most of the terrain within the study area was flat, with the steepest slopes of eight degrees occurring along the Chobe River. The vegetation consisted primarily of deciduous dry woodlands and interspersed grasslands (Gaughan et al., 2012). Kasane, in the northeastern corner of the study area, was the largest town, and outside of this town, human settlements occurred in small villages along roadways mainly on the periphery of the study area. Permanent human settlements were prohibited in national parks; however lodges, campsites, and park offices were located within park boundaries. Roads also occurred throughout at a density of 0.073 km/km^2.

Elephant Data

Aerial surveys to locate elephant carcasses and live elephants were conducted from June to December 2010. Aerial survey methodology followed procedures established by Norton-Griffiths (1978), whereby parallel strip-transects were systematically flown in a fixed-wing plane and animal locations were recorded. Transects were flown at a speed of 160 km/hour and 300 feet above ground level. The study area was divided into 42 sampling units, and transects with each sampling unit where surveyed once on one day to reduce duplicate counting of animals. The distance between strip-transects varied by sampling unit to minimize sampling effort (for detailed methods see Chase, 2011). Sampling units expected to have high to moderate elephant density were surveyed more intensively (2-4 km, n=38) than those with low elephant densities (8 km, n=3). However, NG26 was surveyed at a 1km density at the request of local stake holders. The width of strip transects extended approximately 400 m (two observers covering 200 m); consequently, surveys intensities of 1, 2, 4, and 8 km accounted for 40%, 20%, 10%, and 5% coverage of the sampling unit, respectively. The differing sampling intensities were not biased towards a particular habitat type or landscape feature and would, therefore, not bias habitat selection models (see Appendix A). Orientation and spacing of flight paths were generated using DNR Garmin Sampling Extension in ArcView 3.2 (ESRI, Redlands, California).

The timing of aerial surveys coincided with the peak dry season to increase visibility through the tree canopy. The location, time, sex, and number of elephants were recorded. The sex and age composition of individuals in groups were used to distinguish breeding herds from male herds which contained no females or juveniles. For elephant remains, the age of the carcass was categorized as either a recent carcass (i.e. flesh still present and the ground still moist indicating that the animal died less than a year ago) or as an old carcass (i.e. clean bones, dry ground, and vegetation reestablishing in the rot patch) (Douglas-Hamilton and Hillman, 1981). From the air, observers also recorded whether multiple carcasses were observed in the same location to indicate illegal hunting. While observers also recorded whether tusks had been chopped or removed, park officials also removed tusks from any carcass they find, as did legal hunters. However, natural mortality and hunter related deaths were generally isolated events; therefore, clustering of carcasses provided a better indication of poaching than did presence of tusks. Indications of illegal hunting were only noted in 18 instances, so low sample size precluded further analysis on poaching.

Modelling Animal Locations

We used a resource selection function (RSF) model to identify habitats associated with live elephant and elephant mortality locations. A RSF model compares animal locations to random locations within a logistic regression model, using landscape factors as independent variables. We used a design I approach because individual animals were not uniquely identified and were only sampled once (Manly et al., 2002). A design I approach is made at the population level, where used resources units are sampled for the entire study area (Manly et al., 2002). We then developed three habitat-based models. First, using the live elephant observations, we estimated habitat selection by elephants. Each elephant herd accounted for one observation, resulting in 3 040 live elephant observations. We compared these to random points generated at a density of 1 point per 3 km^2 across the study area, for a total of 24 785 random locations. Next, we estimated the habitat-specific probability of elephant mortality using the 341 elephant carcass observations. The same set of random points was used for the mortality model as in the elephant habitat selection model. Finally, we compared elephant carcass locations to live elephant locations. This model accounts for the reality that elephants can only die in areas where they occur (Nielsen et al., 2004).

Covariates used in the estimation of the three habitat selection models pertained to water, slope, tree cover, human presence, and roads (based on Roever et al., 2012). Surface water was located using data from Tracks4Africa (2010) and was visually validated against Landsat imagery. Missing water bodies were manually digitized into the water layer. Distance to water (km) was then calculated for each location. While surface water can vary substantially across the seasons, the time of death for mortality events was unknown; therefore, we used all water bodies in our estimation (analysis using dry season water availability is in Appendix B). Because elephant locomotion is limited by steep slopes (Wall et al., 2006), slope was calculated in degrees using a 90 x 90 m digital elevation model (Jarvis et al., 2006). Proportion of tree cover was estimated using MODIS Vegetation Continuous Fields (Hansen et al., 2006), which assessed the proportion of tree cover at a 500 x 500 m resolution. To quantify permanent human use across the landscape, we used Landscan (2008) human population data. Landscan data estimates human use over a 24hr period, and includes permanent settlements as well as roads, recreation areas, and other areas where people occur but not necessarily sleep (Landscan, 2008). Areas with >16 people/km^2 were considered relevant for elephant space use (Hoare and Du Toit, 1999); therefore, these areas were identified and distance to these high human-use areas was calculated. Finally, road infrastructure data (Tracks4Africa, 2010) was used to determine the distance (km) of locations from roads. As most roads in the study area were secondary dirt roads, road type was not further differentiated. All geospatial analysis was completed using the Spatial Analyst extension of ArcGIS 10.0 (ESRI, Redlands, California) and Geospatial Modelling Environment (Beyer, 2011).

To determine which habitat variables influenced elephant use and death locations, Akaike's information criterion (AIC) was used to choose a top-model among eight a priori candidate models (Table 4-1; Burnham and Anderson, 2002). Prior to model selection, all variables were tested for correlations and for non-linearity. Using Pearson's correlation coefficient, variables with an $r > 0.60$ were not included in the same model. Correlations occurred between distance to roads and distance to water (Pearson's $r = 0.632$). All continuous variables were examined for nonlinearities using histograms and by examining changes in model fit when including a quadratic term. Model fit of the top-ranked model was evaluated using k-fold cross validation ($k = 5$) and the Spearman rank correlation coefficient (Boyce et al., 2002). Analyses were conducted in R software (R Development Core Team, 2011).

Using the resultant models for where elephants lived and where elephants died, we predicted the relative probability of use and the relative probability of mortality across the study area. The relative probabilities were then classified into ten ordinal categories using the quantile (equal-area) method in ArcGIS 10.0, with the lowest and highest probability equal to 1 and 10, respectively (Nielsen et al., 2006).

Identifying Habitat States

We followed the methods of Nielsen et al. (2006) to define five habitat states based on elephant use and mortality. Habitat states included non-habitat (low use), secondary habitat (moderate use, low mortality), primary habitat (high use, low mortality), secondary risk areas (moderate use, high mortality), and primary risk areas (high use, high mortality) (Figure 4-2). We used the elephant data to define the boundaries between habitat states, using an a priori defined 80% cutoff. Consequently, where 80% of the live elephants occurred was categorized as habitat (use classes 5 to 10, inclusive) and where 80% of mortalities occurred was classified as high risk (mortality classes 7 to 10, inclusive). We then calculated the percentage of each state that occurred within each study region, to ascertain the proportion of effective habitats present within each.

Results

The top-ranked model for all three habitat selection analyses (elephant vs. random, mortality vs. random, and mortality vs. elephant) was model 7 (the global model with water; see Appendix C for full model results). This model had strong support in the elephant vs. random (weight = 1.00) and mortality vs. random (weight = 1.00) analyses. Conversely, in the analysis comparing carcass locations to live elephant locations, the global model with water (Model 7) had a weight of 0.74 and the global model with roads (Model 8) was the second ranked model with a weight of 0.23. These two models were similar in form except that they interchanged the correlated variables, distance to water and distance to road. In all three analysis, the top model provided good fit to data using k-fold cross validation tested using the Spearman rank correlation coefficient ($r_s > 0.86$; Table 4-2).

For the elephant use model, selection was associated with intermediate distance from water, steep slopes, moderate tree cover, and further from humans (Table 4-2). These features were most prevalent in Moremi GR in the western portion of the study area and the WMAs surrounding the Okavango Delta (Figure 4-3a). High elephant use was also prevalent in the central portion of the study area in NG 15, and NG 18, and western Chobe NP. Selection patterns of elephant mortalities were similar to live elephant habitat use for most variables. Elephant mortalities were associated with areas of intermediate distance from water, steep slopes, and intermediate tree cover; however the magnitude of these selection coefficients varied from the elephant use model (Table 4-2). Counter to the elephant use model, mortalities were more closely associated with humans. Across the study area, high mortality areas were located along the periphery of the study area, near areas with higher levels of human occupation (Figure 4-3b).

Results comparing elephant carcass locations to elephant use locations reveal that water, slope, and distance to humans differed significantly between the two. Compared to where they lived, elephants were more likely to die in areas slightly further from water and on steeper slopes (Figure 4-4); however, the most striking difference between use and mortality locations was proximity to humans. Live elephants selected areas which were at intermediate distances from humans, whereas the highest relative probability of mortality occurred in areas near humans. Overall, the predictions of models comparing mortality locations to either elephant locations or random locations were similar (Table 4-2), indicating that mortality was not closely associated with patterns of habitat selection but were instead more closely associated with some other factor, such as human presence.

Based on our classification of habitat states, 15.0% of the study area comprised primary habitat for elephants, while 12.3% were primary risk areas (Table 4-3). Secondary habitat, which had low mortality and moderate use by elephants, comprised 14.6% of the study area, whereas secondary risk areas, with high mortality and moderate use, composed 16.2%. Overall, 42.0% was classified as non-habitat. The study area contained three national parks and one game reserve. Of these, Chobe NP contained the highest proportion of primary (30.0%) and secondary (26.1%) risk areas of any study region, and Makgadikgadi NP had the second highest proportion of non-habitat of any study region and had little (1.0%) primary habitat for elephants. Conversely, Moremi GR had the highest percentage of primary habitat of any study region (51.1%). WMAs also provide substantial amounts of primary and secondary habitat for elephants. The WMAs we called NG north and south comprise 28,058 km^2 of land and they consist of 5,666 km^2 (20%) of primary habitat (Figure 4-5).

Discussion

Our results indicate that elephant use and mortality locations were spatially separated. Elephant mortality locations were concentrated in areas close to human settlements, with 80% of all elephant mortalities occurring within 25 km of high human use areas, an area that accounts for 52% of the study area. Conversely, 50% of live elephants were observed in that same area, and live elephants selected areas of intermediate distance from people (Figure 4-4). Elephant mortalities were, therefore, not proportional to elephant distribution. This is positive for elephant conservation as it shows that elephants were not exhibiting maladaptive selection, whereby individuals select areas that ultimately increase their mortality risk. However, it also suggests that humans contribute to elephant mortalities in the study area. Nielsen et al. (2004) found a similar pattern with grizzly bears, whereby human-induced mortalities reflected patterns of human use rather than of grizzly bear use. However, cause of death for elephants can be difficult to ascertain (Moss et al., 2011). Tusk removal is not a reliable sign of human-caused mortality because game wardens also remove tusks on any carcass observed to discourage the trade of ivory. In this study only 18 of the 341 elephant carcasses showed obvious signs of poaching, and most of these (17 of 18) were within 25 km of high human use areas.

The use of carcass location data is particularly informative when the death of the individual is directly related to the habitat component in which it was found. For example, with predators or human hunters, the carcass of the animal will generally remain in close proximity to the source of risk. However, when the animal succumbs to starvation or a disease, the behaviour of the individual may change in response to the weakened state. Elephants, for example, are dependent on surface water for survival in northern Botswana (Metcalfe and Kepe, 2008), and it has been anecdotally noted, although not statistically verified, that a sick elephant may remain within close proximity to a water source (Haynes, 1988). Here, we found that elephant mortalities were closely associated with water, but at a similar rate as live elephant locations (Figure 4-4). Yet, our study period was not a particularly stressful year; therefore, years of drought may produce very different patterns of mortality. In such instances of nutrition stress and disease, the carcass location may prove to be less informative at a fine spatial scale as examined here. Across a larger spatial scale, however, carcass locations may still provide valuable information on the ability of the region to support elephant populations at the home range or landscape scale.

Most of our carcass observations were of adult elephants, possibly an artifact of their increased visibility from an airplane. Consequently, the relative probability of mortality described in this study is biased towards adults. Other studies examining juvenile mortality among elephants found in 89% of cases the cause of death was natural (i.e. from drought, starvation, disease, predation, etc.; Moss et al., 2011). Once an elephant reaches adulthood, the likelihood of natural mortality declines until the animal reaches the age of 40 years, when age-related factors again increase the risk of natural mortality (Moss et al., 2011). Because our observed carcass locations were of adults, it stands to reason that mortality was heavily biased towards human-dominated landscapes. A further bias in the data could exist as a consequence of the Okavango Delta. No study to date has examined elephant carcass longevity in a marshy environment like the delta, where water could aid in decay and dispersal or obscure carcass visibility from the air. However, if the mortality events observed in this study are largely human-induced, then the low rate of mortality could simply be a consequence of decreased human presence in the delta. Nonetheless, more research needs to be done to verify the cause of death in adult elephants to better distinguish landscape factors associated with natural versus human-induced mortality events.

Our study area in northern Botswana included three national parks, one game reserve, and many wildlife management areas. Because national parks have greater restrictions on animal and land-use practices, it is often assumed that these areas will provide lower mortality and more secure habitat for animals than would areas with fewer restrictions. However, this is not always the case in Africa where high human densities near park boundaries (Wittemyer et al., 2008) may increase incidences of poaching (Metzger et al., 2010; Milner-Gulland and Bennett, 2003) and human-wildlife conflicts (Newmark et al., 1994). Our results support this, as we found that areas designated as national parks and game reserves did not decrease mortality for elephants. The highest proportions of primary risk areas (high use and high mortality) occurred in Chobe NP, where 27% of our observed mortalities occurred; whereas the highest concentrations of primary habitat occurred in Moremi GP and NG-south (Table 4-3). Consequently, the protected designation of an area had less influence on elephant mortality than did the location of the protected area in relation to human occupation; therefore, increased human development in the study area will likely result in a greater abundance of risky areas for elephants.

We opted to use aerial survey data rather than telemetry data to make direct comparisons between elephant abundance and elephant mortality locations. However, the disadvantage of aerial survey data was that data were restricted to the dry season when decreased foliage on trees increased elephant visibility. Therefore, our conclusions of habitat states relate to dry season elephant use. The dry season is the limiting season for this mega-herbivore (Illius, 2006; Trimble et al., 2009), so we consider the dry season best reflects limitations in habitat suitability and ultimately best relates to fitness. Habitat selection patterns are likely to vary in the core wet season (Young et al., 2009), when elephants shift their diet to consume more grasses (Cerling et al., 2006; Codron et al., 2011) and are less dependent on permanent water sources (Harris et al., 2008; Young et al., 2009). Based on our knowledge of elephant use patterns in the area from GPS collar data, we suspect that areas designated as “non-habitat” will be most influenced, particularly in NG-north. This area has a high proportion of grasses and was used readily by elephants in the wet season. We also expect that elephants will be more closely associated with people during the dry season, as human settlements are also concentrated around permanent water, possibly increasing human-wildlife interactions and conflict. For patterns of elephant mortalities, results are less likely to vary with season because the longevity of elephant carcasses means that mortality events could have occurred during any season.

Habitat selection models are often used in the management and conservation of wildlife; however, maladaptive selection by wildlife can result in the conservation of habitats that do little to contribute to the local persistence of the species. By including an indication of risk, we can begin to temper habitat selection estimations to better define habitat suitability. Here we used mortality location data because the large body size and slow decay rate of elephant carcasses makes this data relatively straightforward to obtain (Douglas-Hamilton and Hillman, 1981); however other indicators which directly relate to individual fitness have also been used, such as the habitat selection of a predator (Hebblewhite et al., 2005), and the availability of a limiting resource (Bleich et al., 2010; Nielsen et al., 2010). The next step is to determine if these habitat selection and mortality models relate to demographic responses by the population to determine if these areas of risk also act as attractive sinks (Battin, 2004; Delibes et al., 2001).

