

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

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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; Roeber 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 km². 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/km². 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/km², 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 km². 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 $r > 0.6$ 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 mortality 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 mortality 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 km². 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 km² 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 with 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 km² pixels with a human density of >16 people/km² 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 it is 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 of 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 female, 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 disproportionately as compared to settlements located in less suitable 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/km² occupied only 1,200 km² 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

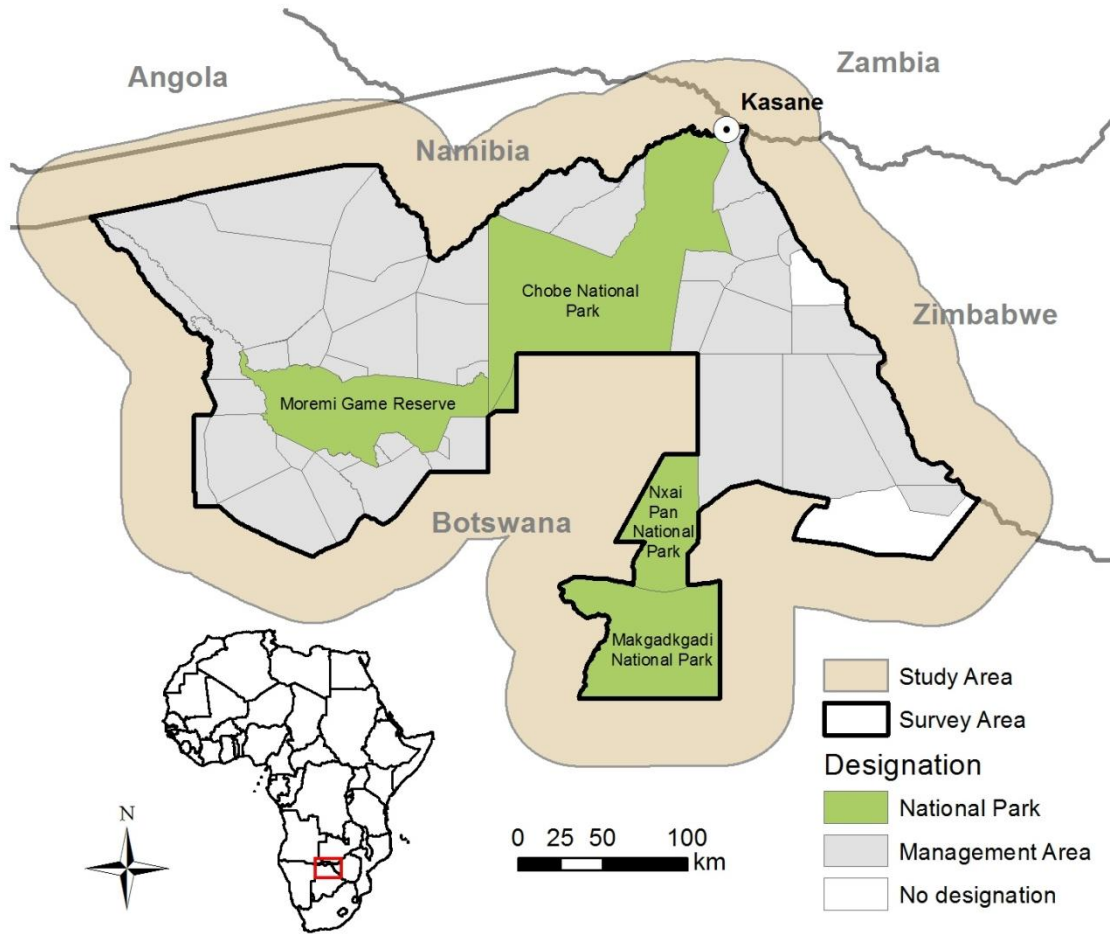


Figure 5-1. Map of the study area located in northern Botswana. The area included three national parks, one game reserve, and multiple wildlife management areas (gray). Aerial surveys were conducted in the survey area, which was buffered by 40 km to accommodate the data obtained from elephants equipped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

