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

Publication Details

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).

Acknowledgements

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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.

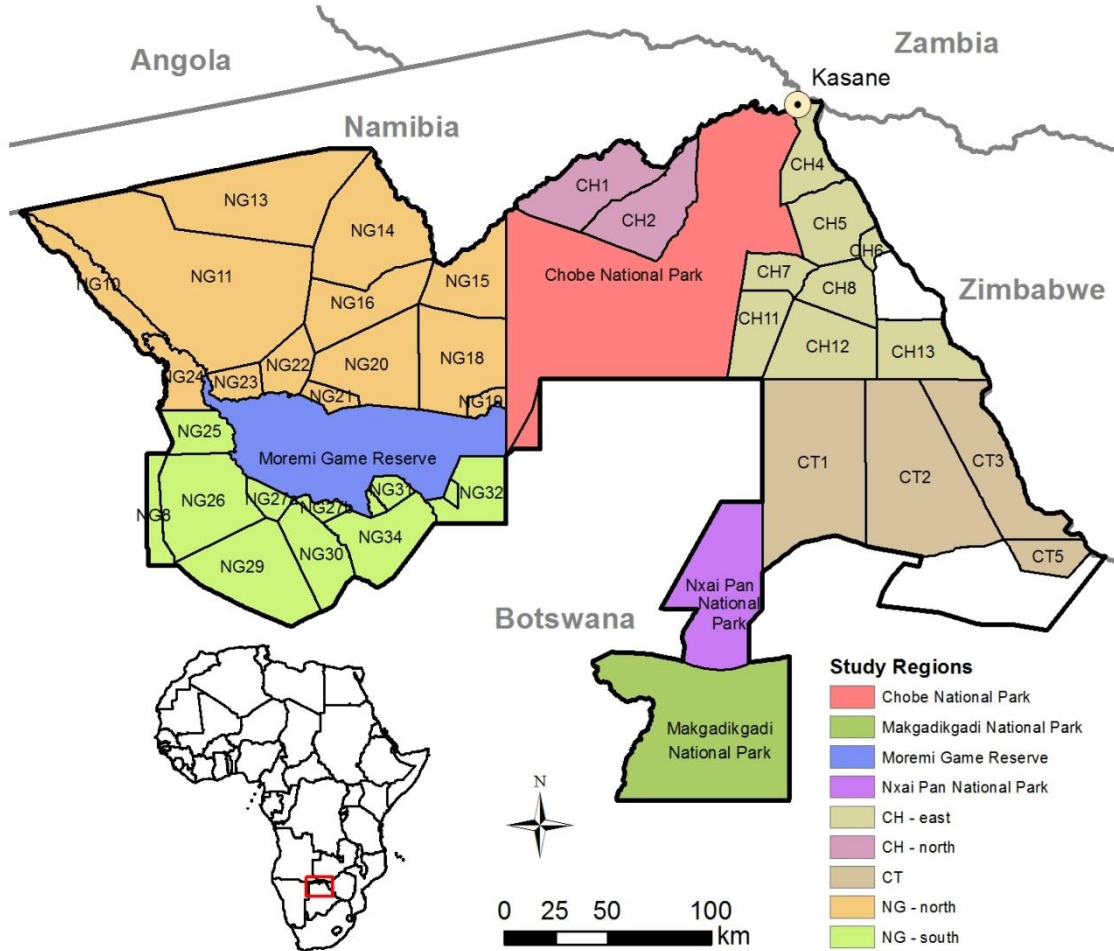|	Non-habitat	Secondary Habitat	Secondary sink	Primary habitat	Primary sink	Total Area (km^2)
Chobe NP	14.6	14.5	26.1	14.8	30.0	10,751
Makgadikgadi NP	66.4	20.1	10.6	1.0	2.0	5,018
Moremi GR	13.6	18.1	7.1	51.1	10.2	4,889