This study is the first to examine habitat-associations of adult elephant mortalities and provide spatially explicit predictions of secure and risky habitats. Understanding the possible habitat variables which could contribute to mortality is the first step towards developing a habitat-based management plan. Balancing factors that contribute to elephant fitness and mortality to stabilize growth is a management option that could help alleviate concerns of elephant overpopulation (van Aarde and Jackson, 2007). Past elephant management entailed fencing populations into protected parks and supplementing water, which often resulted in localized overpopulation (van Aarde and Jackson, 2007). To reduce elephant numbers, managers then resorted to regular but controversial culls (van Aarde et al., 2006). Conversely, the elephant population in northern Botswana has largely escaped this more hands-on management approach, and now provides a model for a self-sustaining population. The areas of primary habitat in the Okavango Delta and central portion of the study area were isolated from human development and could provide a source population to supplement potential risky areas closer to human development on the periphery if our proposed habitat states result in demographic response. This habitat heterogeneity could contribute to regional population stability (Owen-Smith, 2004).

Because elephant have such large roaming areas, habitat-based management requires vast tracks of land to accommodate the habitat heterogeneity for secure and risky areas. To put the area in perspective, the study area is roughly the same size as the combined area of New Hampshire, Massachusetts, and Vermont in the United States. Yet our study area is just a portion of the larger Kavango-Zambezi Transfrontier Conservation Area, which stretches across 320 000 km^2 and five countries, and is home to some 220 000 elephants (Blanc et al., 2007). Across Africa, initiatives to create corridors, link protected areas, and establish transfrontier conservation areas may increase the amount of land available to elephants. By increasing connectivity between protected areas we may be able to support and maintain the natural regulatory processes, such as long distance migrations and habitat heterogeneity, which may have help to limit elephant populations in the past (van Aarde and Jackson, 2007).

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Table 4-1. Structure of the AIC candidate models evaluating elephant habitat use (elephant location vs. random location), elephant mortality risk (mortality location vs. random location), and difference in selection (mortality location vs. elephant location). Distance to water and distance to road were correlated; therefore, they could not be used in the same model.

Model Name	Model
1. Null	
2.Water	Distance to water[1]
3. Nutrients	Distance to water[1] + Proportion tree[1]
4. Water, Food, and Slope	Slope + Distance to water[1] + Proportion tree[1]
5. Human Presence	Distance to humans[2,3] + Distance to road[2]
6. Cover and Humans	Proportion tree[1] + Distance to humans[2,3] + Distance to road[2]
7. Full water	Slope + Distance to water[1] + Proportion tree[1] + Distance to humans[2,3]
8. Full roads	Slope + Proportion tree[1] + Distance to humans[2,3] + Distance to road[2]

[1] Quadratic in all analysis
[2] Quadratic in the elephant vs. random analysis
[3] Quadratic in the mortality vs. elephant analysis

Table 4-2. Coefficients (β) and standard errors (SE) for the top-ranked AIC models. An asterisk (*) was used to indicate where the confidence intervals did not overlap with zero. Model fit using k-fold cross validation and the Spearman rank correlation coefficient (r_s) is also presented.

	Elephant vs. Random			Mortality vs. Random			Mortality vs. Elephant		
	β	SE		β	SE		β	SE	
Distance to water†	0.73	0.55		5.31	1.80	*	4.29	1.90	*
(Distance to water†)^2	-0.15	0.02	*	-0.28	0.06	*	-0.12	0.06	
Slope	0.15	0.04	*	0.40	0.07	*	0.27	0.09	*
Proportion tree	6.24	0.67	*	13.36	2.23	*	4.38	2.48	
(Proportion tree)^2	-17.98	2.28	*	-38.83	8.01	*	-14.86	8.34	
Distance to humans†	2.92	0.46	*	-4.52	0.46	*	-8.05	1.45	*
(Distance to humans†)^2	-0.04	0.01	*				0.05	0.03	
Model fit (r_s)	1.00			0.96			0.87		

† Coefficients multiplied by 100

Table 4-3. Percent composition of habitat states occurring within each study region.

	Non-habitat	Secondary Habitat	Secondary sink	Primary habitat	Primary sink	Total Area (km^2)
Chobe NP	14.6	14.5	26.1	14.8	30.0	10,751
Makgadikgadi NP	66.4	20.1	10.6	1.0	2.0	5,018
Moremi GR	13.6	18.1	7.1	51.1	10.2	4,889
Nxai Pan NP	35.8	27.9	8.1	9.5	18.7	2,518
CH – east	42.1	9.8	19.3	9.0	19.7	6,977
CH – north	39.1	0.5	43.2	0.1	17.2	2,884
CT	84.1	3.0	11.2	0.4	1.3	10,002
NG – north	42.6	14.7	18.7	15.3	8.7	19,683
NG – south	10.4	33.1	7.0	36.5	13.0	8,375
Total Area	42.0	14.6	16.2	15.0	12.3	74,354

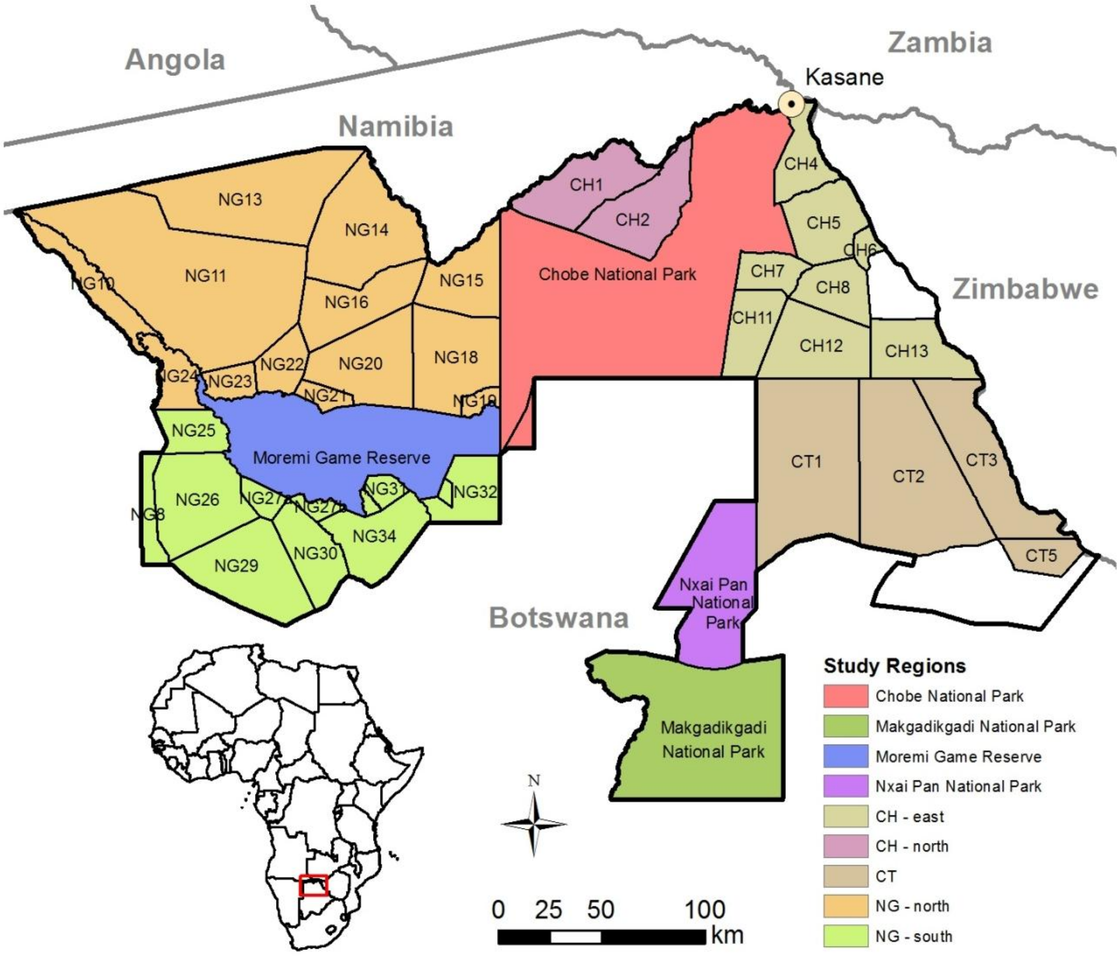


Figure 4-1. Map of the study area located in northern Botswana. The area included three national parks, one game reserve, and multiple wildlife management areas which were grouped and referred to as study regions.

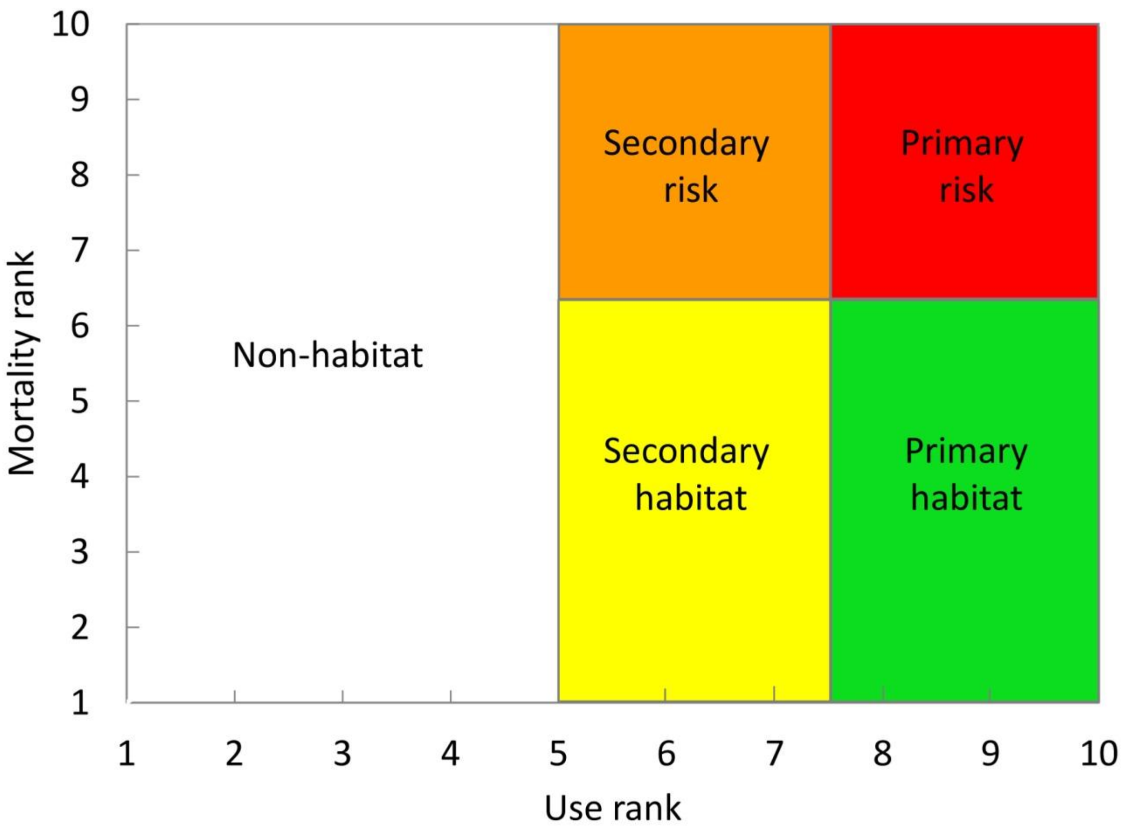


Figure 4-2. Five habitat states categorized based on relative probability of use (ten ordinal bins from 1-low to 10-high) and relative probability of mortality (ten ordinal bins from 1-low to 10-high) for elephants. This figure was adapted from Nielsen et al. (2006).

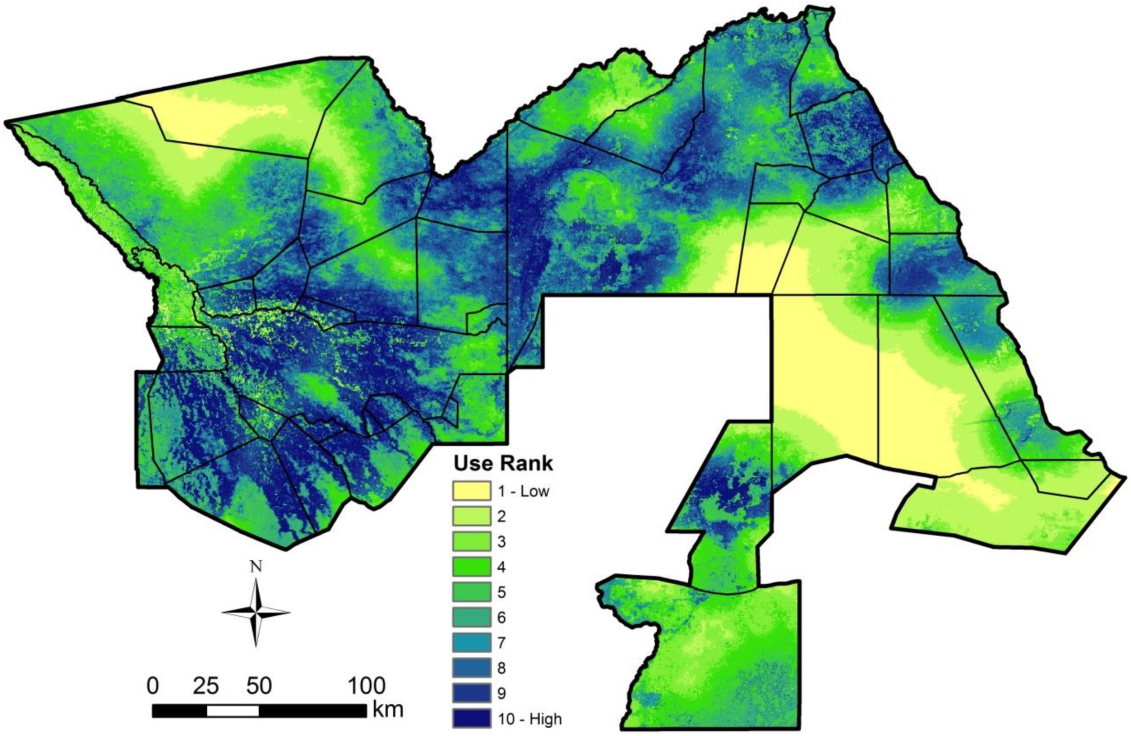
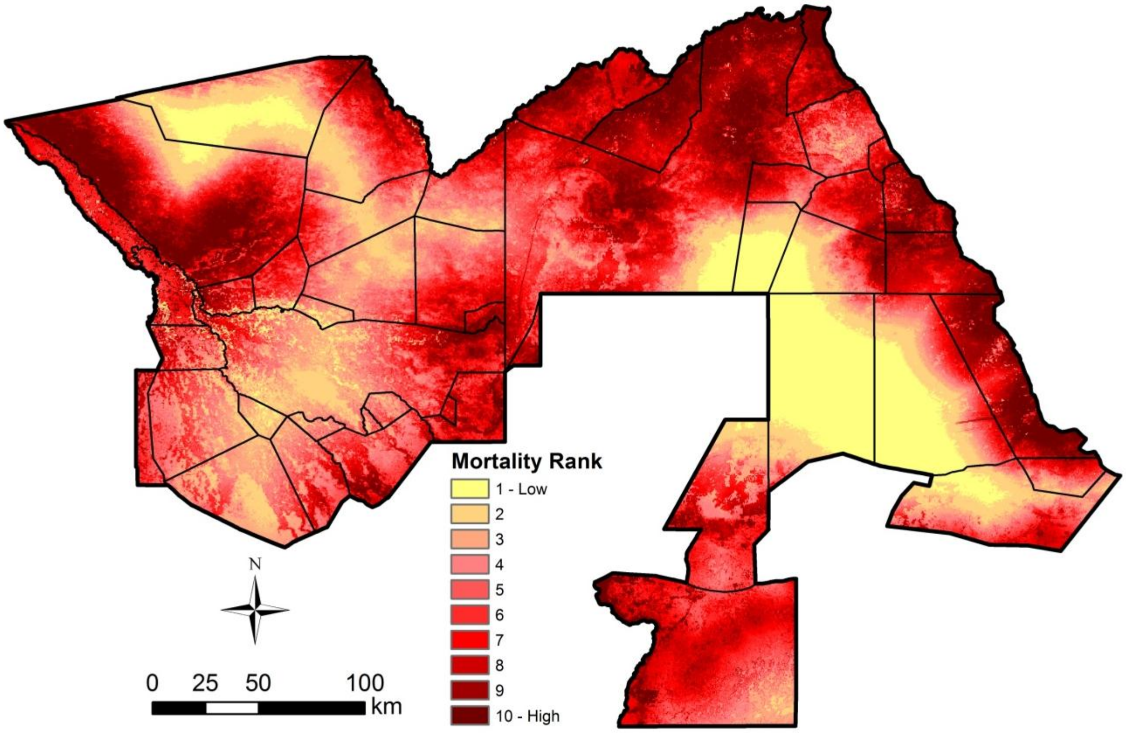


Figure 4-3. (a)



(b)

Figure 4-3. Relative probability of use (a) and relative probability of mortality (b) for elephants based on logistic regression models and binned into 10 ordinal classes. Relative probability of mortality represents year-round mortality events, whereas relative probability of use pertains to dry season (June – December) occurrence. Black lines indicate jurisdictional boundaries.