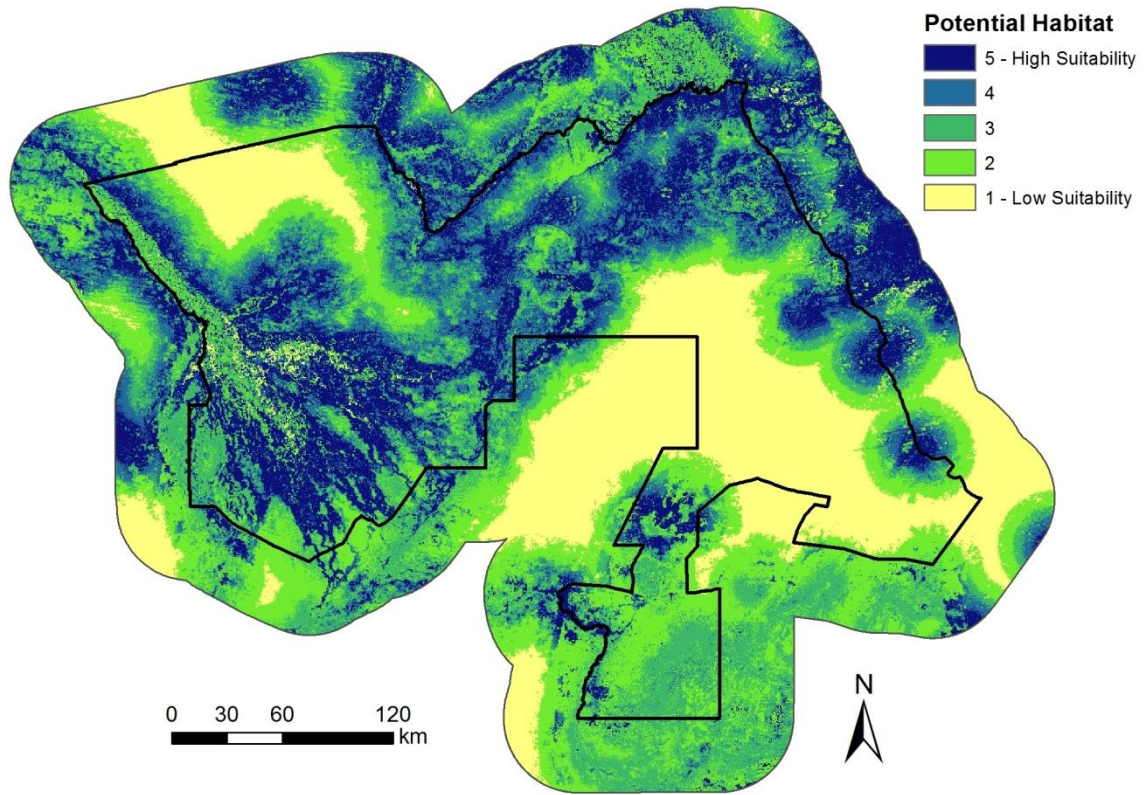