Nxai Pan NP	35.8	27.9	8.1	9.5	18.7	2,518
CH – east	42.1	9.8	19.3	9.0	19.7	6,977
CH – 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.
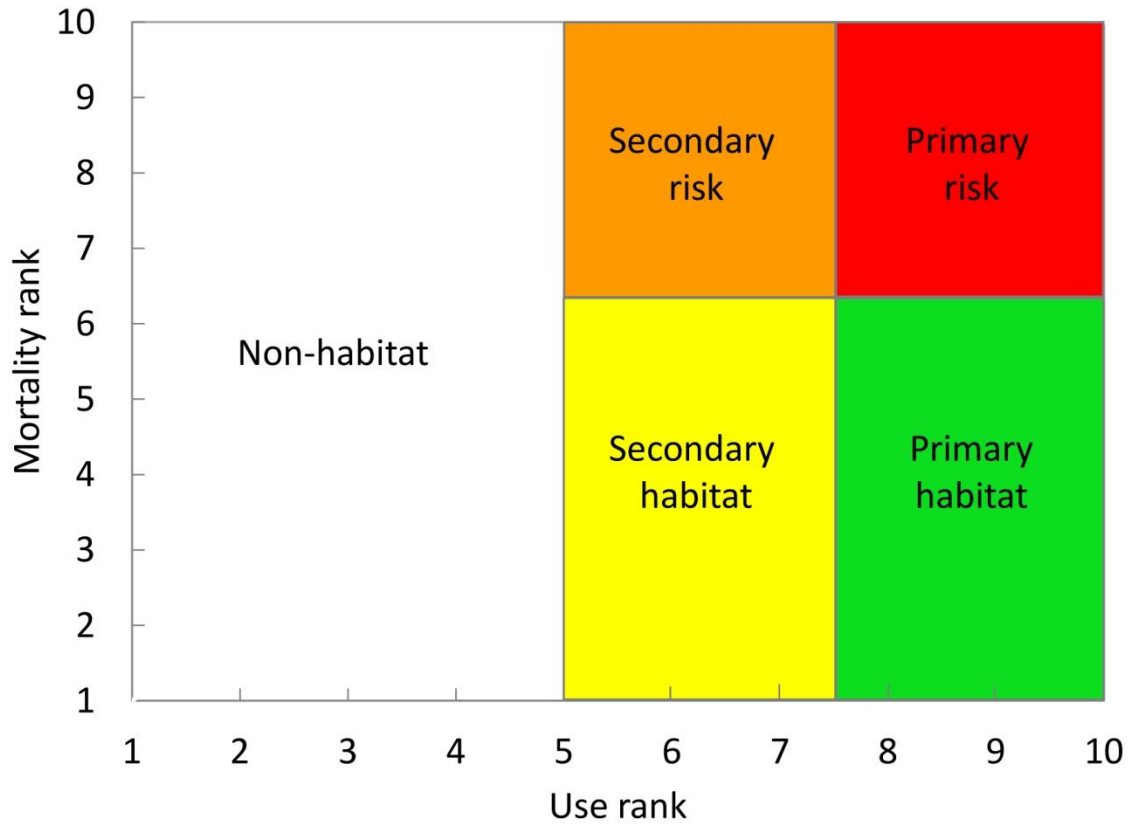
Figure 4-2. Five habitat states categorized based on relative probability of use (ten ordinal bins from 1-low to 10-high) and relative probability of mortality (ten ordinal bins from 1-low to 10-high) for elephants. This figure was adapted from Nielsen et al. (2006).
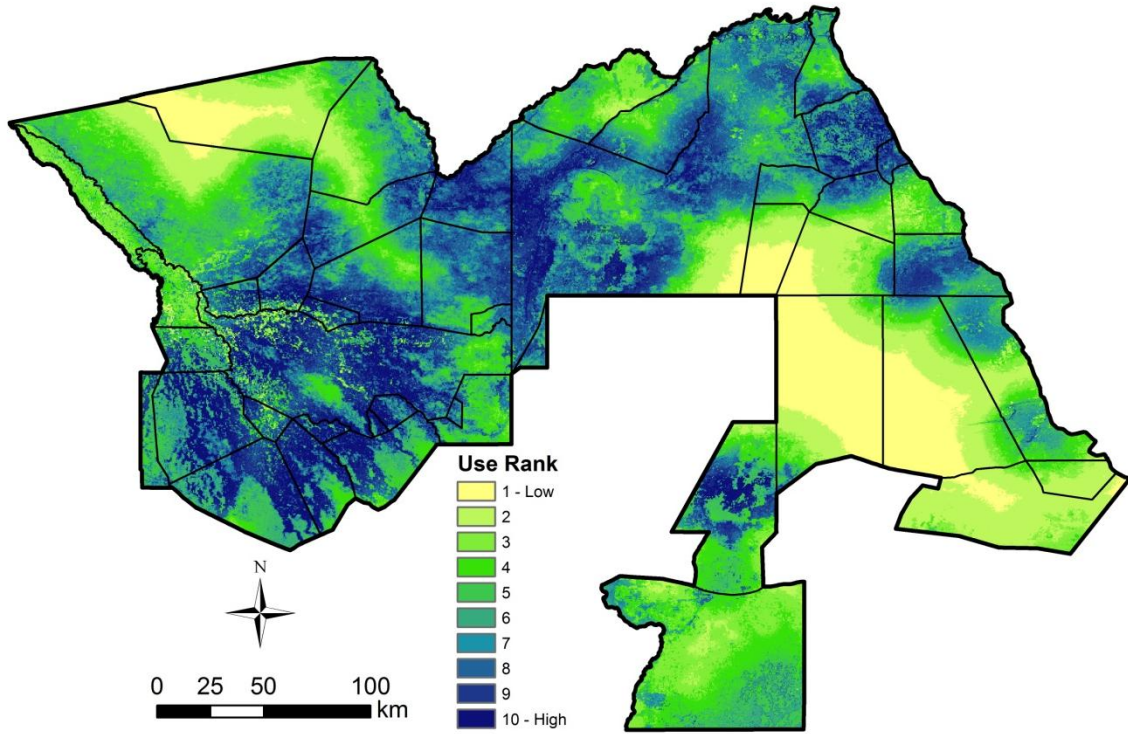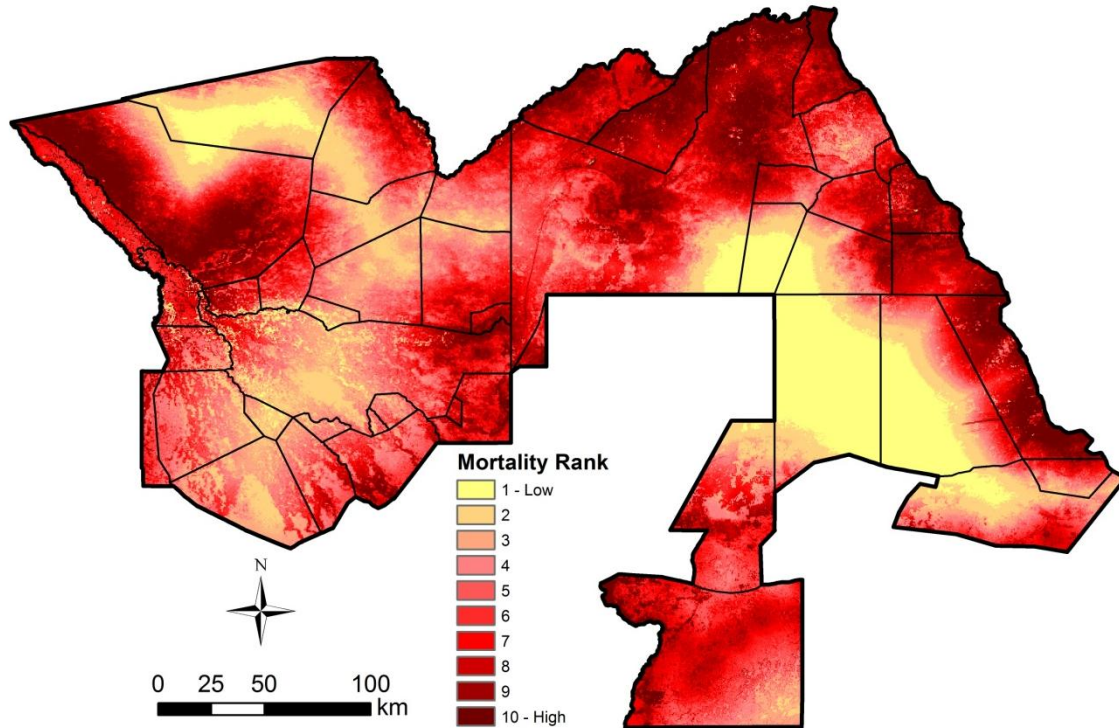
Figure 4-3. (a)