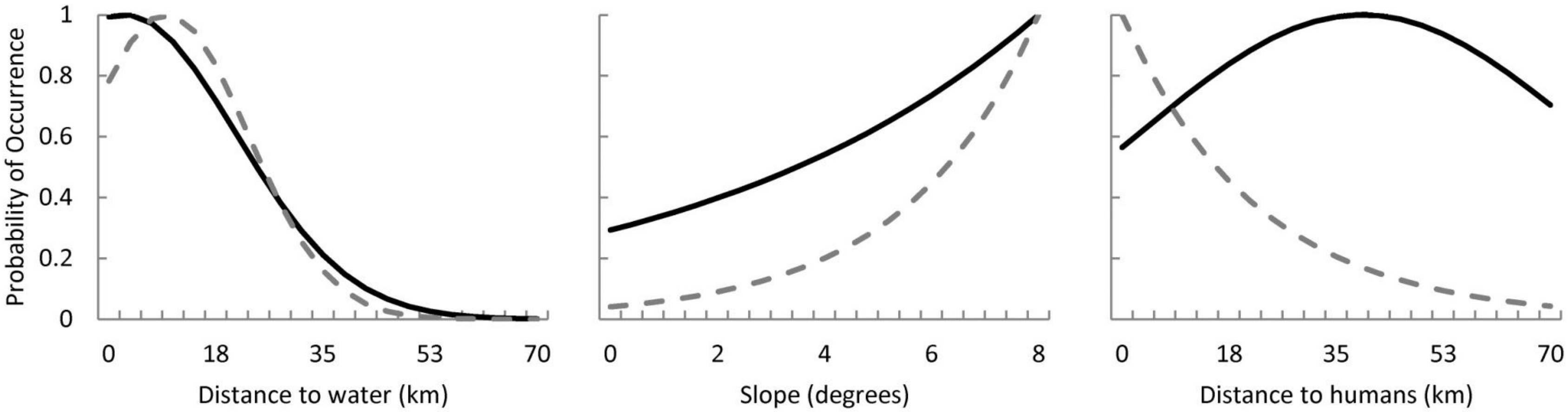


Figure 4-4. Relative probability of occurrence for live elephant (solid black) and elephant carcass (dashed gray) locations as a function of distance to water, slope, and distance to humans.

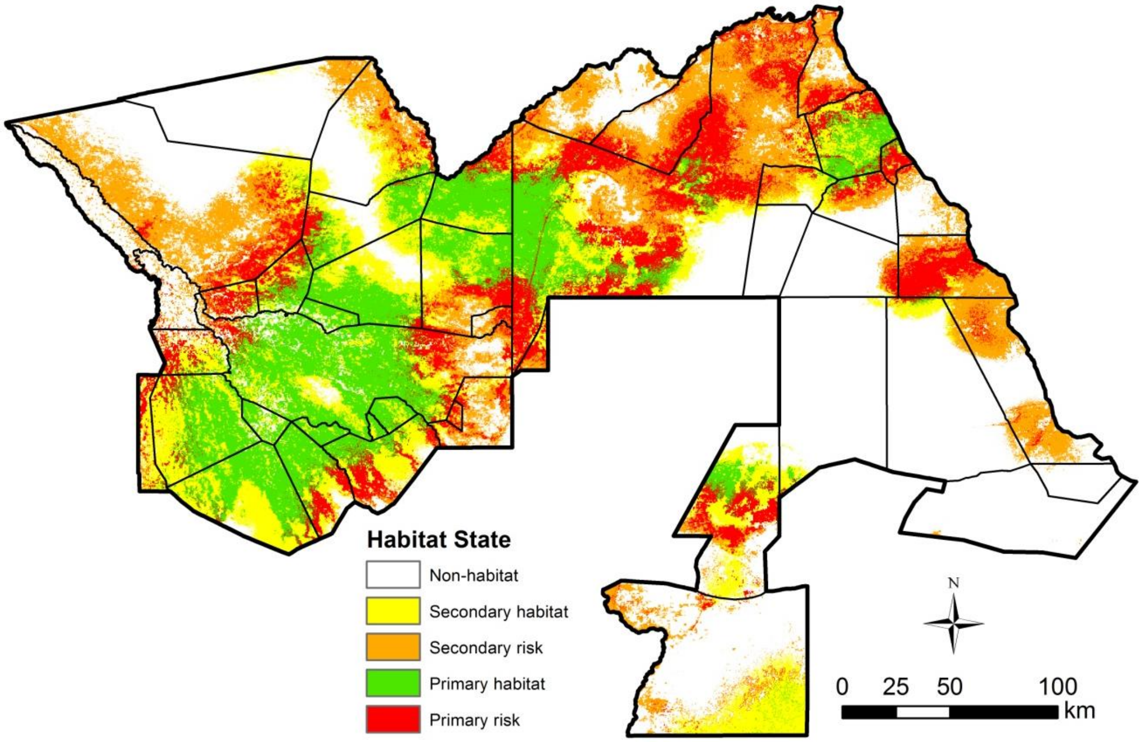


Figure 4-5. Habitat states for elephants in northern Botswana. Non-critical habitats represent areas of low elephant occurrence. Primary and secondary habitats represent areas with high to moderate use and low mortality. Primary and secondary risk areas represent regions with high mortality and high to moderate use by elephant.

Appendix A.

Test for potential biases caused by the stratified sampling design of the aerial surveys

Appendix A, Table 4-4. Transects were sampled more intensively when elephant density was known or suspected to be higher in the region. To ensure this did not introduce a source of bias, we sub-sampled the aerial survey transects and retained only points observed along 4km transect intervals. We then reran the logistic regression models with the sub-sampled data (sub-sampled) and compared the results to that of the original data (original). The sign of the coefficient did not vary, and the significance varied only for the elephant vs. random model for the "slope" covariate. The beta coefficients, however, did vary between the sub-sampled and original datasets.

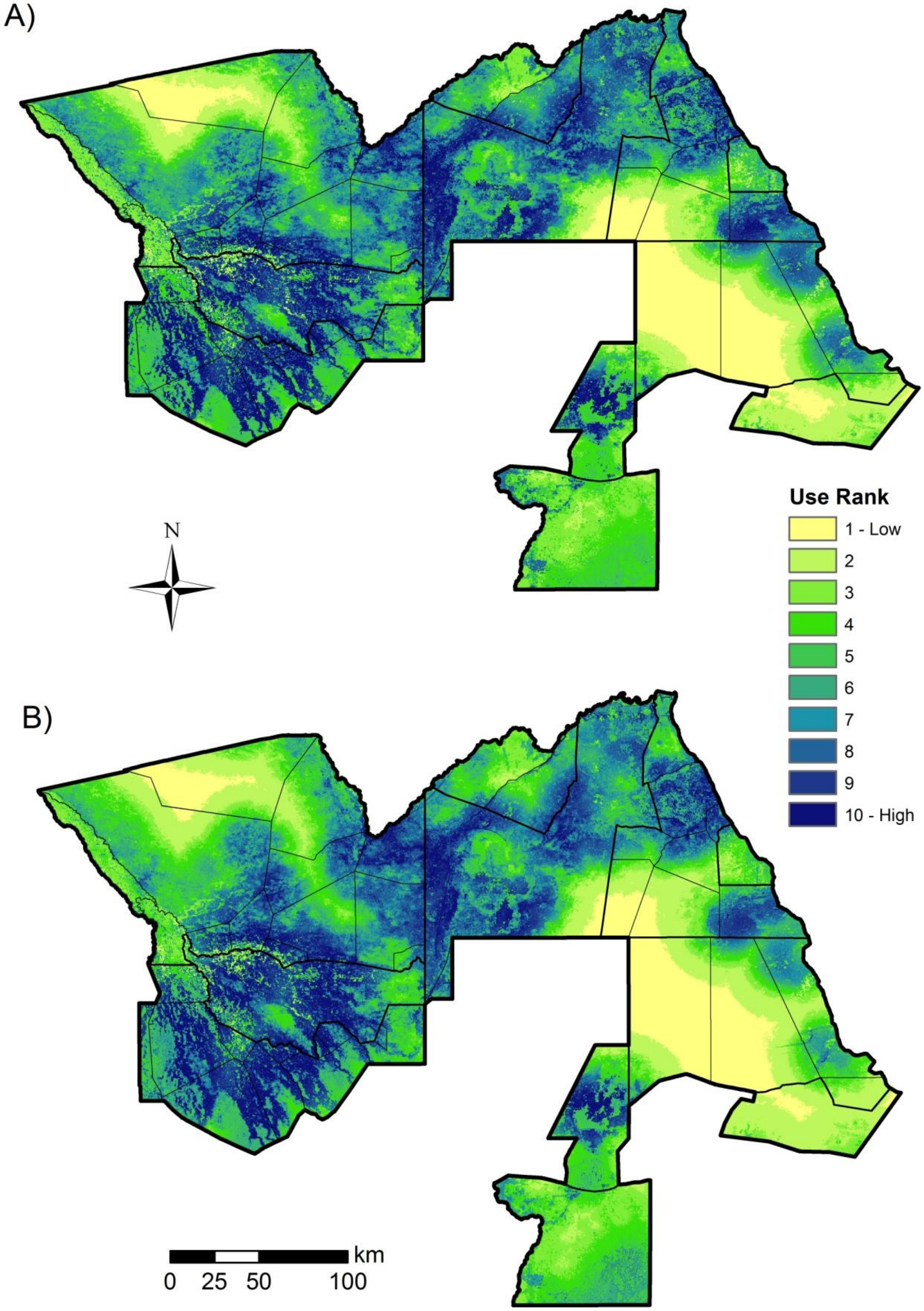
	Sub-sampled			Original			% Change
	β	SE		β	SE		in β
1) Elephant vs. Random							
Intercept	-3.06	0.10	*	-2.65	0.08	*	15.3%
Distance to water[a]	1.02	0.64		0.73	0.55		40.5%
(Distance to water[a])^2	-0.13	0.02	*	-0.15	0.02	*	-14.7%
Slope	0.06	0.06		0.15	0.04	*	-60.7%
Proportion tree	7.45	0.85	*	6.24	0.67	*	19.5%
(Proportion tree)^2	-20.40	2.88	*	-17.98	2.28	*	13.5%
Distance to humans[a]	1.82	0.56	*	2.92	0.46	*	-37.6%
(Distance to humans[a])^2	-0.02	0.01	*	-0.04	0.01	*	-36.4%
2) Mortality vs. Random							
Intercept	-4.73	0.22	*	-4.30	0.18	*	9.9%
Distance to water[a]	4.02	2.04	*	5.31	1.80	*	-24.3%
(Distance to water[a])^2	-0.21	0.07	*	-0.28	0.06	*	-25.0%
Slope	0.28	0.10	*	0.40	0.07	*	-31.5%
Proportion tree	13.61	2.67	*	13.36	2.23	*	1.9%
(Proportion tree)^2	-36.12	9.24	*	-38.83	8.01	*	-7.0%
Distance to humans[a]	-4.41	0.56	*	-4.52	0.46	*	-2.3%

a- Coefficient value and standard error multiplied by 100

Appendix A, Table 4-5. The elephant vs. random logistic regression model had the greatest differences in beta (β) coefficients when comparing the model produced from sub-sampled data to that of the original data. Therefore, we wanted to see how these changes influenced the relative probability of use surface. We created the probability surface for the sub-sampled model using identical methodology as the original data, and then subtracted it from the original probability surface to test for differences. The majority of the study area retained the same probability of use score (56.3%) or changed by ± 1 class (39.0%). Only 4.7% of the study area differed by more than ± 2 classes.

Difference	Percent of study area	Area (km^2)
< -4	0.0%	3
-3	0.1%	95
-2	1.3%	972
-1	16.4%	12,226
0	**56.3%**	**41,866**
1	22.6%	16,773
2	3.2%	2,383
3	0.0%	1
> 4	0.0%	1
Total*		74,321

* Total differs slightly from the value listed in the study area section because this calculation was based on square pixels.



Appendix A, Figure 4-6. Relative probability of use surfaces created using the sub-sampled (A) and original (B) data and binned into 10 ordinal categories.

Appendix B.

Model results using estimated dry season water availability

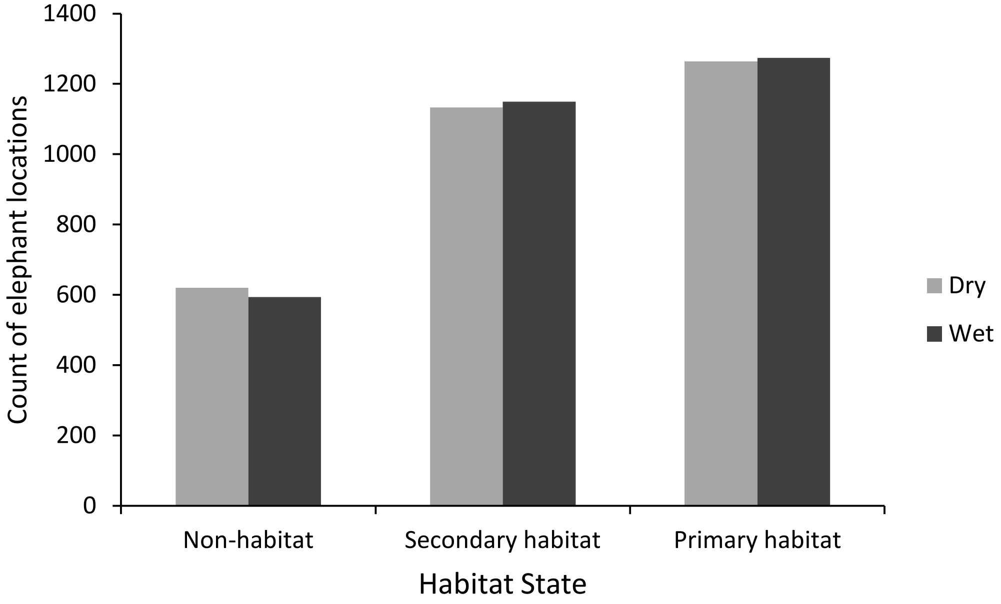
Appendix B, Table 4-6. Results of AIC model selection using dry season water availability. AIC values, change in AIC (ΔAIC), and the model weight (w) are presented for the three habitat selection models tested. The top model is presented in bold. Top models do not vary from those observed using the wet season water availability.