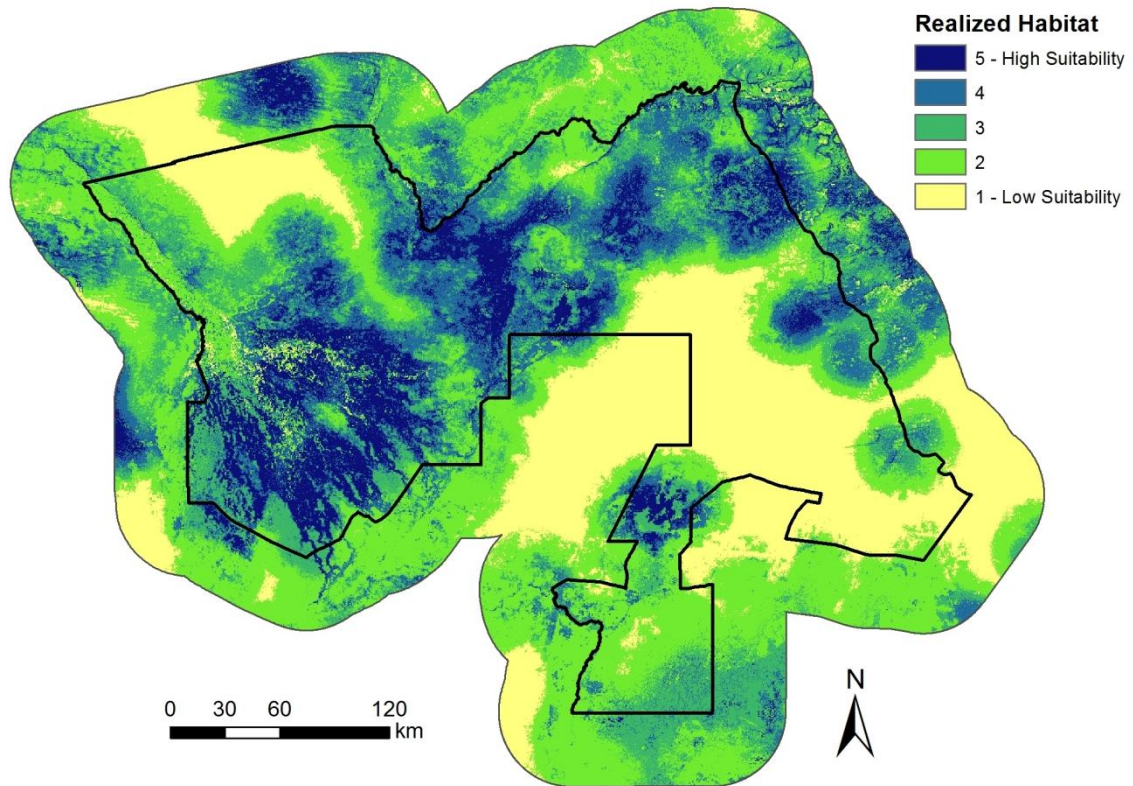


