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Determinants of protected area boundary crossings by savannah elephants, *Loxodonta africana*

by

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ABSTRACT

When elephants leave primary protected areas (PPAs), such as national parks and game reserves, they may come into conflict with people residing on the adjoining land. In this study, I attempted to determine why African savannah elephants leave the PPAs in which they were collared. To accomplish this, I used telemetry locations of collared elephants in PPAs throughout southern Africa and investigated whether a range of intrinsic and extrinsic variables could explain why elephants crossed the boundaries of the PPAs. Adjoining many of the PPAs were secondary protected areas (SPAs), which consisted of community conservancies, and collectively with the PPAs formed clusters of protected areas. Most (45 of 49) elephants roamed beyond the PPAs but they remained within the clusters of protected areas. The elephants utilised both the PPAs and the SPAs and appeared to not feel threatened when using the SPAs. The reasons for elephants leaving PPAs varied both seasonally and between the sexes. The females roamed beyond the PPAs more during the wet season than the dry season, whereas, for males there was no seasonal difference. During the wet season, female and male habitat selection was similar within and beyond the PPAs. During the dry season, more females and males beyond the PPAs selected for areas close to people, which could be indicative of water. The proportion of male and female home ranges beyond PPAs did not increase with increasing density of elephant populations within the PPAs, nor did the proportion of female home ranges beyond PPAs increase with increasing population growth rate of elephant populations within the PPAs. Therefore, high numbers of elephants within the PPAs did not drive elephants beyond the boundaries. Contrastingly, the proportion of male home ranges beyond the PPAs did increase with increasing population growth rate. However, the results were inconclusive due to small sample size. This study confirms that elephants are utilising the SPAs as well as the PPAs. Therefore, the importance of including the SPAs in conservation actions for elephants cannot be over-emphasized.

SUMMARY

When elephants roam beyond primary protected areas (PPAs), such as national parks, they may come into contact with people. Therefore, it is important to try to explain the reasons for elephants leaving PPAs. In this thesis I used the GPS locations of elephants across southern Africa to investigate whether a range of explanatory variables could explain the roaming of elephants beyond PPAs. I divided the study into two parts based on scale. At the location-scale, I compared displacement rates per hour of elephants within and beyond PPAs, and investigated differences in seasonal and spatial use of the areas beyond PPAs. Additionally, I compared elephant habitat selection within and beyond PPAs. At the home range-scale, I investigated whether elephants from more arid areas had a larger area of their home range beyond PPAs than elephants from wetter areas. I then determined whether the variability in the proportions of the home ranges beyond PPAs could be explained by a range of intrinsic and extrinsic variables.

The displacement rates of the elephants were similar within and beyond the PPAs. The habitat selection patterns of elephants were also similar within and beyond the PPAs, but for the dry season selection for areas close to people when the elephants were beyond the PPAs. Females spent more time beyond PPAs during the wet season, and females from wetter PPAs had a larger area of their home range beyond PPAs than females from more arid PPAs. There were no seasonal differences in the amount of time that males spent beyond PPAs and during both seasons they concentrated their activities beyond the PPAs. Additionally, during both seasons males from PPAs with higher population growth rate had a larger proportion of their home range beyond the PPAs. However, these results were inconclusive due to small sample sizes. The area of males' dry season home ranges beyond PPAs was larger in more arid areas than wetter areas. Adjoining many of the PPAs were secondary protected areas

(SPAs) consisting of community conservancies. Together with the PPAs, the SPAs formed clusters of protected areas in which the elephants remained.

Therefore, this study shows that the reasons for elephants leaving the PPAs varied both seasonally as well as between the sexes. However, the elephants did utilise both the PPAs and the SPAs. During the dry season, when water was limited elephants selected for areas close to human settlements within the SPAs, which was probably indicative of selection for water as many settlements are built along rivers or close to water. This study highlights the importance of conserving both the PPAs and the SPAs. The SPAs can then act as a buffer between the PPAs and areas of high human densities.

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I would like to thank my supervisor, Professor Rudi van Aarde for his guidance, criticism and patience throughout the duration of this thesis. His passion for science and elephants has inspired me and driven me to do the best work that I can. I am very grateful to him for allowing me to be involved in the elephant project, something which I hold very close to my heart.