	Elephant vs. Random			Mortality vs. Random			Mortality vs. Elephant		
Model	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w
1	19199	929	0.00	3612	296	0.00	2213	225	0.00
2	18471	201	0.00	3483	166	0.00	2209	220	0.00
3	18401	131	0.00	3452	136	0.00	2204	215	0.00
4	18396	126	0.00	3423	107	0.00	2187	199	0.00
5	18776	506	0.00	3428	112	0.00	2034	45	0.00
6	18719	449	0.00	3384	68	0.00	2034	45	0.00
7	**18270**	**0**	**1.00**	**3316**	**0**	**1.00**	**1988**	**0**	**1.00**
8	18703	433	0.00	3365	48	0.00	2028	40	0.00

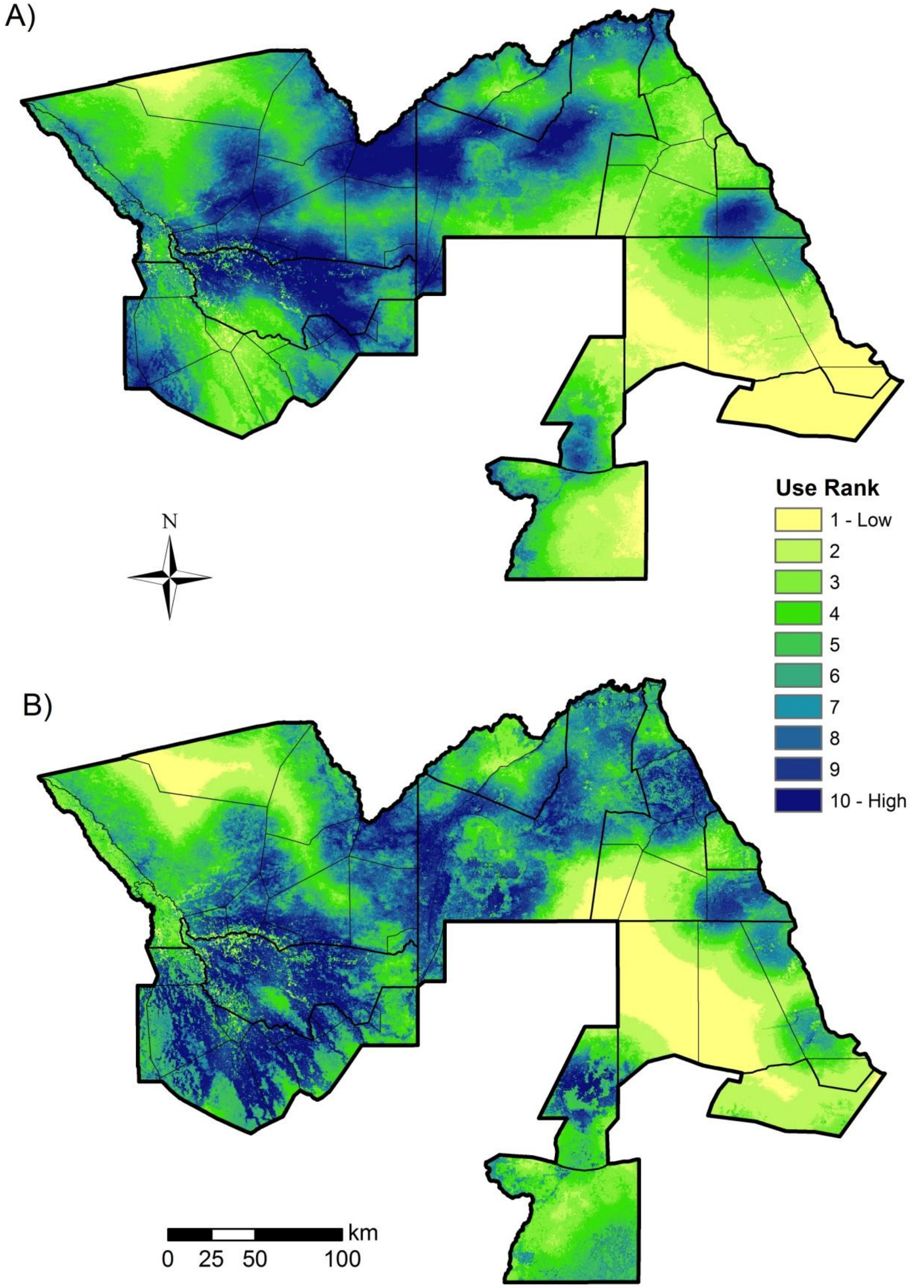
Appendix B, Table 4-7. Beta coefficients (β) and standard errors (SE) for the top-ranked AIC models. Because water varies seasonally, we compared model results estimated using water availability during the dry season (only permanent lakes and rivers were filled) with that of the wet season (all water sources). An asterisk (*) indicates where the confidence intervals did not overlap with zero. Model fit was good ($r_s > 0.96$) for all models.

	Dry Season Water			Wet Season Water		
	B	SE		β	SE	
1) Elephant vs. Random						
Intercept	-2.18	0.08	*	-2.65	0.08	*
Distance to water[a]	-4.65	0.33	*	0.73	0.55	
(Distance to water[a])^2	0.02	0.01	*	-0.15	0.02	*
Slope	0.15	0.04	*	0.15	0.04	*
Proportion tree	4.98	0.67	*	6.24	0.67	*
(Proportion tree)^2	-16.00	2.22	*	-17.98	2.28	*
Distance to humans[a]	3.69	0.47	*	2.92	0.46	*
(Distance to humans[a])^2	-0.04	0.01	*	-0.04	0.01	*
2) Mortality vs. Random						
Intercept	-4.10	0.18	*	-4.30	0.18	*
Distance to water[a]	2.38	1.27		5.31	1.80	*
(Distance to water[a])^2	-0.09	0.03	*	-0.28	0.06	*
Slope	0.40	0.07	*	0.40	0.07	*
Proportion tree	11.81	2.21	*	13.36	2.23	*
(Proportion tree)^2	-35.01	7.86	*	-38.83	8.01	*
Distance to humans[a]	-4.67	0.49	*	-4.52	0.46	*
3) Mortality vs. Elephant						
Intercept	-1.61	0.23	*	-1.45	0.24	*
Distance to water[a]	8.20	1.38	*	4.29	1.90	*
(Distance to water[a])^2	-0.14	0.02	*	-0.12	0.06	
Slope	0.32	0.09	*	0.27	0.09	*
Proportion tree	3.10	2.48		4.38	2.48	
(Proportion tree)^2	-11.95	8.37		-14.86	8.34	
Distance to humans[a]	-9.99	1.49	*	-8.05	1.45	*
(Distance to humans[a])^2	0.07	0.03	*	0.05	0.03	

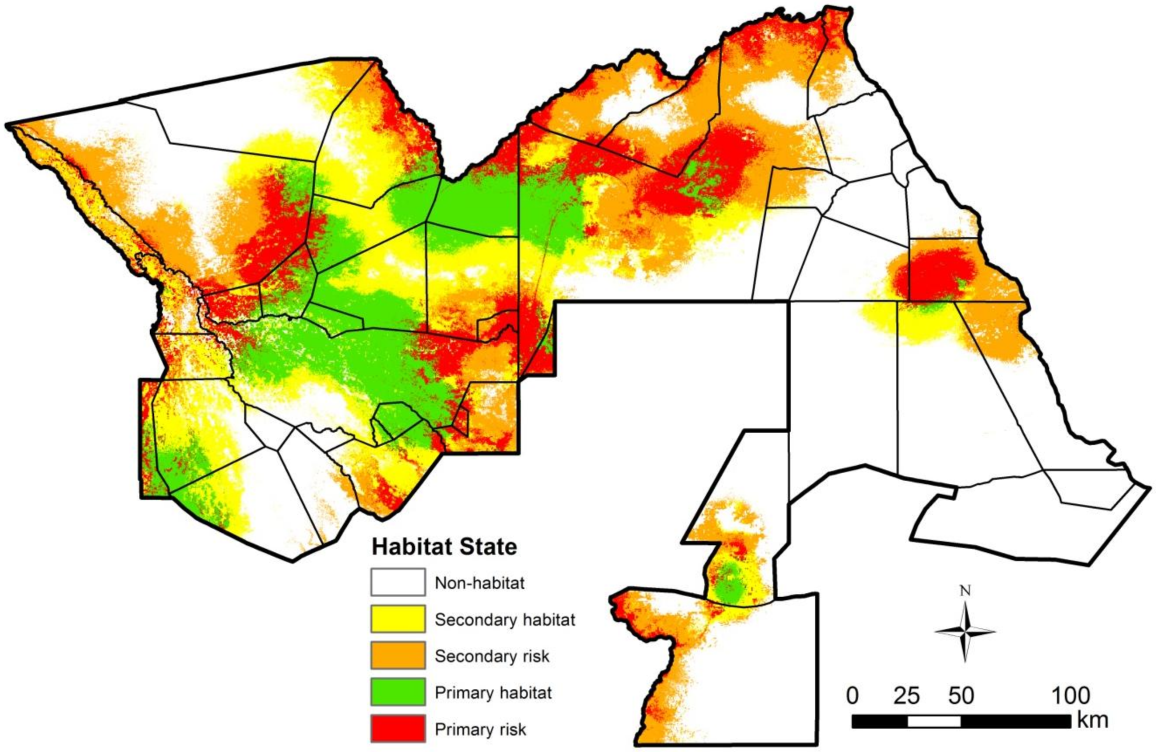
a- Coefficient value and standard error multiplied by 100



Appendix B, Figure 4-7. While model fit was good when using either the dry season or wet season water availability, the wet season water availability did a slightly better job at predicting the elephant use locations. The wet season probability surface had fewer locations in non-habitat and more locations in secondary and primary habitat than did the dry season probability of use model.



Appendix B, Figure 4-8. Relative probability of use predicted using dry season water availability (A) and wet season water availability (B) and binned into 10 ordinal categories.



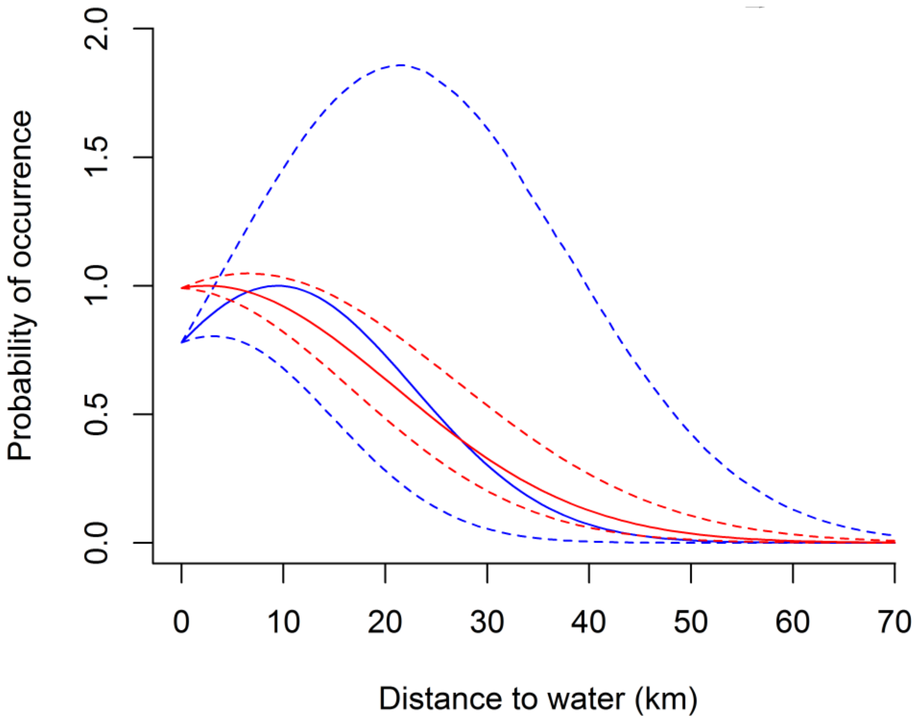
Appendix B, Figure 4-9. Habitat states for elephants calculated using the relative probability of use model estimated using dry season water availability and relative probability of mortality model estimated using wet season water availability. Seasons varied between the models because elephant use locations were observed in the dry season only, whereas elephant carcasses persist for several years so the mortality event could have occurred during any season.

Appendix C.

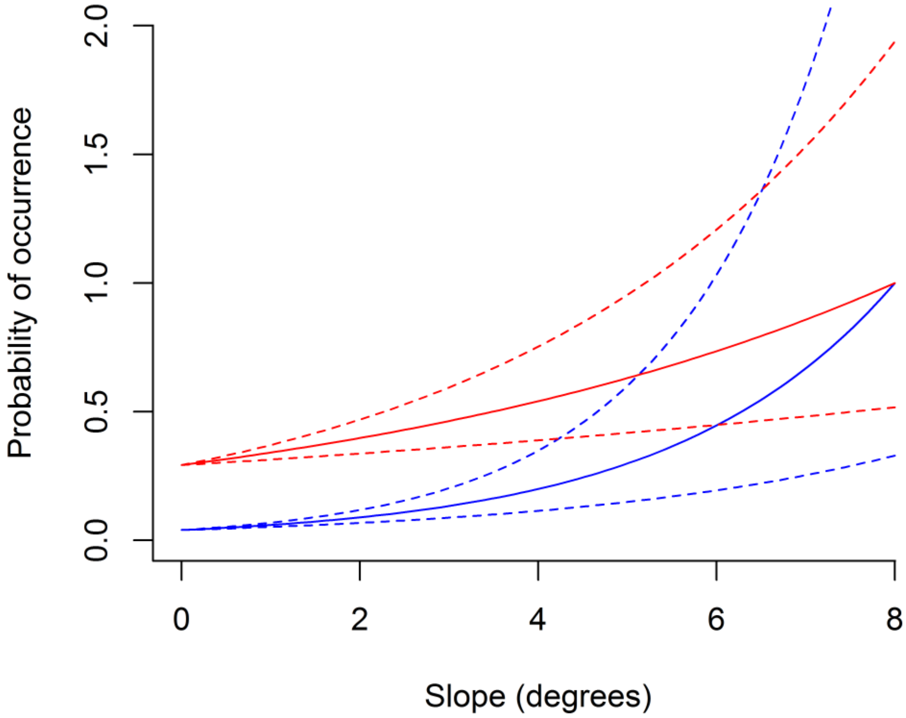
Full model results

Appendix C, Table 4-8. Results of AIC model selection. AIC values, change in AIC (ΔAIC), and the model weight (w) are presented for the three habitat selection models tested. The top model is presented in bold.