Figure 5-2. (a)



(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.

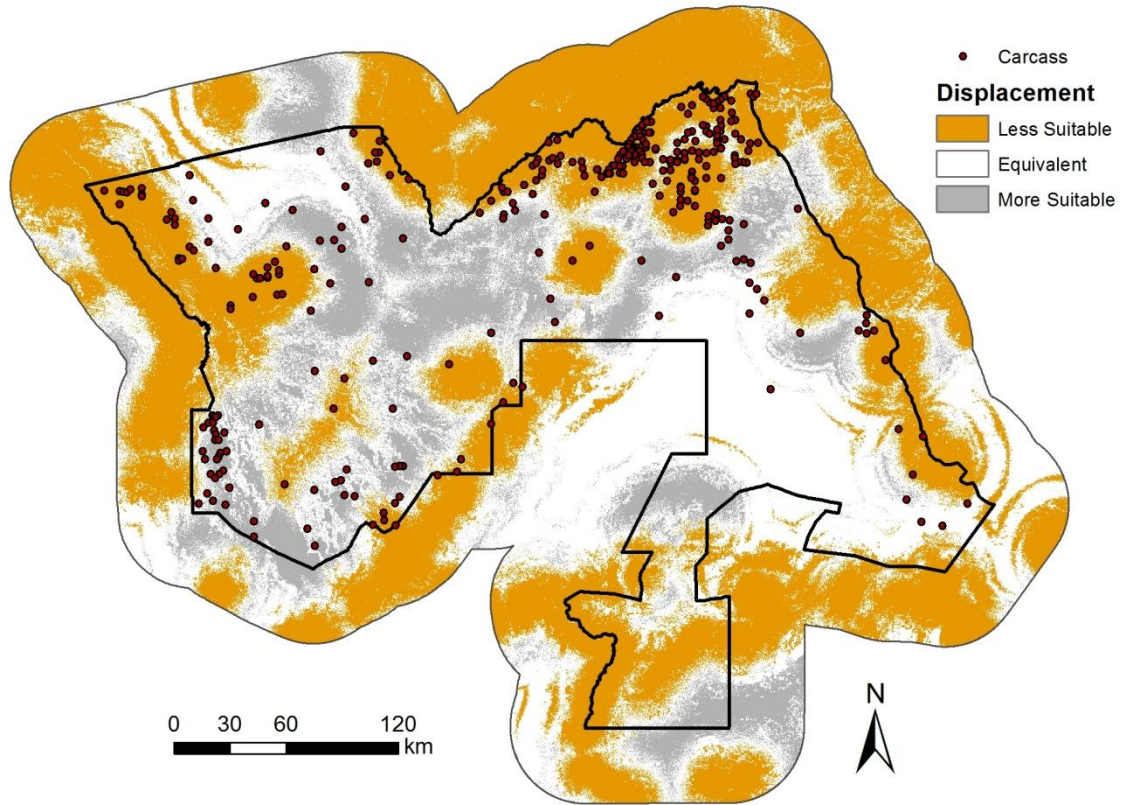


Figure 5-3. Potential habitat minus realized habitat and overlaid with elephant carcass locations. Less suitable areas (orange) specify where elephants were effectively displaced due to the presence of humans, and this represents the conflict zone. Fifty nine percent of elephant mortalities ($n = 341$)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

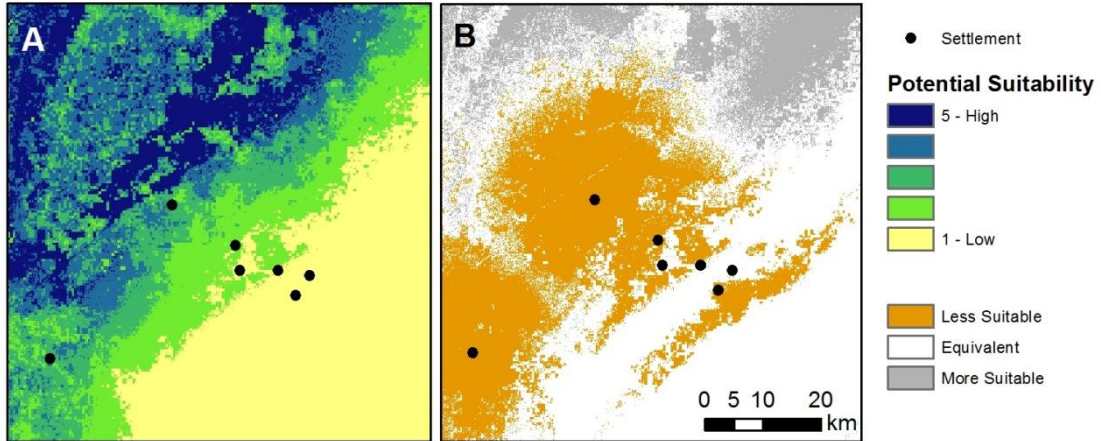


Figure 5-4. An illustrative example of how habitat suitability around human settlements (a) influenced elephant displacement (b). Settlements located in highly suitable elephant habitats had larger displacement areas around the settlement (classified as “less suitable”), an area which extended up to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