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DISCLAIMER

I, Tamara Lee declare that the thesis, which I hereby submit for the degree of *Magister Scientiae* (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Tamara Lee

30 August 2012

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CHAPTER 1

INTRODUCTION

The formation of formally protected areas in southern and eastern Africa began in the 1890s with the mandate of wildlife preservation (Western, 2003). Most of these protected areas were national parks and reserves that excluded indigenous people from entering or utilising resources from within them (deGeorges and Reilly, 2009). Since the World Parks Congress in Bali in 1982 the importance of including local people in conservation has been acknowledged and the purpose of protected areas has evolved from purely conservation to include livelihood benefits to local people for whom utilisation of the resources is essential (e.g. Abensperg-Traun, 2009; Naughton-Treves *et al*., 2005). Furthermore, in 1994 a category system for protected areas was created consisting of six categories as guidelines for international categorising of protected areas (see Table 1).

Table 1. The six IUCN categories for protected areas based on IUCN (1994). Categories I to IV represent primary protected areas (PPAs) and categories V and VI represent secondary protected areas (SPAs).

IUCN category	Description
I (a and b)	Strict nature reserve or wilderness area, managed primarily for strict protection.
II	National park, managed primarily for recreation and ecosystem protection.
III	Natural monument, managed primarily for conserving natural features.
IV	Habitat/Species management area, managed primarily for conservation through active management
V	Protected landscape/seascape, managed primarily for landscape/seascape conservation and recreation
VI	Managed resources protected area, managed primarily for the sustainable use of natural ecosystems.

Wildlife populations in several East and southern African protected areas are declining for a variety of reasons (Ogutu and Owen-Smith, 2003; Stoner *et al*., 2007; Ogutu *et al*., 2009; Western *et al*., 2009; Ogutu *et al*., 2011), most thereof either directly or indirectly related to human activities (Stoner *et al*., 2007; Ogutu *et al*., 2009; Western *et al*., 2009; Ogutu *et al*., 2011). In Tanzania, these declines are more pronounced in game-controlled areas and unprotected areas than in national parks (strict protection) and game reserves (allow tourist hunting) (Stoner *et al*., 2007). The game-controlled areas only allow extractive resource use under licence, while game reserves allow tourist hunting. In Kenya, the declines in populations within national parks and reserves mirror those in adjoining ranchlands and unprotected areas (Western *et al*., 2009). However, it is speculated that changing the ranchlands into community conservancies (SPAs) will help to halt the decline in wildlife numbers as the local communities will have a greater interest in conserving wildlife (Ogutu *et al*., 2009; Western *et al*., 2009; Ogutu *et al*., 2011).

In southern Africa community-based natural resource management (CBNRM) has been adopted to try and integrate conservation and the rights of indigenous people (Nelson and Agrawal, 2008). CBNRM occurs in secondary protected areas (SPAs; IUCN categories V and VI), which adjoin many primary protected areas (PPAs) that consist of national parks and game and wildlife reserves (IUCN categories I – IV). Collectively these form clusters of protected areas across the sub-continent. Consequently, SPAs extend the areas available for utilisation by wildlife, especially when considering that nearly 60%[1] of the 16%[2] of southern

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[1] This figure was calculated from the sizes of SPAs given in the World Database on Protected Areas 2009 (http://www.wdpa.org). I included protected areas in the IUCN categories V and VI as well as the unknown category.

[2] This average was calculated from the 2011 Millennium Development Goals Report released by the IUCN and UNEP-WCMC (2011). For each country the percentage of protected area coverage for the year 2008 was used, Footnote continued on the next page.

Africa set aside for conservation related activities comprises of protected areas in IUCN categories V and VI.

The parks and reserves are generally state-controlled. Human habitation in some PPAs is restricted and in some cases have multiple management objectives, most of which centres on the maintenance of biological diversity. Conversely, the SPAs are generally community conservancies where people live, albeit at low densities, and are allowed to utilise the natural resources and receive money through non-consumptive activities such as tourism. These areas therefore have multiple management objectives (Hoekstra *et al*, 2005). The SPAs aim to allow the resident people to gain some benefit from the wildlife with which they share their land. Many of these SPAs may act as buffers between the parks and areas of higher human density and greater land transformation. These areas therefore add to the amount of land available to wildlife and may be important for conservation (Abensperg-Traun, 2009).