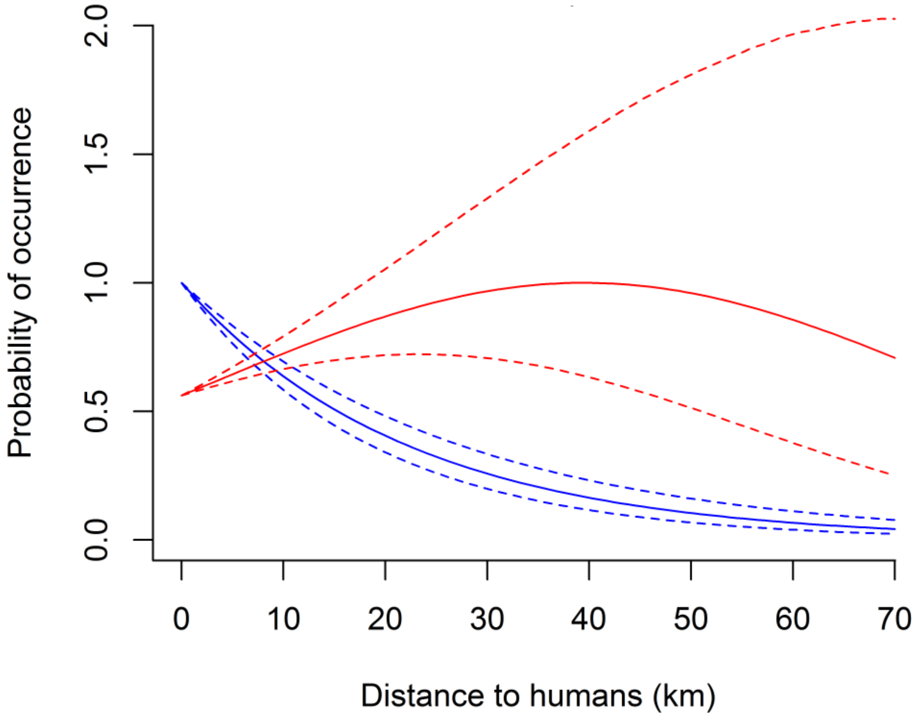
	Elephant vs. Random			Mortality vs. Random			Mortality vs. Elephant		
Model	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w
1	19199	827	0.00	3612	290	0.00	2213	187	0.00
2	18541	169	0.00	3507	186	0.00	2202	176	0.00
3	18434	62	0.00	3468	146	0.00	2196	170	0.00
4	18429	57	0.00	3434	112	0.00	2177	151	0.00
5	18776	404	0.00	3428	106	0.00	2034	8	0.01
6	18719	347	0.00	3384	63	0.00	2034	8	0.01
7	**18372**	**0**	**1.00**	**3322**	**0**	**1.00**	**2026**	**0**	**0.74**
8	18703	331	0.00	3365	43	0.00	2028	2	0.23



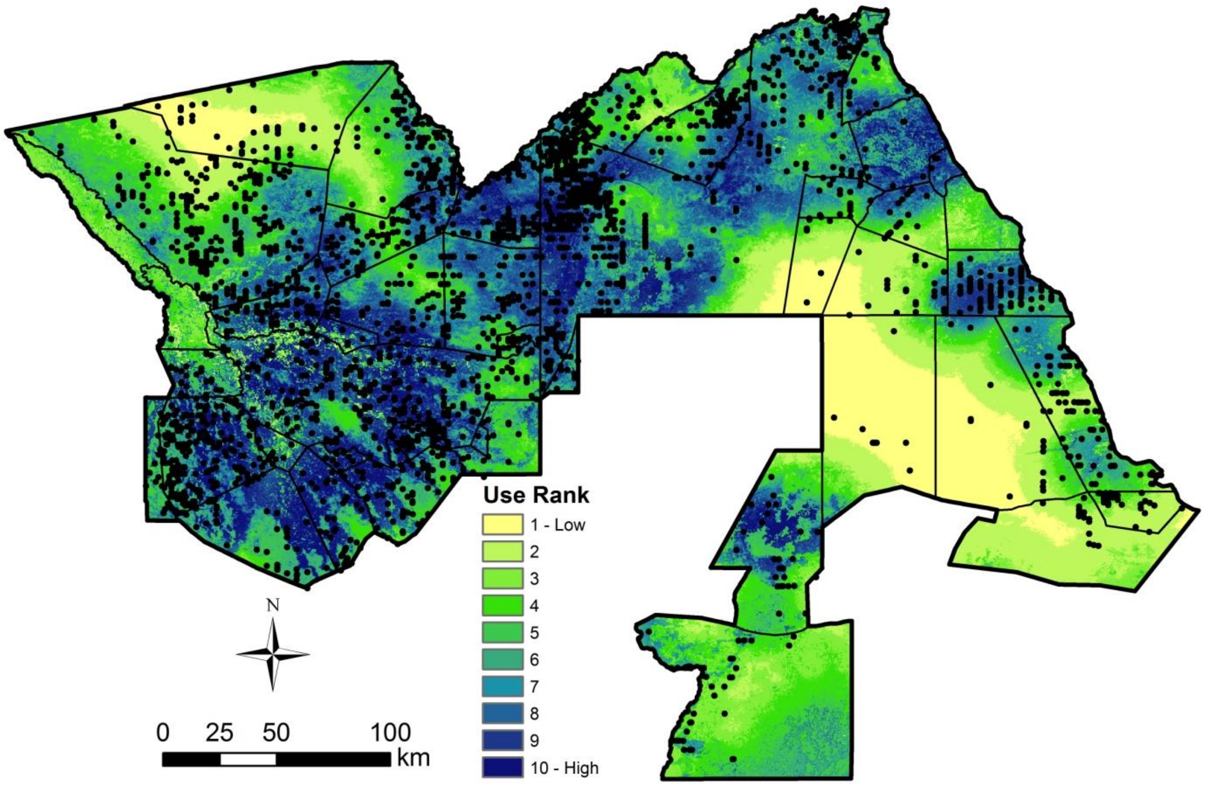
Appendix C, Figure 4-10. Relative probability of occurrence as a function of distance to water for live elephant (red) and elephant carcass (blue) with 95% confidence intervals (dotted line).



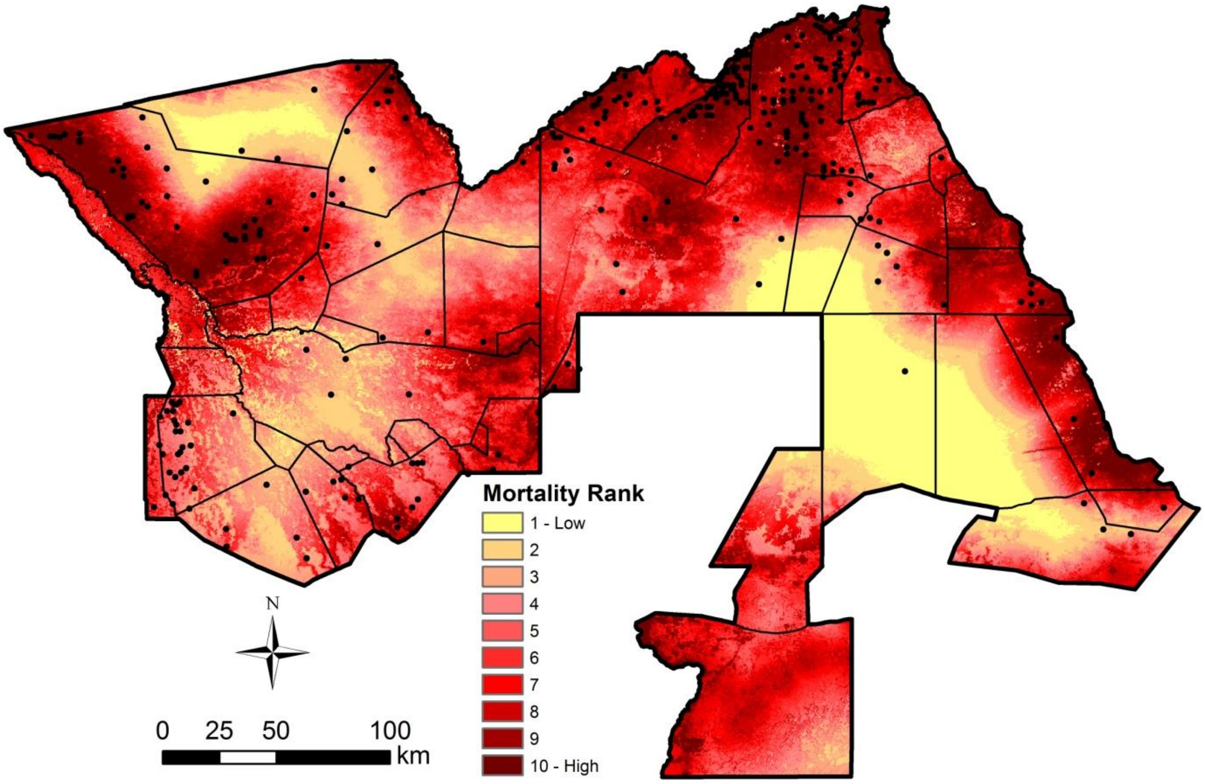
Appendix C, Figure 4-11. Relative probability of occurrence as a function of slope for live elephant (red) and elephant carcass (blue) with 95% confidence intervals (dotted line).



Appendix C, Figure 4-12. Relative probability of occurrence as a function of distance to humans for live elephant (red) and elephant carcass (blue) with 95% confidence intervals (dotted line).



Appendix C, Figure 4-13. Relative probability of use for elephants binned into 10 ordinal classes and overlaid with the live elephant observations (n=3 040) noted during the aerial survey (black dots).



Appendix C, Figure 4-14. Relative probability of mortality binned into 10 ordinal classes and overlaid with the elephant carcass observations (n=341) noted during the aerial survey (black dots).

Chapter 5. Similarity in habitat preferences impedes human-elephant coexistence

Publication Details

Roever, C.L., van Aarde, R.J., Chase, M.J. Similarity in habitat preferences impedes human-elephant coexistence. Ecology Letters, *in preparation*. R.J. van Aarde supervised the study, and M.J. Chase provided all of the aerial survey and telemetry data.

Abstract

Large conservation areas protect charismatic species and epitomize African savannahs, as do rural areas where people and wildlife live sympatrically but not always harmoniously. Incentives to include rural areas into conservation networks are lucrative and promise to improve conservation effectiveness. However, we show that in northern Botswana where a quarter of Africa's savannah elephants live, people occupy habitats that are sought after by elephants. Elephants trying to access resources in these areas then face increased mortality, particularly in the most suitable habitats. To mitigate this risk, elephants responded by selecting less suitable habitats. Consequently conservation strategies that promote human-wildlife coexistence may prove unsuccessful, particularly when resource competition leads to wildlife mortality. Conservation should ensure that people do not limit wildlife's access to prime habitat.

Introduction

The goal of national parks is to protect and preserve biodiversity in an increasingly human-dominated world; however, they are proving to be insufficient for the conservation of many large mammals (Morrison et al., 2007). Large mammals need large parks to preserve populations and to maintain ecosystem processes (van Aarde and Jackson, 2007). However, parks often fall short in both size and location (Rodrigues et al., 2004). To remedy these shortcomings, conservation networks are being developed to help link isolated populations and enlarge protected areas (Gonzalez et al., 1998; van Aarde and Jackson, 2007). Yet these initiatives often incorporate land where people live and hence increases contact between wildlife and people. Co-occurrence then leads to human-wildlife conflict to the detriment of both wildlife and conservation.

Efforts to deter wildlife from the human domain can often be compromised if people place their homes and infrastructure near places where animals need or want to be. A basic premise of ecology is that all habitats are not of equal value for a given species, and a large branch of conservation research is invested in identifying and protecting important habitats to ensure species persistence (e.g. Cabeza et al., 2004; Nielsen et al., 2006). However, across the globe, areas transformed through human activities generally overlap with areas of greatest ecological value. Human development coincides with areas of high biodiversity (Balmford et al., 2001) and areas with high net primary productivity (O'Neill and Abson, 2009). In mountainous areas human development occurs in valley bottoms, and in arid areas development occurs around rivers and lakes. Yet valley bottoms are associated with warmer temperatures and riparian habitat used by carnivores (Noss et al., 1996; Roever et al., 2008), and the rivers and lakes of arid environments are essential for the survival of many species (Fritz et al., 2003; Brawata and Neeman, 2011; Bhola et al., 2012). Human presence in these highly favorable areas invariably leads to high rates of human-wildlife conflicts, as both humans and wildlife compete for the same limited and valuable resource (e.g. Jackson et al., 2008).

It is often assumed that wildlife is simply displaced by human activity and anthropogenic features (McLellan and Shackleton, 1988; Whittington et al., 2005; Okello, 2009). However, displacement can occur only when suitable alternatives exist, and because resources are finite and spatially explicit, displacement may not be an option for wildlife. Many resources are essential for species survival, and animals will take greater risks to access those resources as they become increasingly limited. This is known as the predator-sensitive food hypothesis (Sih, 1980; Sinclair and Arcese, 1995); however here, we propose that humans may induce a similar response. Humans are a source of mortality for many species, and if humans choose to develop near rare and essential resources, animals are forced to take greater risks to access those resources. This can result in a variety of direct and indirect consequences for local wildlife populations, ranging from increased mortality (Benn and Herrero, 2002) to subtle shifts in animal behaviour and habitat selection (Harju et al., 2011; Latham et al., 2011).

Here, our goal is to quantify the spatial overlap between humans and prime wildlife habitat, and identify the consequences for the mortality and habitat use of a large mammal species, the African savannah elephant (*Loxodonta africana*). Elephants regularly come into conflict with humans, and a large collection of studies exist to mediate this conflict (Osborn and Parker, 2003). Yet these studies often focus on deterring elephants through various means including electrified fencing and noise (O'Connell-Rodwell et al., 2000), bees (King et al., 2009), or capsaicin derived from chillies (Hedges and Gunaryadi, 2009). While some deterrents are effective, they are ultimately a symptomatic response that does little to address why conflicts are occurring (Jackson et al., 2008). They also ignore the human factors that may contribute to increased human-wildlife interactions. We propose that human development of prime habitats causes competition between elephants and humans, creating detrimental effects for elephants trying access essential resources which are located near people.

Using aerial survey data, we modelled potential and realized habitat suitability as a consequence of human presence. The difference between these two suitability indexes identified areas of effective habitat loss due to humans, which we coin the “conflict zone.” We then looked at several aspects of influence from this conflict zone. First, we examined how the location of the human settlement in high or low suitable elephant habitat influenced the size of the conflict zone around a settlement. Next, we quantified incidences of mortality within and outside of the conflict zone, particularly in relation to habitat suitability. We expect that human presence and habitat suitability will interact to incur greater numbers of mortalities for elephants. Finally, we examined whether elephants collared with GPS telemetry collars shifted their selection in the conflict zone in order to decrease their mortality risk.

Methods

Study area

The study area was located in northern Botswana and encompassed an area of 74,355 km^2. The north and eastern portion of the study area was bounded by jurisdictional borders for the countries of Namibia and Zimbabwe (Figure 5-1). The study area included Chobe National Park, Makgadikgadi National Park, Moremi Game Reserve, and Nxai Pan National Park. The rest of the study area comprised multiple wildlife management areas, where legal hunting was allowed between the months of April and September. The largest human settlement at the periphery of the study area was the town of Kasane, which had a population of 9,127 people in 2011 (Botswana Central Statistics Office, 2011). Other smaller human settlements were located along roadways mainly on the periphery of the study area. Within national parks, people were present at hotels, campsites, and park offices. Road densities were relatively low at 0.073 km/km^2. Vegetation in the study area was composed primarily of deciduous dry woodlands with interspersed grasslands (Gaughan et al., 2012), and terrain was relatively flat, with the steepest slopes of eight degrees occurring along the Chobe River.