(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.
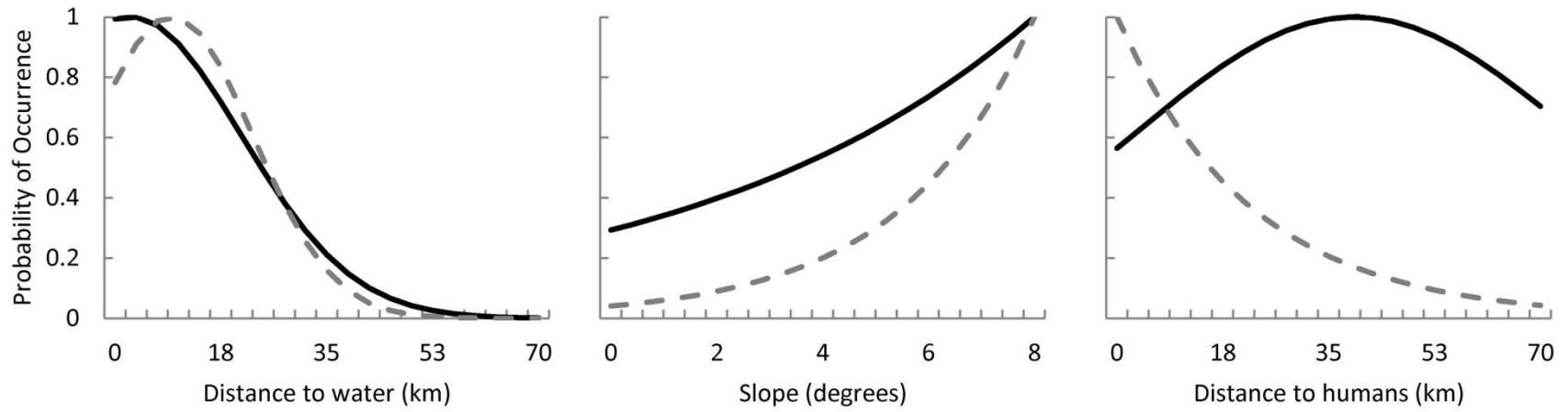
Figure 4-4. Relative probability of occurrence for live elephant (solid black) and elephant carcass (dashed gray) locations as a function of distance to water, slope, and distance to humans.
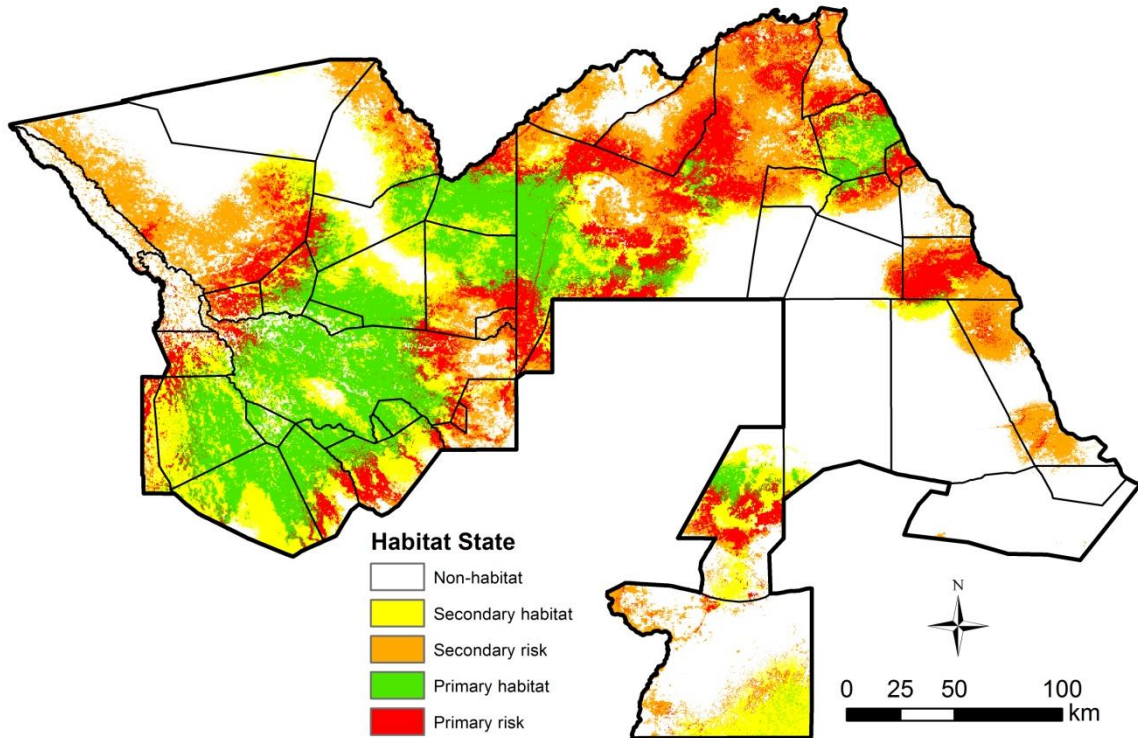
Figure 4-5. Habitat states for elephants in northern Botswana. Non-critical habitats represent areas of low elephant occurrence. Primary and secondary habitats represent areas with high to moderate use and low mortality. Primary and secondary risk areas represent regions with high mortality and high 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.
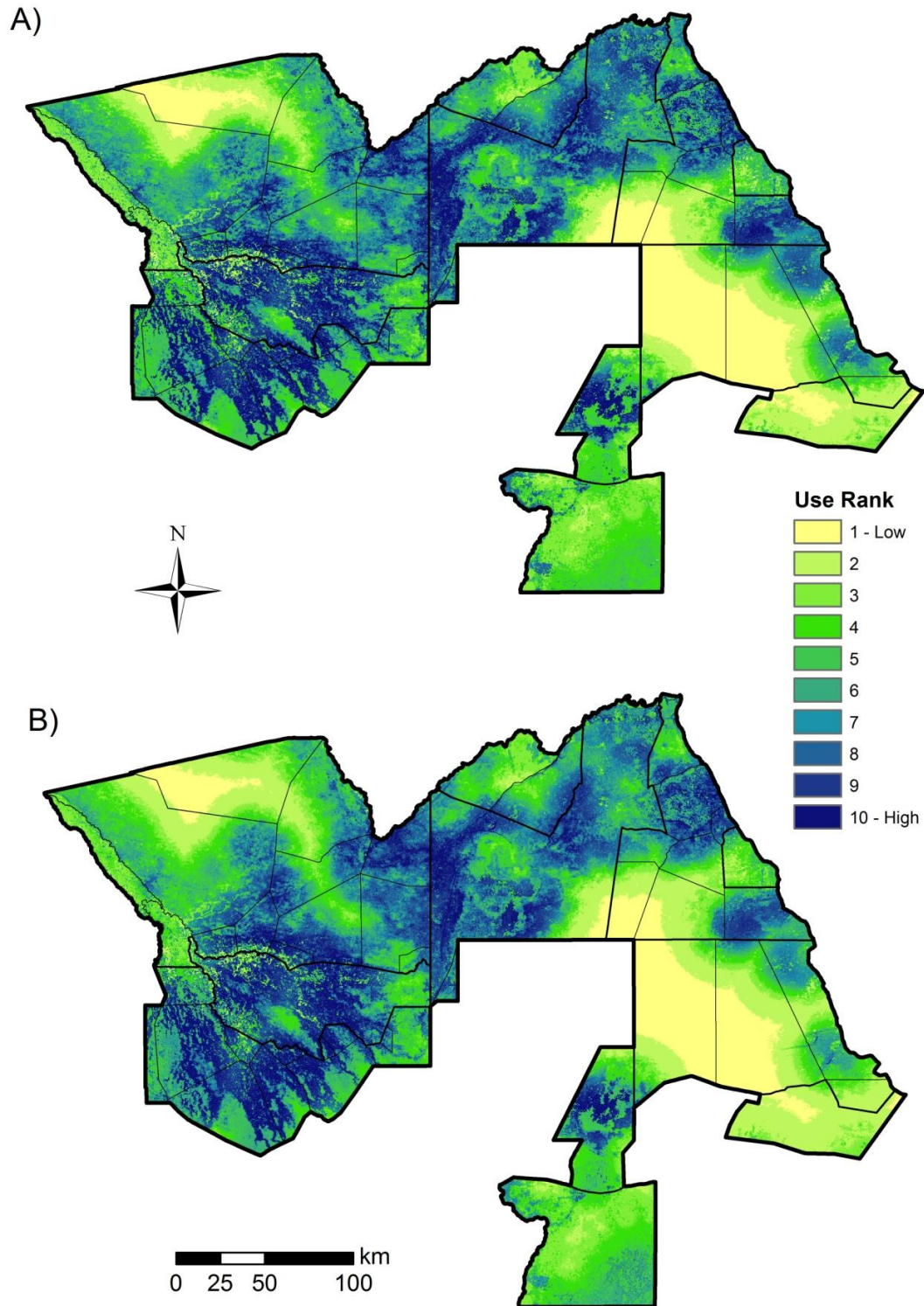
	Sub-sampled			Original			% Change
	β	SE		β	SE		in β
1) Elephant vs. Random							
Intercept	-3.06	0.10	*	-2.65	0.08	*	15.3%
Distance to water[a]	1.02	0.64		0.73	0.55		40.5%
(Distance to water[a])^2	-0.13	0.02	*	-0.15	0.02	*	-14.7%
Slope	0.06	0.06		0.15	0.04	*	-60.7%
Proportion tree	7.45	0.85	*	6.24	0.67	*	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.