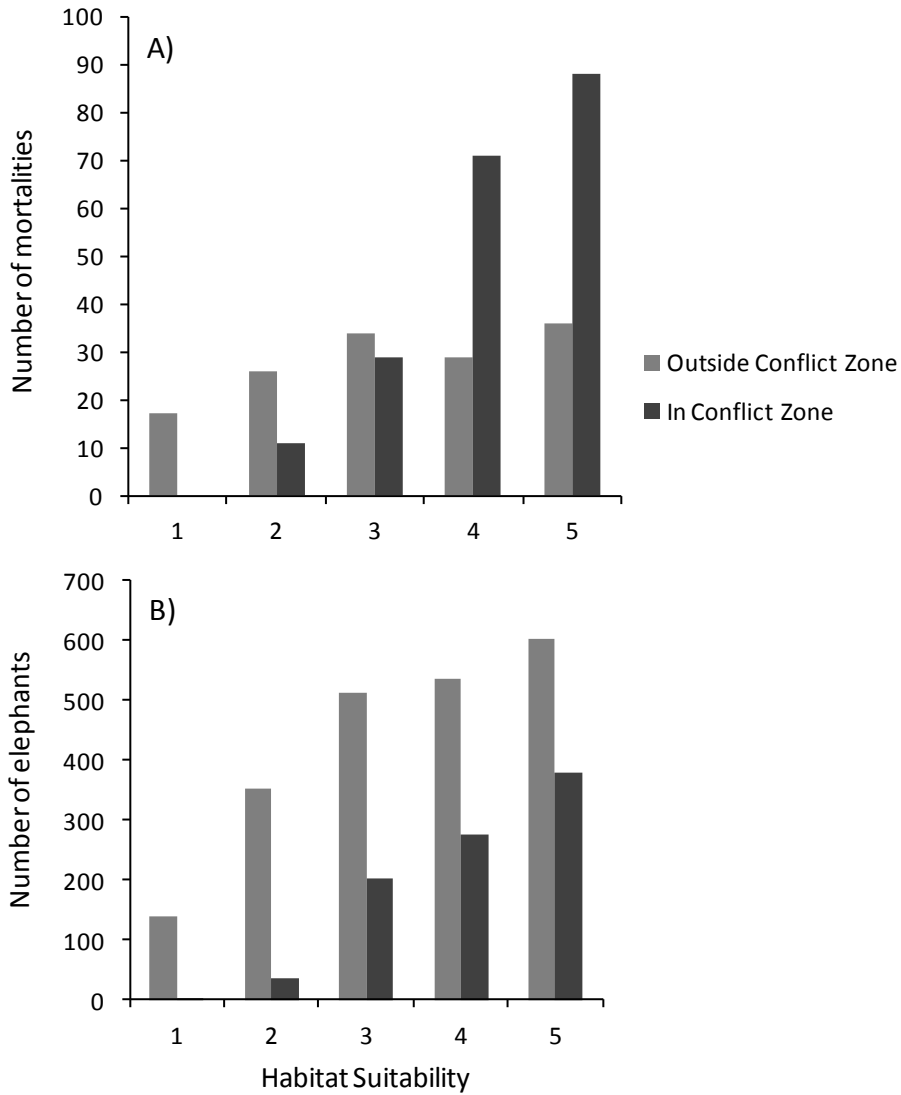


Figure 5-5. The number of elephant mortalities (A) and observed elephants (B) within and outside of the conflict zone as a function of the potential habitat suitability (low=1, high=5).