Elephant Data

Elephant location data was obtained using two independent methodologies, aerial survey estimates to assess the locations of all individuals in the population and telemetry collar data to obtain detailed spatial information for several individuals. Aerial surveys were conducted during the dry season of 2010 between the months of June to December. Following the methods of Norton-Griffiths (1978), parallel strip-transects were flown at a speed of 160km/hour and 300 feet above ground. Two observers, positioned on either side of the plane, recorded the location of elephants seen within a 400 m wide strip. Tape placed on the windows helped observers to maintain a consistent observation distance. Observers recorded the location, time, sex, and number of elephants. They also recorded any elephant carcass observed, along with the condition of the carcass and any signs of poaching. The survey area was divided into 42 sampling units and sampling intensity (or the distance between parallel strip-transects) of each unit varied to minimize sampling effort. Units with higher populations of elephants were surveyed more intensively. Survey intensities varied from 1, 2, 4, and 8 km, which accounted for 40, 20, 10, and 5 percent coverage of the sampling units. Because the varying survey intensities were not biased towards a particular habitat type, we inferred that it would not influence habitat selection models. The orientation and spacing of flight paths was determined using DNR Garmin Sampling Extension in ArcView (ESRI, Redlands, California). For more detailed description of the aerial surveys see Chase (2011).

Within the study area, Elephants Without Borders has been fitting telemetry collars on elephants since 2001, and they maintain a database of telemetry data with varying collaring dates and relocation intervals. For the purposes of this study, we included data collected at hourly intervals from June to December 2010 and therefore during the same period as the aerial survey. We only used individuals (3 females and 5 males) for which at least 1,000 locations were recorded during the study period, resulting in a total of 17,349 locations. We then created 95 percent kernel home ranges for each individual using Geospatial Modelling Environment (Beyer, 2011). We tested the BCV2, LSCV, Plugin, and SCV bandwidth estimators from the 'ks' library in R (Duong, 2012) and found that SCV produced the most appropriate kernel density estimates based of the distribution of locations.

Habitat covariates

To model habitat selection, we used a suite of landscape layers which are known to account for elephant space use (Roever et al., 2012), namely water, slope, tree cover, and human presence. Dry season surface water was identified using data from Tracks4Africa (2010) and was manually validated against Landsat imagery. Distance to water (km) was then calculated for each location. Next, slope (degrees) was calculated from a 90 m digital elevation model (Jarvis et al., 2006), and proportion of tree cover was obtained at a 500 m resolution using the MODIS Vegetation Continuous Fields product (Hansen et al., 2006). Finally, we quantify human use across the landscape using Landscan (2008) human population data. Originally estimated as human density at a 1 km resolution, we identified areas with greater than 16 people/km^2 , which was the lowest published density where elephants avoid human settlements (Hoare and Du Toit, 1999). We then calculated distance to these high human-use areas. All geospatial analysis was completed using the Spatial Analyst extension of ArcGIS 10.0 (ESRI, Redlands, California) and Geospatial Modelling Environment (Beyer, 2011).

Habitat selection models

Using the aerial survey data, we first quantified potential and realized habitats for elephants using resource selection function models. We used a design I approach because individuals were not uniquely identified and individuals were only sampled once (Manly et al., 2002). Since elephants often occur in herds, each elephant herd accounted for one location resulting in a sample size of 3,040 locations. Within a logistic regression model, elephant location data was compared to random locations distributed across the study area at a density of 1 point per 3 km^2. The same set of elephant and random locations were used for both the potential and the realized habitat models.

We then created two models of elephant use. To model potential habitat use, we examined selection for water, slope, and tree cover and excluded the variable pertaining to human presence. This created an estimation of selection for landscape features not related to human presence. Next, we created the model for realized habitat use by further including the covariate for human presence. For both models, all variables were tested for non-linearity by examining histograms and, when warranted, testing model fit with the inclusion of a quadratic term. Correlations between variables were tested using Pearson's correlation coefficient. Variables with an $r > 6.0$ were not included together in the same model; however, we found no evidence of correlations. Model fit of the top-ranked model was evaluated using k-fold cross validation ($k = 5$) and the Spearman rank correlation coefficient (Boyce et al., 2002). Analyses were conducted in R (R Core Team, 2012).

Using the resultant potential and realized habitat models, we predicted the probability of use by elephants across the study area. These predictions were also projected to a 40 km wide buffer around the study area because six of the eight collared elephants left the study area bounds during the tracking period. The habitat models estimated a probability of use in continuous values, but to make direct comparisons between the two maps, we classified the continuous values into 5 ordinal bins using the quantile method in ArcGIS 10.0, with the lowest use equal to 1 and the highest equal to 5 (Nielsen et al., 2006). We then subtracted the potential habitat from the realized habitat to identify areas of displacement as a function of human presence. This allowed us to quantify the zone of influence that is a consequence of human presence (henceforth referred to as the conflict zone) without introducing a need to arbitrarily assign a distance buffer around human settlements.

Assessing the consequences of human presence

Finally, we assessed how mortality locations and individual selection preferences were influenced by the presence of humans. Using the mortality data, we partitioned morality events based on location within or outside of the conflict zone. We then used a logistic regression to test whether there was a relationship between the morality locations and habitat suitability (using the potential habitat use index). Mortality locations were compared to random locations generated at a density of 1 point per 3 km^2. Separate models were developed for locations occurring within and outside of the conflict zone. If competition exists between humans and elephants for highly suitable habitat, we expect to see a stronger relationship between habitat suitability and mortality event in the conflict zone.

Finally, we used the elephant telemetry data to examine how individual elephants modified selection patterns as a consequence of their location with respect to the conflict zone. For each animal, we modelled selection for the five habitat suitability classes from the potential habitat model using a logistic regression model, withholding habitat class five. We compared telemetry locations (1) to random locations (0) generated at a density of 1 point per km^{2}to test selection relative to availability. Based on habitat selection theory, selection for the habitat classes should increase with increasing habitat suitability. We then qualitatively compared selection by elephants which were always outside of the conflict zone to those which had greater than 20 percent of their home range in the conflict zone.

Results

Habitat selection for water, slope, and tree cover were similar for the potential and realized habitat selection models (Table 5-1, Figure 5-2). Elephants selected areas close to water, with steep slopes, and with intermediate tree cover. Slopes in the study area are mostly associated water sources and this could explain the apparent selection for steep slopes. In the realized habitat selection model, elephants avoided areas near people, and the model exhibited a slightly quadratic relationship, suggesting that elephants also avoid areas far from people.

By subtracting the potential habitat from the realized habitat model, we identified areas where use decreased as a function of human presence (i.e. the conflict zone). The conflict zone accounted for 43 percent of the buffered study area (Figure 5-3). Settlements located in less suitable elephant habitat had little to no conflict zone, while settlements in highly suitable habitats had conflict zones extending up to 21 km from the settlement edge (Figure 5-4, see Figure 5-7 in Appendix A). However, few human settlements occurred in areas unsuitable for elephants. Only 3 percent of the 1 km^2 pixels with a human density of >16 people/km^2 occurred in areas classified as 1 on the potential habitat use index. Unsuitable areas accounted for 20 percent of the buffered study area.

The displacement model also predicted decreased use by elephants of the central Okavango Delta (Figure 5-3). This is an artifact of the quadratic relationship for the human covariate, as distances far from people had slightly decreased use in the realized habitat model. Its remote location in the delta, however, means that is it unlikely to be an area of increased conflict; therefore, we reclassified this band of conflict zone as beyond the conflict area for the mortality and telemetry analysis. When examining elephant mortalities, 58 percent of carcasses were located in the conflict zone, an area that accounted for only a third (31 percent) of the aerial survey area (Figure 5-3). Mortality risk increased as a function of habitat suitability both inside (beta = 0.433, se = 0.074) and beyond (beta = 0.257, se = 0.059) the conflict zone. However, the slope of the coefficient in the conflict zone was nearly double to that beyond, and in highly suitable habitat inside the conflict zone we counted nearly double the number of carcasses than in similar habitat beyond the conflict zone (Figure 5-5). Consequently, when elephants were in the conflict zone, mortality risk increased more markedly as a function as habitat suitability.

One of the 8 elephants that we tracked had most of his home range within the conflict zone. Four (2 males, 2 females) elephants used areas both inside and outside of the conflict zone, and three (1 females, 2 males) had almost all of their home ranges beyond the conflict zone (Table 5-2). Selection for the one female and two males which were outside of the conflict zone conformed to our expectation of increasing use with increasing habitat suitability (Figure 5-6). These individuals used habitat classes 1 and 2 as they were available and had positive selection for classes 3 and 4. Only one male (EM0192) had positive selection for habitat class 2.

The pattern of selection among individuals within the conflict zone did not follow our expectations. For females, EF0196 selected habitat classes 1 and 2 and EF0194 selected classes 2 and 3. All males had negative or neutral selection for all habitat classes. Both males and females within the conflict zone had negative or neutral selection for habitat class 4, whereas outside of the conflict zone all individuals had positive selection for this class.

Discussion

We demonstrated that human occupation of highly suitable wildlife habitats has escalating implications for elephants in northern Botswana. First, humans tended to settle in areas that were highly suitable for elephants, and in so doing, decrease habitat suitability disproportionally as compared to settlements located in less suitably habitats. For example, we found that settlements located in highly suitable habitat reduced habitat suitability for elephants up to 21 km from the settlement edge (Figure 5-4). This area of reduced suitability was defined as the conflict zone. Second, we found that mortality was more likely to occur in the conflict zone than elsewhere. Not only did mortality generally increase, but mortality in highly suitable habitats near people was twice as high as background levels, indicating that human-elephant conflict was more intense in highly suitable habitats than in those less suitable (Figure 5-5). Finally, habitat selection by elephants changed as a consequence of human presence. While female elephants used less suitable habitats when in the conflict zone, males showed a negative or neutral selection for all habitat categories. Furthermore, all individuals outside of the conflict zone selected for the highest habitat suitability category; all animals within the conflict zone avoided or had neutral selection for these areas.

The behavioural and mortality effects that human presence has on elephants imply competition. Both elephants and people benefit from rivers. For elephants, rivers provide water and riparian vegetation and large trees provide shade (Kinahan et al., 2007), all of which are essential during the extreme climatic conditions that prevail during the dry season in our study area. Proximity to water is also essential for rural people, as the relatively fertile soils and surface water provides for the needs of their cattle and crops. Therefore, both elephants and people prefer to be close to water, and as humans are also a source of mortality for elephants, elephants must take greater risks to access a resource that is limiting (Sih, 1980; Sinclair and Arcese, 1995). In response to people, elephants used less suitable habitats, possibly making it more difficult for individuals to fulfill their nutritional and other daily requirements. Displacement from prime habitat may also influence movement rates, which could be particularly detrimental for breeding herds. For these mixed herds of females and offspring, roaming distances are likely to increase, and increased roaming distances reduces survival in young elephants (see Young and van Aarde, 2010). The spatial displacement (behavioural response) and reduced survival (demographic response) due to the presence of people, suggests that elephants lose out in this apparent competitive interaction with people.

While others have shown that placement of human settlements near reserves contributes to human-elephant conflict (Graham et al., 2010), we further demonstrate that it is the placement of those settlements in the most suitable habitats that contributes to elephant mortality. Crop fields located around settlements is a good example; as the settlements are located in areas already coveted by elephants, the crops may further lure animals close to people. While researches have generally taken a symptomatic approach to repel elephants from human settlements (Jackson et al., 2008), this approach may contribute to detrimental attitudes towards elephants. Symptomatic solutions aim to modify the behaviour of wild animals to conform to human rules of good conduct and may perpetuate ideas that elephants are “problems” which must be dealt with accordingly. Even the term “conflict” is inherently combative (Lee and Graham, 2006). Here, however, we show that elephants do shift their behaviour to decrease interactions with people. In the town of Kasane, elephants access water at night possibly to avoid people (personal observation), and they moved closer to human settlements at night during the dry season, when water is limiting (Jackson et al., 2008). Ultimately, efforts to deter elephants from human settlement will continue to have limited success because they work against the inherent behaviour of elephants. A more successful approach would be to regulate human behaviour or, if necessary, spatially separate humans and elephants to reduce competition altogether.

A behavioural shift in habitat selection patterns has been documented as a response to predators (e.g. Creel et al., 2005); however, it has not been well documented in response to humans. We found only one study qualifying changes in selection as a function of human activity (Harju et al., 2011). Yet, these changes in selection patterns could have important consequences for conservation. Habitat selection studies are often used to inform conservation decisions (e.g. Nielsen et al., 2006; Chetkiewicz and Boyce, 2009). However, if selection is estimated in an area occupied by humans, then selection by animals could be biased towards less suitable habitats. As a consequence, habitat protection measures would incorrectly protect habitat of inferior quality. Habitat selection by individuals also influences habitat structure. For instance, elk in Yellowstone National Park have reduced willow recruitment (Ripple and Larsen, 2000), and elephants at high densities due to water supplementation and fencing have caused dramatic changes to woodlands (Western and Maitumo, 2004; Chafota and Owen-Smith, 2009). Just as wolf reintroduction into Yellowstone caused a cascade of behavioural changes in elk which resulted in decreased selection for willow and its subsequent recovery (Fortin et al., 2005), human presence could initiate similar changes in selection patterns, resulting in unexpected or unpredictable changes to vegetation structure.

Human-wildlife competition may further call into question the modern conservation paradigm that promotes human-wildlife coexistence through corridors, habitat preservation, and low-impact human use (Woodroffe et al., 2005). Coexistence initiatives attempt to make human-use areas more hospitable to wildlife, and they rely on decreasing human-induced mortality. However, these initiatives will likely prove unsuccessful if humans and wildlife are competing over the same limited resources, particularly when the consequence of this competition is mortality of wildlife. If human occupation increases on the landscape and human patterns of habitat selection remain unchanged, elephant’s access to waterways will be further impeded. Appropriate zoning of these highly coveted habitats will likely be necessary to reduce human-elephant competition and provide for the safety and sustenance of both wildlife and people.

Ultimately, habitat suitability plays a key role in the impact human development will have on wildlife, reducing effective habitat, increasing mortality, and shifting selection patterns to less suitable habitats. While these changes were not unexpected, the magnitude of the response by elephants to humans was unanticipated. Human settlement of greater than 16 people/km^2 occupied only 1,200 km^2 of the buffered study area, comprising 0.7 percent of the landscape. These settlements in Botswana are mostly small villages with cleared land immediately around the village which was hand or animal-tilled. There was also little motorized noise. Yet, even this low-level human presence had far-reaching consequences for elephants, resulting in a conflict zone which comprised 43 percent of the greater study area. Consequently, in 43 percent of the study area, elephant mortality was higher than background levels and elephant behaviour was altered.

Habitat utilization in the absence of humans can never be truly known given the current, widespread distribution of people. But using present-day habitat selection patterns, we can attempt to estimate displacement and other consequences of human activity. Here, we identified habitats of high suitability using aerial survey data, and quantified individual use and mortality risk within these habitat categories. While this method has limitations, it standardized what was a very complex landscape, and it ultimately helped to identify changes in selection as a consequence of human activity. We have provided evidence that human activities have compounding effects on elephants, and habitat suitability plays a key role in the magnitude of the influencing factors. As human development increases on the landscape, it will be increasingly important to identify how human presence alters animal behaviour. In particular, ecologists must consider the implications of resource competition between humans and wildlife. Human habitat selection patterns and resource needs are often congruent with those of wildlife, as shown here, and human develop of high-quality habitats could magnify our impacts to those species.

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Table 5-1. RSF models for potential and realized habitat use. Estimated using elephant aerial survey data (one point per elephant herd at one time period).