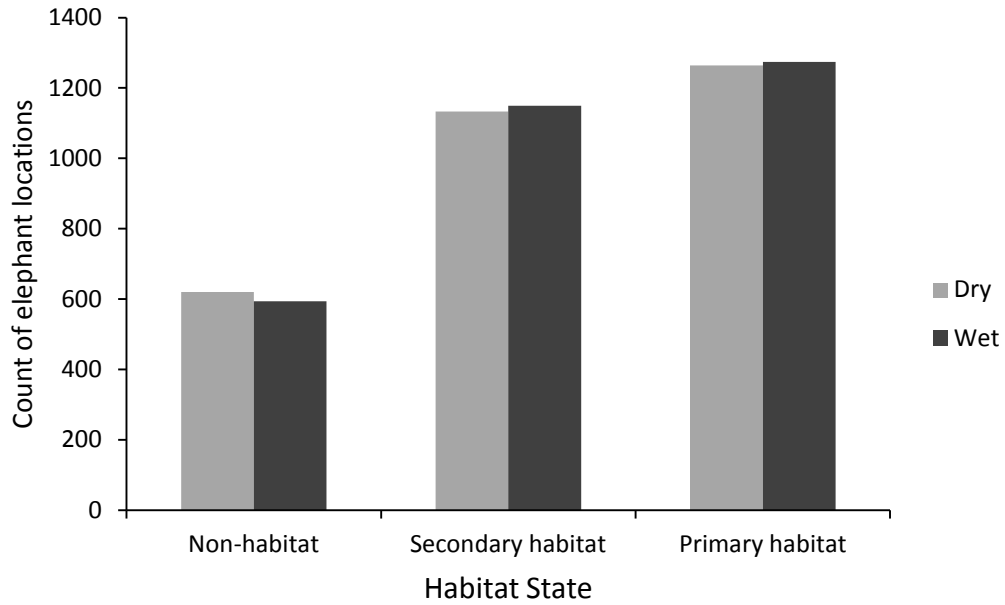**Model results using estimated dry season water availability**