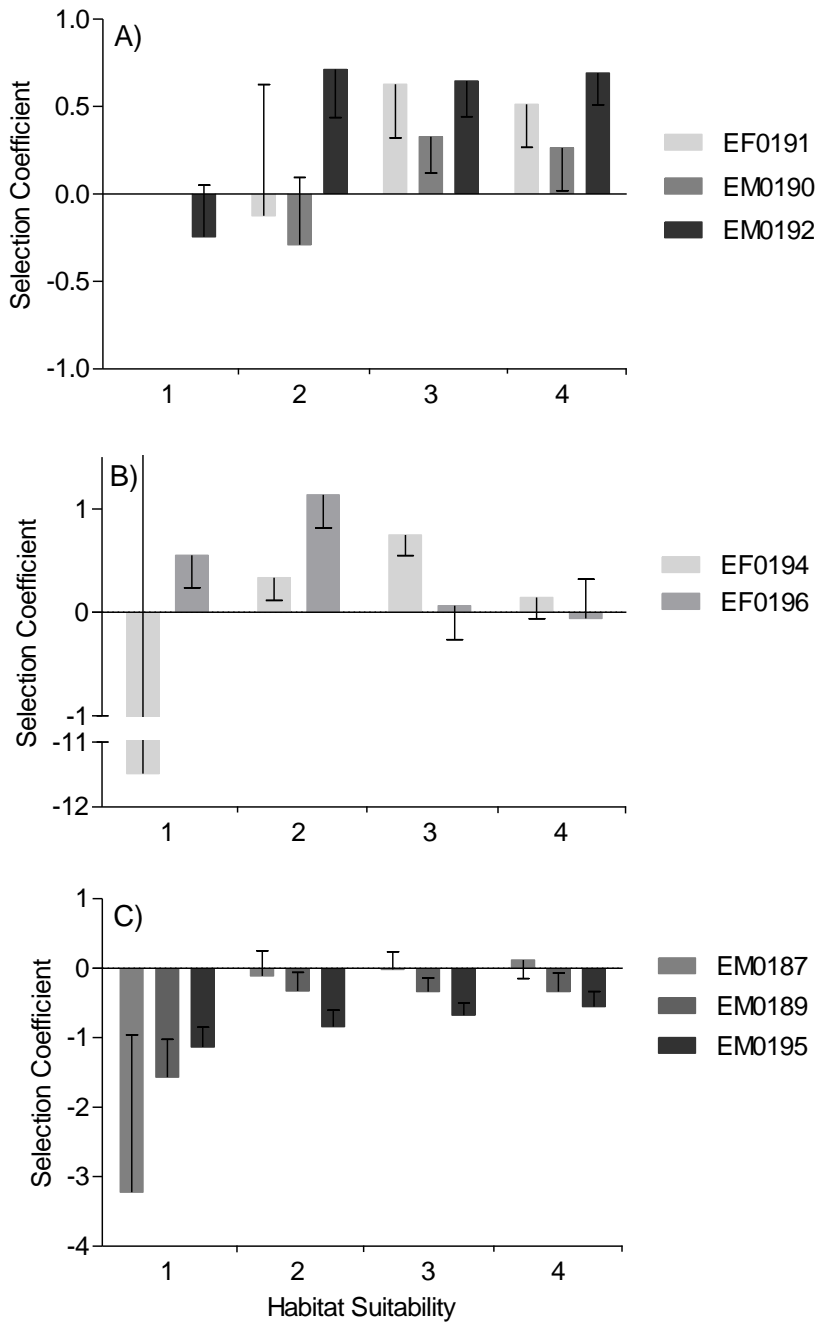
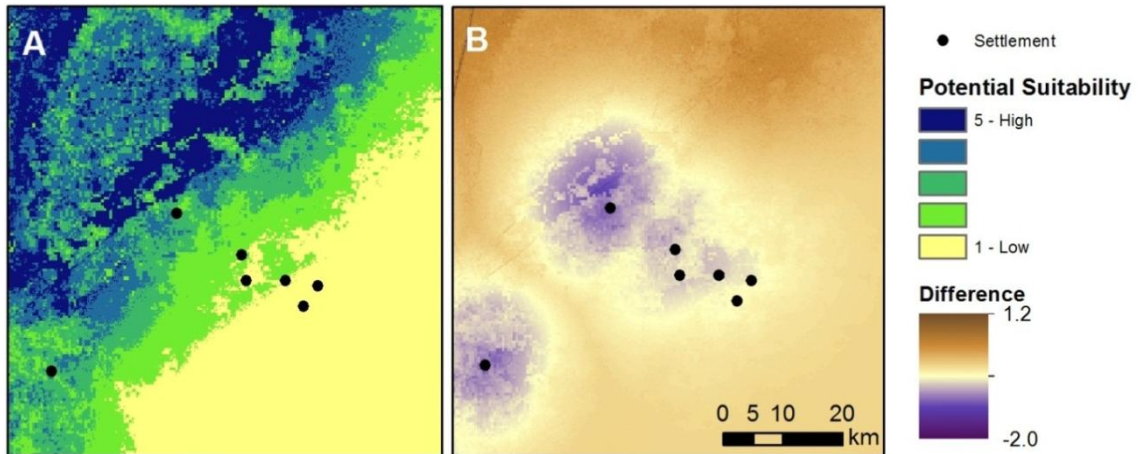


Figure 5-6. Based on habitat selection theory, we expect individuals to avoid less suitable habitat (negative selection coefficient) and select more suitable habitat (positive selection coefficient). This pattern occurs for female and male elephants with home ranges outside

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.