	Potential			Realized		
	Coefficient	SE		Coefficient	SE	
Distance to water	0.004	0.006		0.007	0.006	
(Distance to water)^2	-0.001	<0.001	*	-0.001	0.000	*
Slope	0.124	0.044	*	0.154	0.044	*
Proportion tree	6.551	0.673	*	6.237	0.673	*
(Proportion tree)^2	-19.060	2.280	*	-17.980	2.280	*
Distance to humans	-	-		0.029	0.005	*
(Distance to humans)^2	-	-		-0.001	<0.001	*
Spearman $\bar{r}_s$	0.985			1.000		

Table 5-2. Home range statistics for telemetry collared elephants between June and December 2010.

Elephant ID	Sex	Telemetry locations (n)	Home range size (km^2)	Percent in conflict zone
EM0187	M	3,450	409	85
EF0194	F	1,805	1,388	59
EM0189	M	3,010	730	52
EF0196	F	1,175	2,704	43
EM0195	M	1,152	2,801	22
EM0192	M	1,792	1,668	1
EF0191	F	1,826	412	1
EM0190	M	3,139	788	0

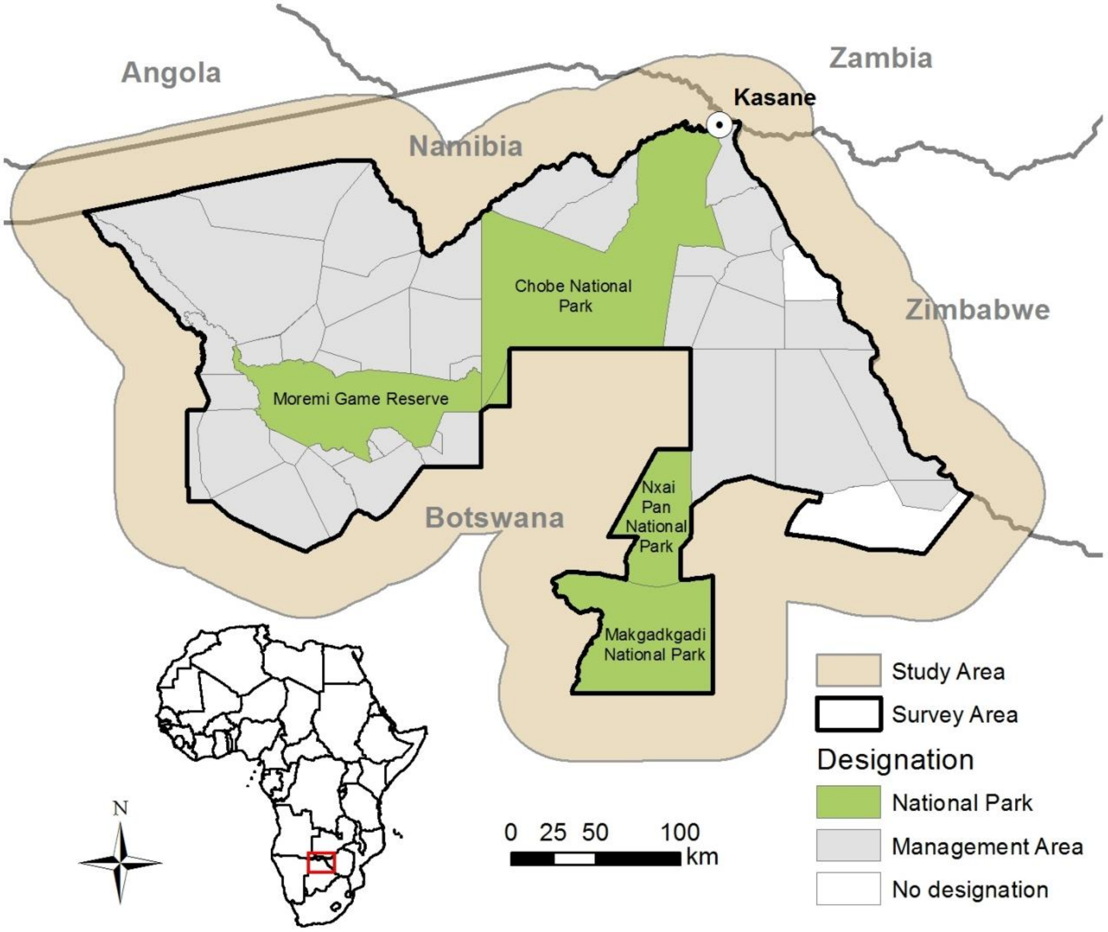


Figure 5-1. Map of the study area located in northern Botswana. The area included three national parks, one game reserve, and multiple wildlife management areas (gray). Aerial surveys were conducted in the survey area, which was buffered by 40 km to accommodate the data obtained from elephants equipped with telemetry collars.

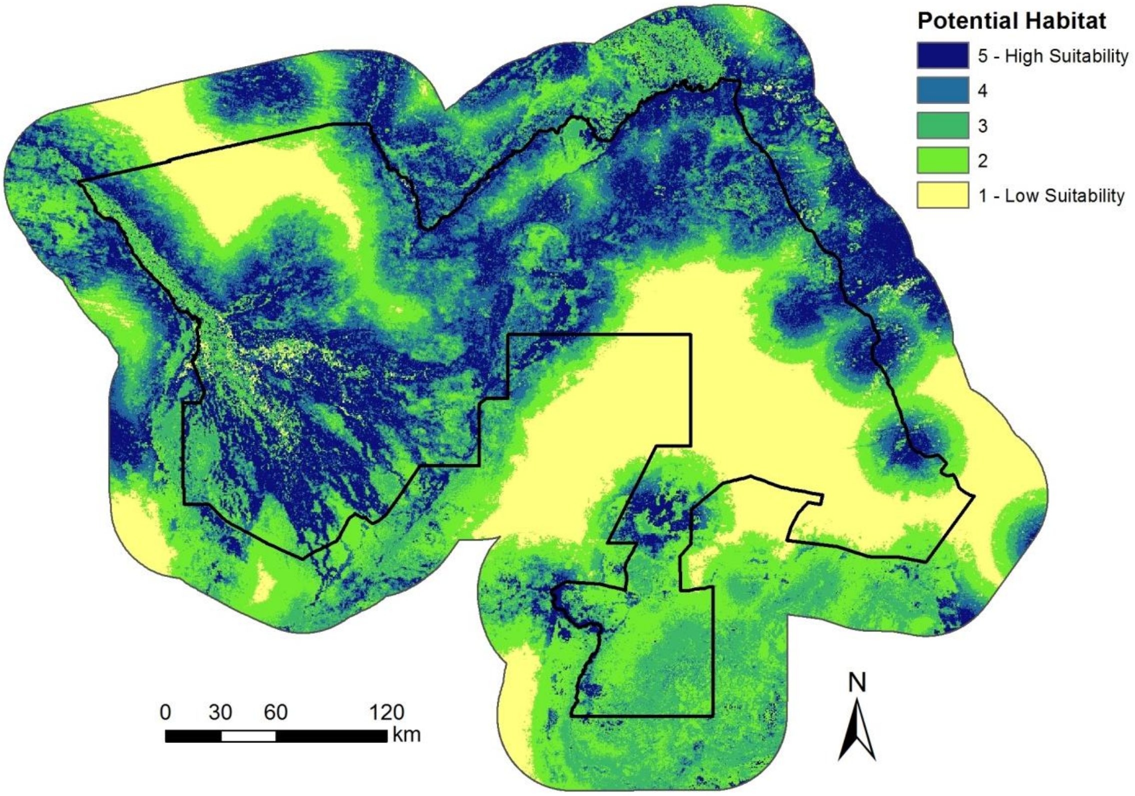
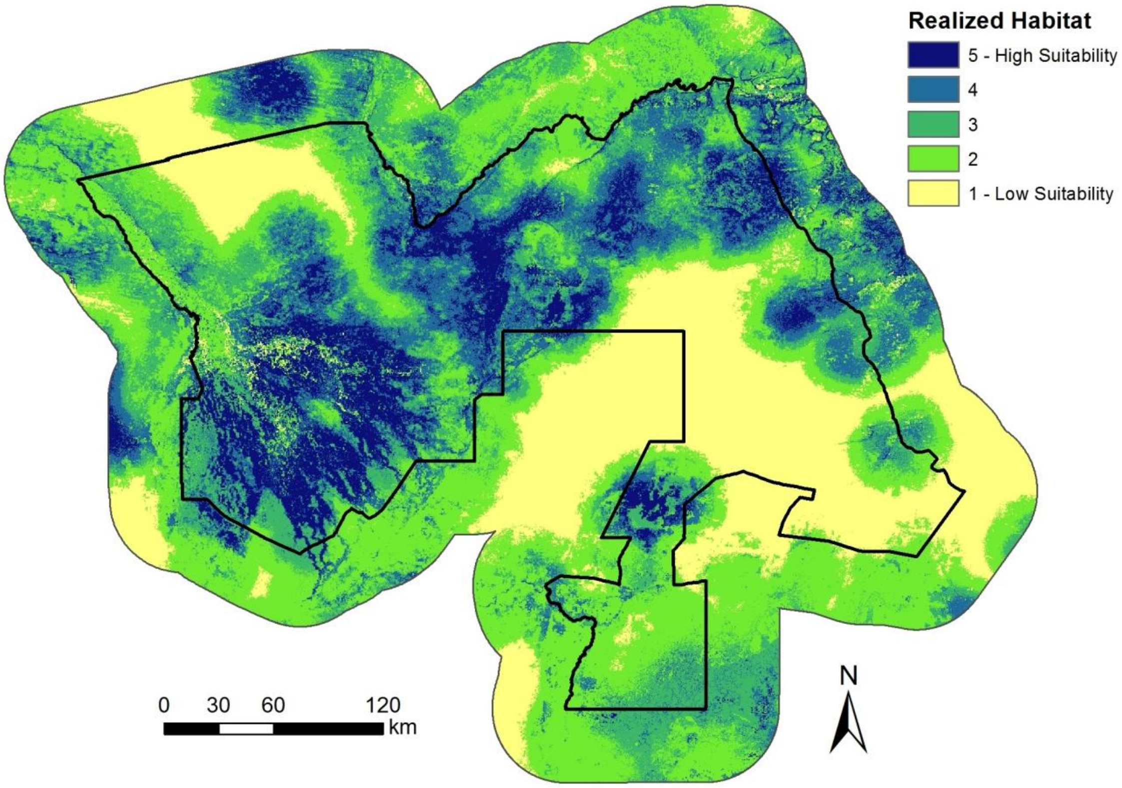

Potential Habitat
5 - High Suitability
4
3
2
1 - Low Suitability
0
30
60
120
km
N

Figure 5-2. (a)



(b)

Figure 5-2. Potential habitat (a) and realized habitat (b) for elephants. Habitat use is reduced in the realized habitat model due to the presence of humans. Habitat selection indexes were estimated beyond the aerial survey area (black line) at a distance of 40 km.

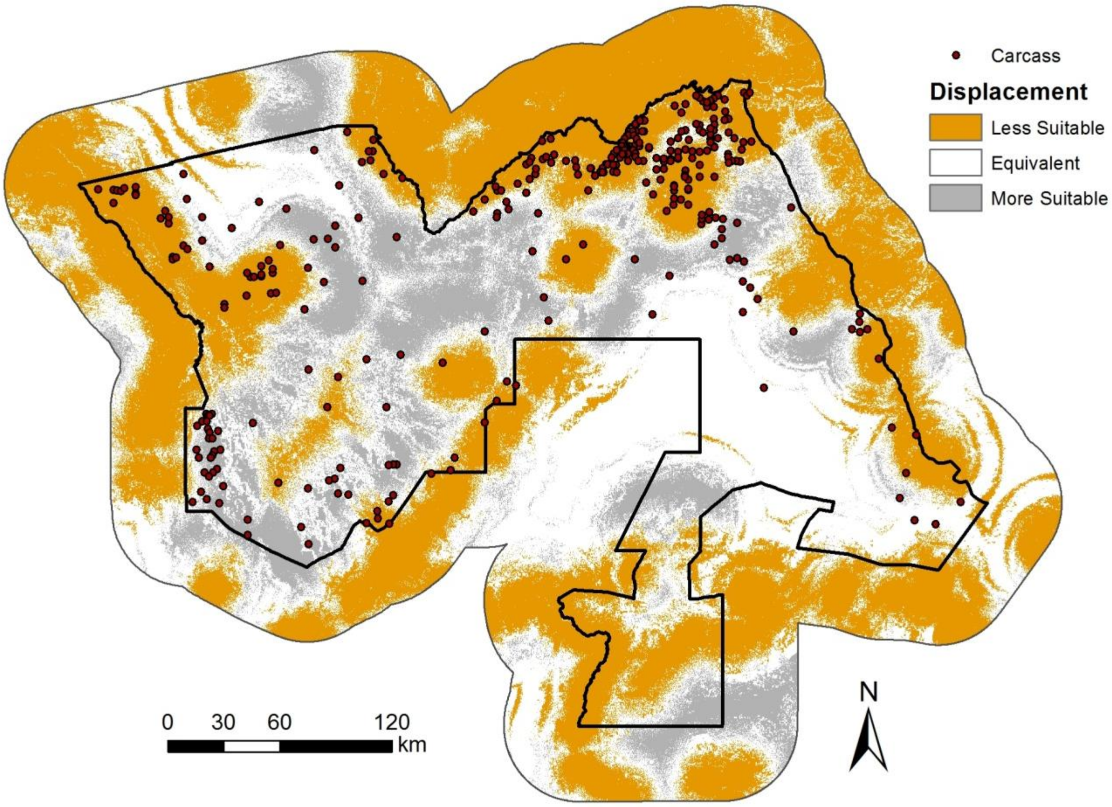


Figure 5-3. Potential habitat minus realized habitat and overlaid with elephant carcass locations. Less suitable areas (orange) specify where elephants were effectively displaced due to the presence of humans, and this represents the conflict zone. Fifty nine percent of elephant mortalities (n = 341) occurred in this conflict zone, an area that encompassed only 31 percent of the aerial survey area (black line).

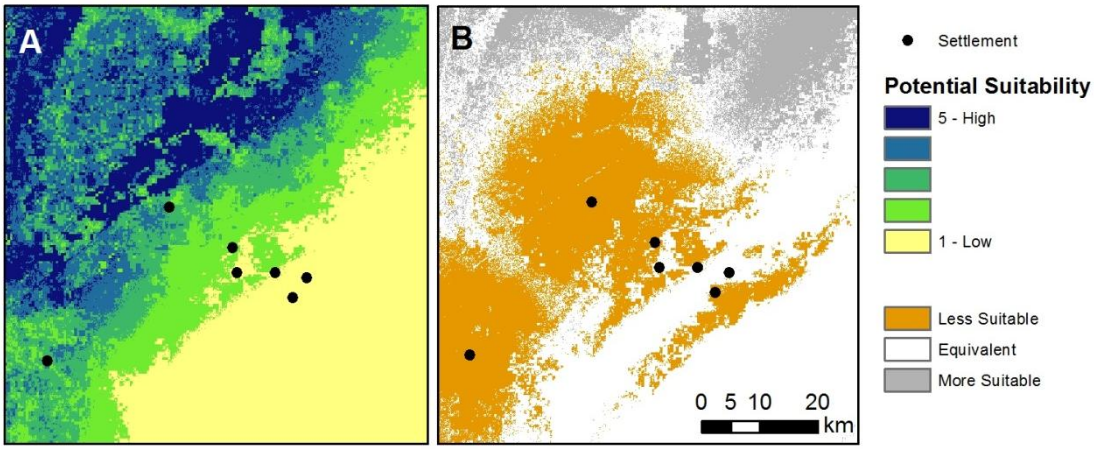


Figure 5-4. An illustrative example of how habitat suitability around human settlements (a) influenced elephant displacement (b). Settlements located in highly suitable elephant habitats had larger displacement areas around the settlement (classified as "less suitable"), an area which extended up to 21 km from the village edge.