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.

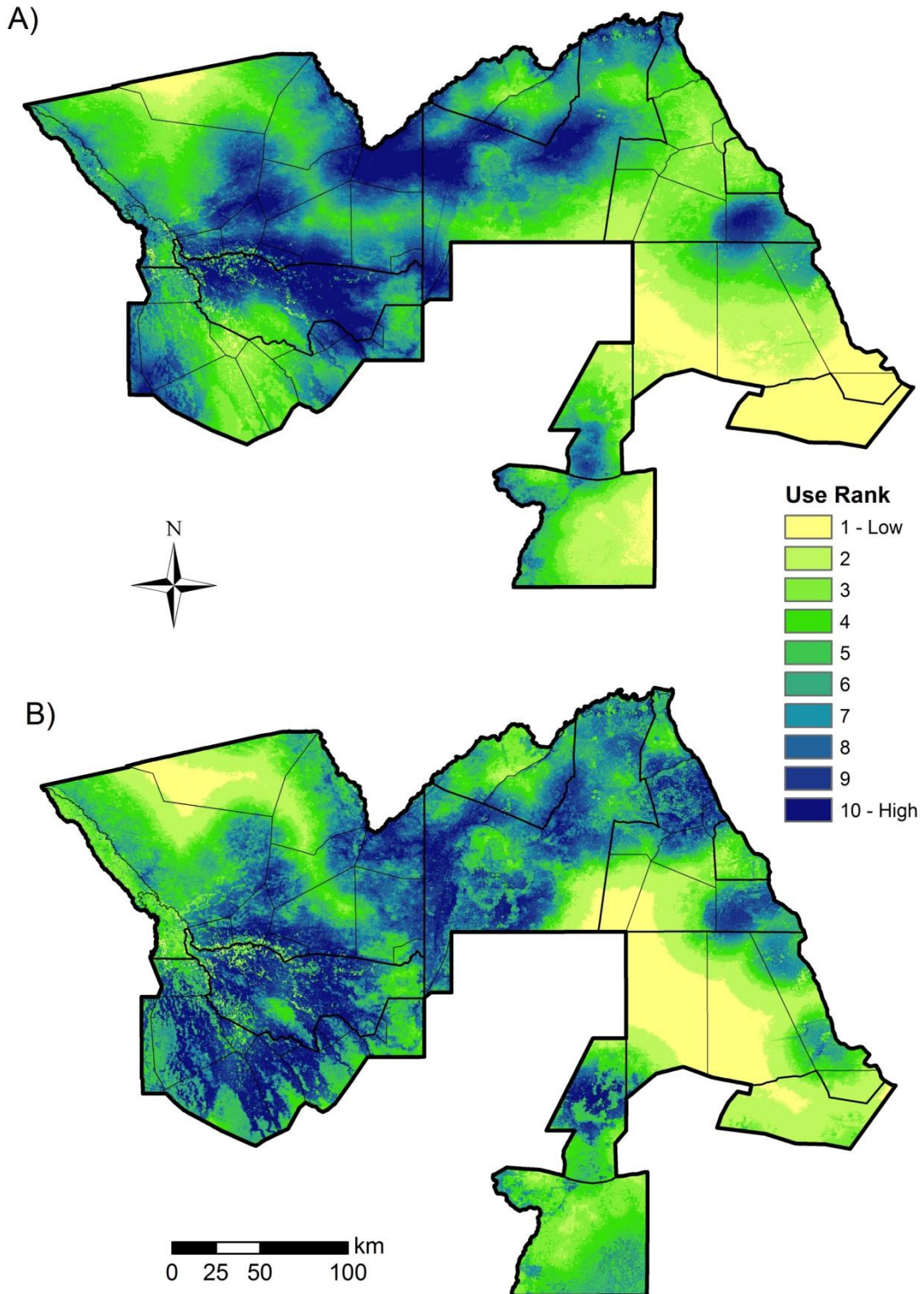| Model	Elephant vs. Random			Mortality vs. Random			Mortality vs. Elephant		
	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w
1	19199	929	0.00	3612	296	0.00	2213	225	0.00
2	18471	201	0.00	3483	166	0.00	2209	220	0.00
3	18401	131	0.00	3452	136	0.00	2204	215	0.00
4	18396	126	0.00	3423	107	0.00	2187	199	0.00
5	18776	506	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.