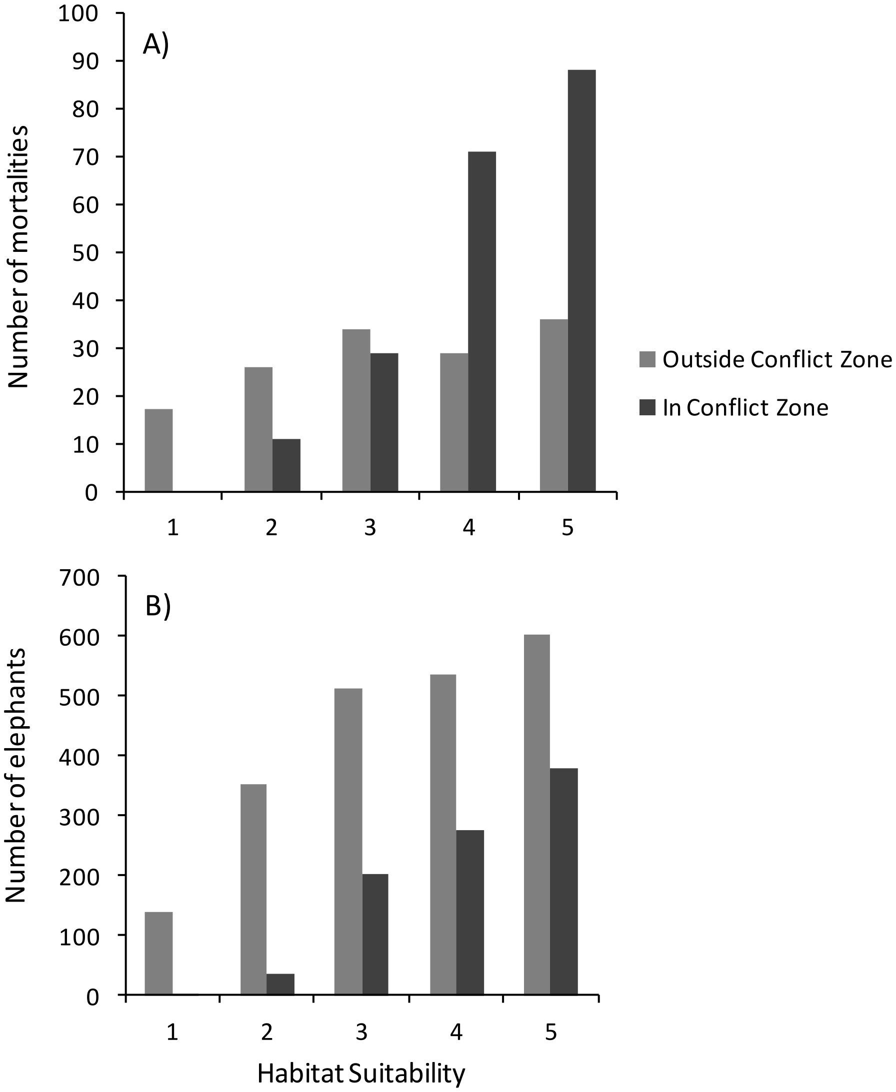


Figure 5-5. The number of elephant mortalities (A) and observed elephants (B) within and outside of the conflict zone as a function of the potential habitat suitability (low=1, high=5).

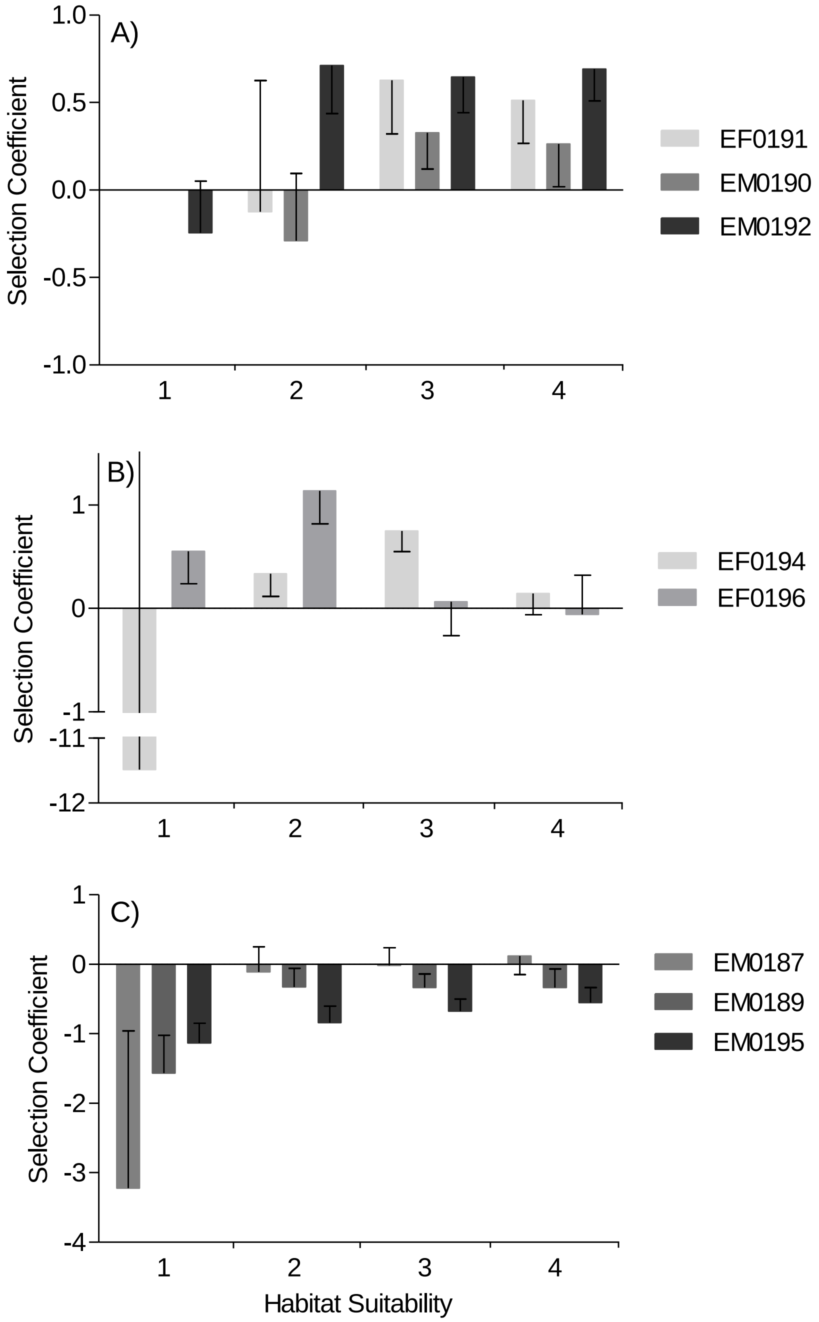
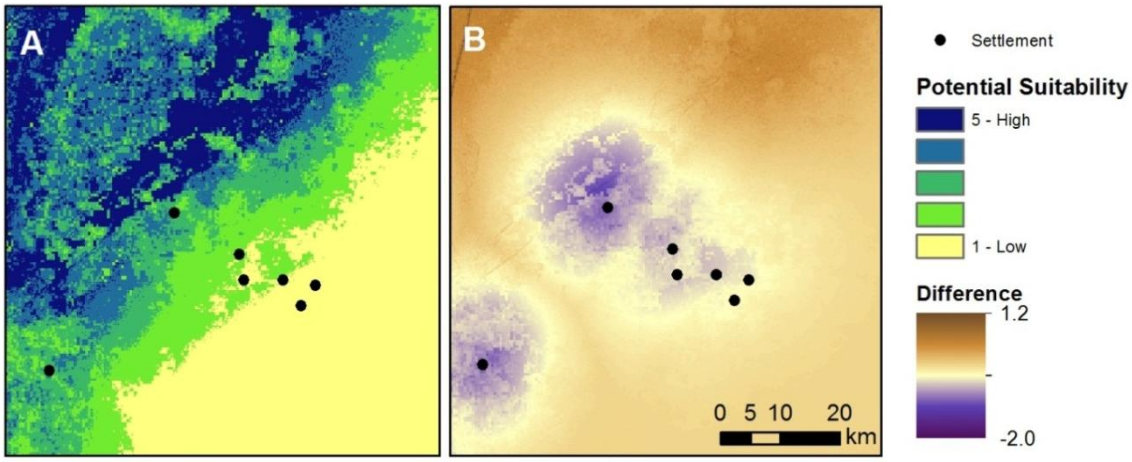


Figure 5-6. Based on habitat selection theory, we expect individuals to avoid less suitable habitat (negative selection coefficient) and select more suitable habitat (positive selection coefficient). This pattern occurs for female and male elephants with home ranges outside

of the conflict zone (a). For individuals with at least 20 percent of their home range in the conflict zone, females (b) selection less suitable habitat and males (c) select all habitats less than available. Habitat suitability category 5 was withheld as the reference category, and if the confidence interval crossed zero, selection was not significantly different from available.

Appendix A.

Supplemental Figure



Appendix A, Figure 5-7. An illustrative example of how the location of human settlements in low or high quality habitats (A) reduced habitat suitability (B). A negative difference denotes a decrease in habitat suitability as a function of human presence. The difference values are based on the original, continuous habitat suitability values for the potential and realized habitat indexes, before they were converted into categorical values.

Chapter 6. General Conclusions

A habitat-based management plan for any species begins with the two-step process of first investigating the species distribution (i.e. where does it occur?) and continues by examining more fine scale questions on habitat utilization (i.e. what contributes to its presence in this area?). Developing a thorough knowledge of spatial patterns and selection processes is then used to help inform management decisions, conserve suitable habitat, and promote population persistence and stability (e.g. Boyce and McDonald 1999; Chetkiewicz et al. 2006; Larson et al. 2004; Nielsen et al. 2006). Within a habitat-based management plan, parks and protected areas are generally assumed to serve as the cornerstone for species conservation (e.g. Gaston et al. 2008). In reality, however, the world's parks and protected areas were often delineated following a very different set of criterion, preserving geological features (DiSilvestro 1993), areas of low productivity (Andrew et al. 2011), or other areas where humans were discouraged to live due to the prevalence of disease (Bengis et al. 2003). Consequently, protected areas often do not meet the spatial requirements of populations, particularly for large mammals (Cantú-Salazar and Gaston 2010; Hanks 2001; Morrison et al. 2007; Woodroffe 2000).

To increase the efficacy of parks in conserving large mammals, initiatives are striving to increase connectivity between once isolated protected areas, creating megaparks (van Aarde and Jackson 2007) and Transfrontier Conservation Areas (Hanks 2001, 2003). For elephants, the hope is that increasing connectivity between parks will promote regional population stability through the spatial structuring of population within the proposed framework of a metapopulation (van Aarde and Jackson 2007). Within a metapopulation, asynchronous population dynamics between interconnected subpopulations that are separated by distance could support regional population stability (Driscoll 2007; Olivier et al. 2009). However a metapopulation makes no predictions about habitat quality (Armstrong 2005), even though it is likely that spatial heterogeneity of resources and risks drives asynchrony (van Aarde and Jackson 2007; van Aarde et al. 2006). Conversely, the habitat-based approach focuses on identifying high-quality habitat, with little regard for demography (Armstrong 2005). For elephants, management may require the integration of the metapopulation concept to stabilize demography and the habitat-based approach to test assumption, model feasibility, and identify areas most conducive to support the structuring of a metapopulation.

In this thesis, I use habitat suitability models to test two pre-requisites for the spatial structuring of a population. The first thereof relates to the potential connectivity between populations. I found that the current spatial structuring of suitable elephant habitats allows for connectivity between populations; however connectivity was limited by a lack of surface water in the west and high human densities in the east (Chapter 3). Connectivity models based on habitat suitability allow for spatially explicit predictions of connectivity which then need to be validated with targeted field surveys. Studies on the genetic structuring of populations could assist efforts to evaluate whether modelled corridors are functional and used by elephants (e.g. McRae et al. 2008). From a study in progress on the genetic structure of elephant populations in the central portion of the study area, it appears that the male elephants are dispersing between populations (A. de Flamingh, *personal communication*). Yet, genetic studies are limited in their ability to explain the landscape factors contributing to connectivity, and they do not provide spatially explicit predictions which can be used to delineate and conserve corridors between subpopulations. When used in conjunction with the habitat-based approach, we may obtain a greater understanding of whether landscape features allow for connectivity and whether such structural corridors are actually functional linkages.

Next, a metapopulation assumes asynchronous population dynamics (Driscoll 2007; Olivier et al. 2009), and landscape heterogeneity could drive this asynchrony (van Aarde and Jackson 2007; van Aarde et al. 2006). Therefore, using a habitat-based approach I next investigated landscape factors that could contribute to heterogeneity in selection and mortality in northern Botswana. I found spatial heterogeneity in habitat selection patterns by elephants, as well as heterogeneity in the location of mortality events (Chapter 4). Both sources of heterogeneity were linked to landscape characteristics. Elephants selected areas close to water, where slopes are steep, and with moderate tree cover, and they had higher mortality risk when near humans (Chapter 4), particularly in highly suitable habitats (Chapter 5). The consequences that such functional heterogeneity may have for the structuring of populations need further investigation.

This thesis contains research across a spatial scale unprecedented in any single-species habitat selection study to-date, incorporating elephant populations across seven countries and a wide ecological gradient. Yet many questions still remain, and my hopes are that this research can serve as a baseline for these future studies. What remains is to identify the critical habitat components that contribute directly to demographic performance. This knowledge gap exists because the spatial and temporal scales with which habitat selection and demography operate are at odds. Habitat selection decisions occur at a fine scale, yet these fine-scale decisions have implications for the lifetime fitness of the individual and ultimately the demographic performance of the population across generations (Gaillard et al. 2010). Yet, the scale at which these processes operate is unknown for elephants. It may be that resource availability during a particular season (Illius 2006), at a particular stage in an individual’s life (Trimble et al. 2009), or during a particularly difficult drought year unobserved for decades (e.g. Booth et al. 2012) has the greatest influence on shaping elephant population dynamics. This information would be invaluable in linking the habitat and metapopulation concepts, as habitat could then be used to directly predict, or potentially manipulate, elephant demographic performance.

Here, the metapopulation concept has provided a unifying framework by which to identify key questions. These questions were then addressed using a habitat-based approach, and the results contribute to the body of knowledge developing around the metapopulation concept. The large spatial scale on which I examined elephant's utilization of heterogeneous habitats effects the distribution of elephant and contributes to how they use space. Similarly, the uneven distribution of deaths and their association with people suggests that humans may contribute to the spatial distribution of elephants. Hence the structuring of elephants across space may be driven by the heterogeneity of resources and risks, as proposed by van Aarde and Jackson (2007), and this could contribute to the structuring of populations across space, possibly as a metapopulation.

As the largest land mammal in the world, savannah elephants also have large spatial requirements (van Aarde et al. 2008); therefore, it is understandable that elephant management ultimately comes down to space. While elephants can survive in small, isolated parks, the demographic processes that regulate population numbers cannot. A metapopulation for elephants may provide a solution (van Aarde and Jackson 2007). In southern Africa, human densities remain relatively low and natural habitats are still abundant in many areas, so we must plan for the future of these lands to ensure they meet the needs of both wildlife and people. The benefits of this framework are not one-sided, as communities near these natural landscapes often perform better than those far from parks (Ntumi 2012). This heterogeneous environment, with population sources that are beneficial for elephants and population sinks that support sustainable human needs, then creates a mutually beneficial system which ultimately serves to stabilize elephant numbers across a broad spatial scale.

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