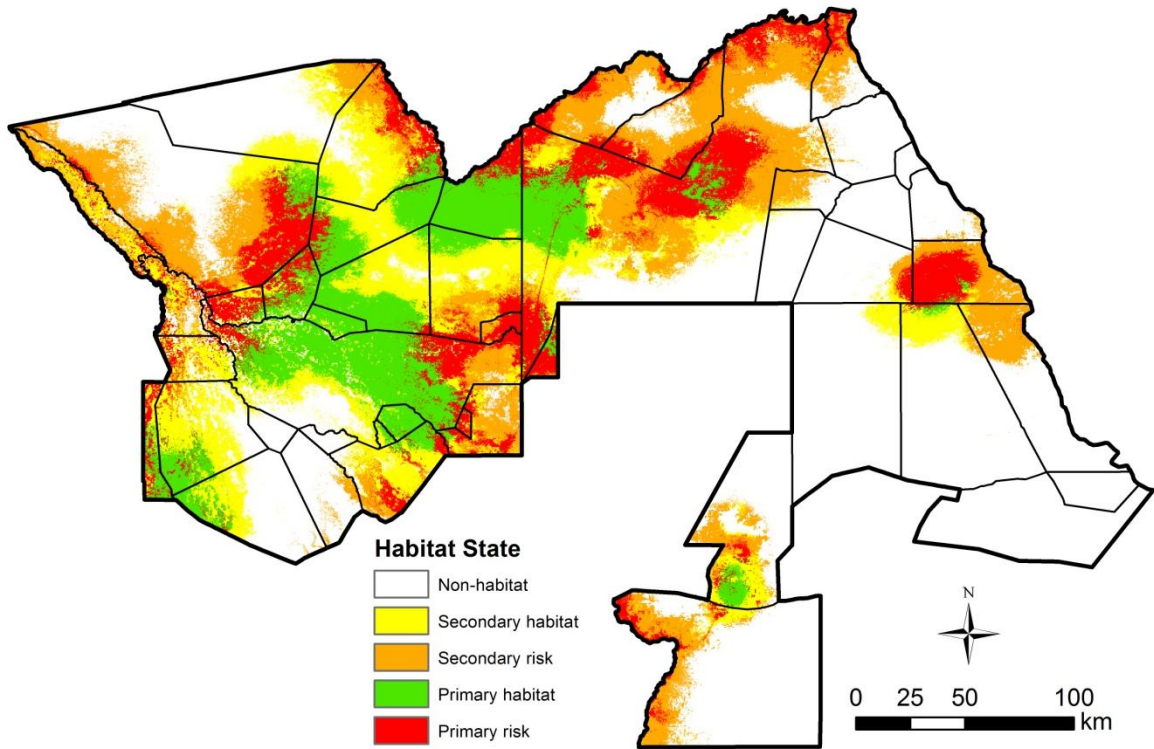|	Dry Season Water			Wet Season Water		
	B	SE		β	SE	
1) Elephant vs. Random						
Intercept	-2.18	0.08	*	-2.65	0.08	*
Distance to water[a]	-4.65	0.33	*	0.73	0.55	
(Distance to water[a])^2	0.02	0.01	*	-0.15	0.02	*
Slope	0.15	0.04	*	0.15	0.04	*
Proportion tree	4.98	0.67	*	6.24	0.67	*
(Proportion tree)^2	-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.

Use Rank

- 1 - Low
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
- 10 - High

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.
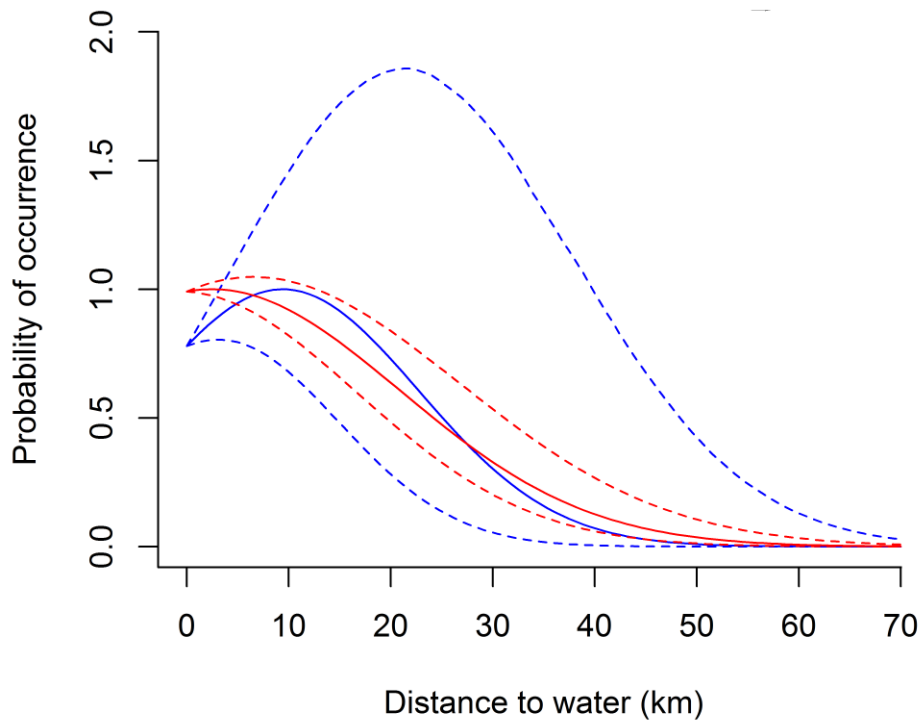
Habitat State

- ☐ Non-habitat
- ☐ Secondary habitat
- ☐ Secondary risk
- ☐ Primary habitat
- ☐ Primary risk

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.
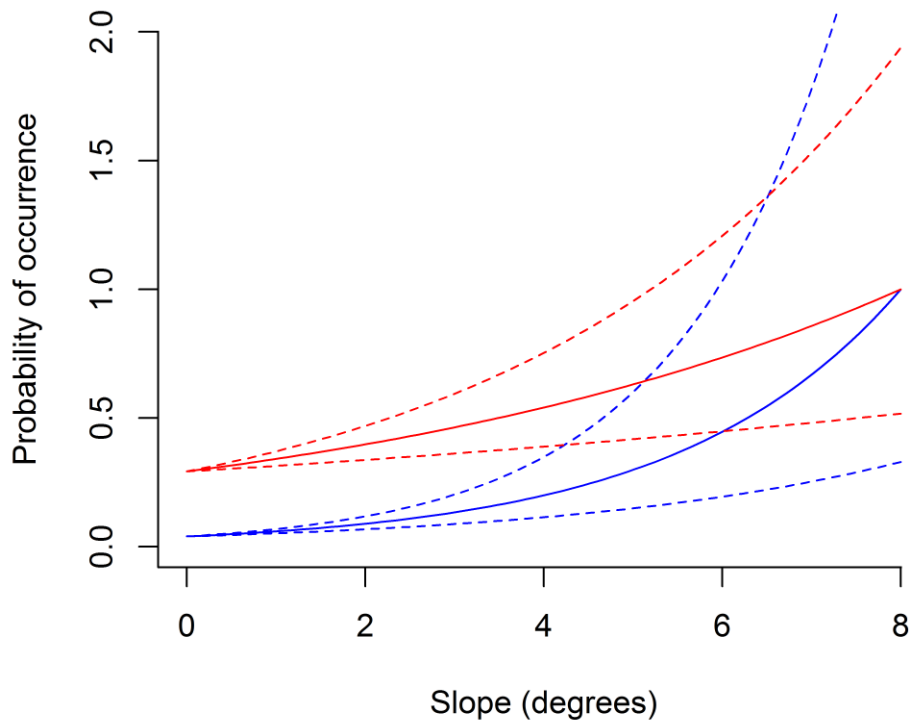
Appendix C.

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.
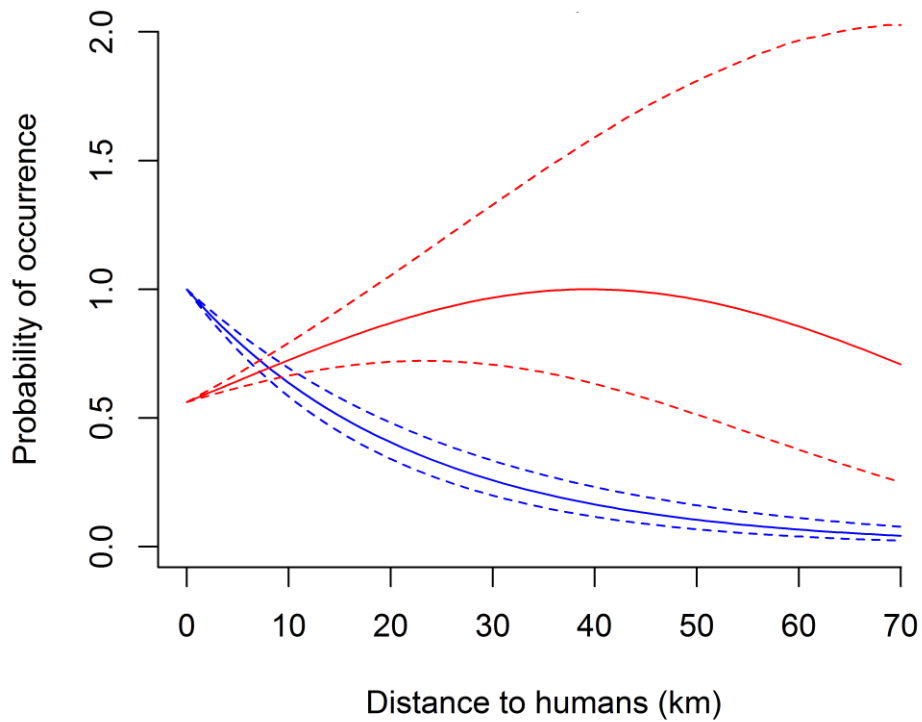
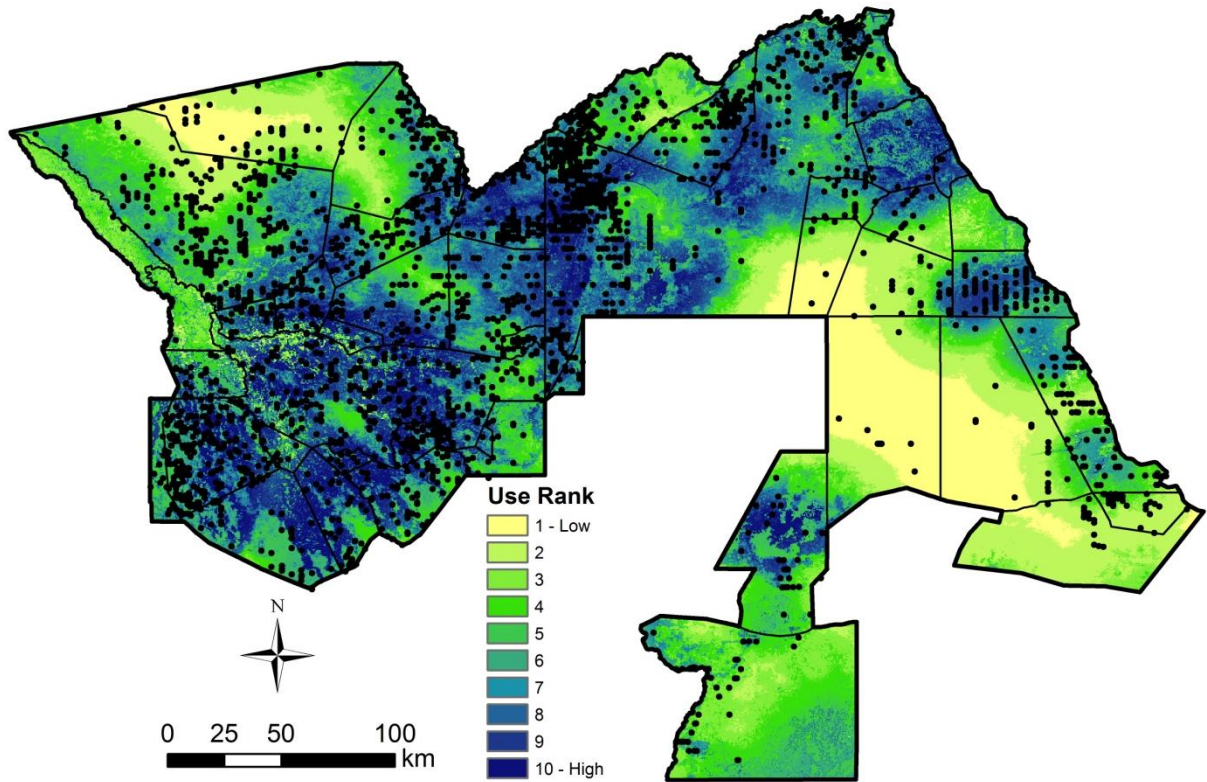| Model	Elephant vs. Random			Mortality vs. Random			Mortality vs. Elephant		
	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w
1	19199	827	0.00	3612	290	0.00	2213	187	0.00
2	18541	169	0.00	3507	186	0.00	2202	176	0.00
3	18434	62	0.00	3468	146	0.00	2196	170	0.00
4	18429	57	0.00	3434	112	0.00	2177	151	0.00
5	18776	404	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).
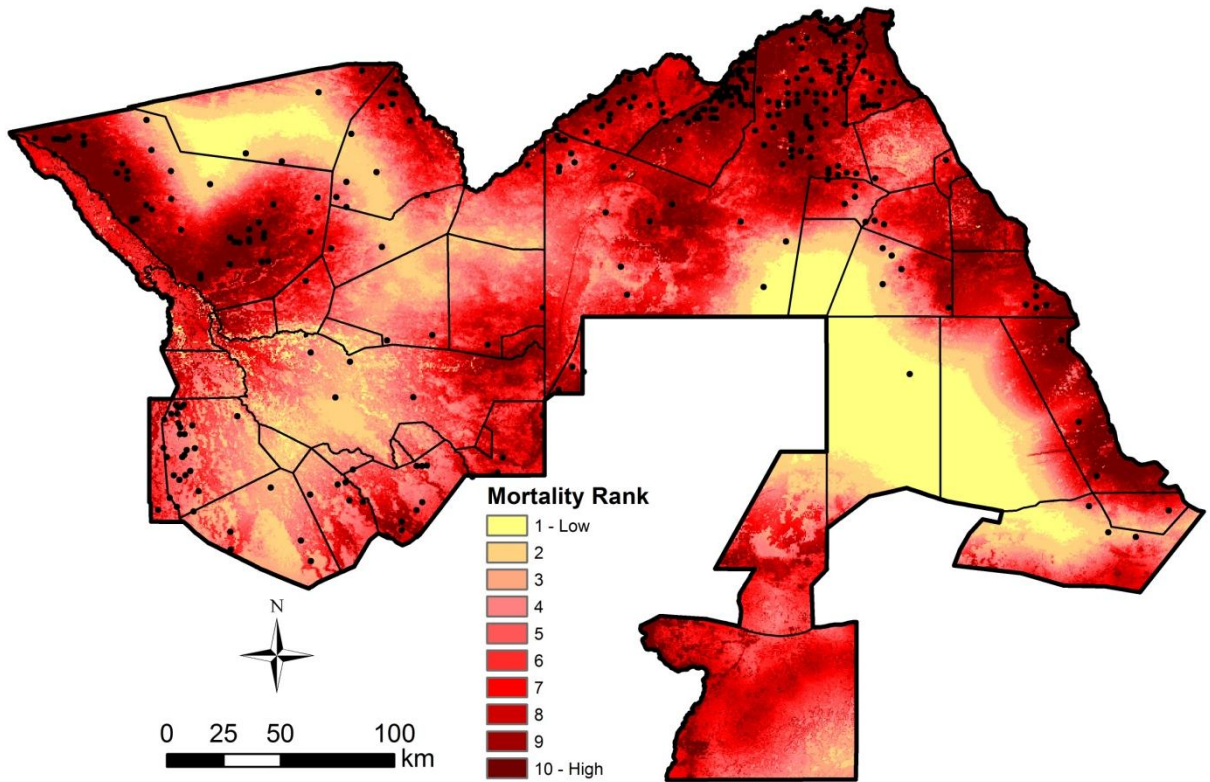
Appendix C, Figure 4-11. Relative probability of occurrence as a function of slope for live

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).