The isolation and restriction of movement of wildlife within PPAs may be caused by habitat loss, and the erection of fences and building of roads (Newmark, 2008). One way to halt the isolation of southern Africa's PPAs is through the clustering of existing national parks and reserves, usually with adjoining or surrounding SPAs, into megaparks (van Aarde *et al*., 2006; van Aarde and Jackson, 2007). Megaparks should increase the range available to elephants and other wildlife, while benefitting local people. Van Aarde and Ferreira (2009) advocated the recognition of eight clusters of protected areas across southern Africa, which would allow the elephant sub-populations within the clusters to be managed as a unit and/or a metapopulation.

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to correspond with the calculation of the extent of SPAs above. The countries included were: Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe.

Another example of integrated land-use in conservation is biosphere reserves. Biosphere reserves consist of core areas of strict legal protection and adjoining buffer areas in which research, education, and training take place and local people may live (Batisse, 1982). Therefore, these reserves are protected while allowing for research and monitoring of the ecosystems within their boundaries.

The relatively recent efforts to establish Transfrontier Conservation Areas (TFCAs) may address some of the shortcomings of existing protected areas (see Hanks, 2003). The development of these TFCAs, which are supported by the Southern African Development Community (SADC)[3], aims to conserve biodiversity while promoting the alleviation of poverty (Hanks, 2003).

TFCAs are areas that straddle two or more countries and which are dedicated to the protection and maintenance of biodiversity, natural and cultural resources (Singh, 1999). They usually are part of a larger ecoregion and consist of one or more PPAs as well as SPAs (Singh, 1999; Sandwith *et al.*, 2001). Ecologically, TFCAs are established to protect ecosystems that span international boundaries. Their purpose is to re-establish seasonal migration routes, which have been disrupted by fences or other barriers, and increase the area for plant and wildlife populations, thereby decreasing their extinction rates (Singh, 1999). TFCAs are a prominent and increasingly implemented tool in conservation (e.g. Smith *et al.*, 2008).

Elephant populations are often fragmented and compressed into PPAs (van Aarde and Jackson 2007). In southern Africa human populations have increased and purportedly contributed to the fragmentation of elephant populations (Hoare and du Toit, 1999; Osborn

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[3] SADAC consists of 14 southern African countries, which promote economic cooperation in the region.

and Parker, 2003; Ntumi *et al*., 2009). Some elephant populations have been compressed into isolated PPAs due to fencing, high human densities beyond the PPAs, or even water supplementation, which encourages elephants to remain within PPAs throughout the year, thereby disrupting seasonal movements as well as modifying elephant range use (Grainger *et al*., 2005; van Aarde *et al.*, 2006; 2008). Elephants confined to PPAs may have negative effects on the vegetation as well as other wildlife within the PPAs (Western and Maitumo, 2004; de Beer *et al*., 2006; Guldemond and van Aarde, 2008).

Throughout much of the southern African region elephants are able to roam beyond the boundaries of PPAs and often onto adjoining SPAs (Roever *et al*., 2013; CERU, unpublished data). As the elephants move into surrounding areas they may come into contact with people resulting in elephants altering their behaviour (Galanti *et al*., 2006; Graham *et al*., 2009; Boettiger *et al*., 2011) and possibly leading to human-elephant conflict (HEC) (Hoare, 1999; Parker and Osborn, 2001; Sitati *et al*., 2003; Osborn, 2004; Chiyo *et al*., 2005; Jackson *et al*., 2008), which can result in people losing their crops or lives, and in elephants being harassed and killed (Ntumi, 2012). Generally, males are more involved in HEC than females and the crop raiding occurs mostly at night (Hoare, 1999; Jackson *et al*., 2008; Graham *et al*., 2010; Chiyo *et al*., 2011). Therefore, efforts at mitigating HEC may benefit from an understanding of why elephants are leaving PPAs.

Elephant movements, home range sizes, and spatial distributions may be influenced by the presence of PPAs (Douglas-Hamilton *et al*., 2005), the distribution of water (Grainger *et al*., 2005; de Beer and van Aarde, 2008; Harris *et al*., 2008; Roever *et al*., 2012), primary productivity (Loarie *et al*., 2009a; Young *et al*., 2009a, b; Marshal *et al*., 2011), topography (Wall *et al*., 2006), proportions of different vegetation types (Harris *et al*., 2008), human settlements associated with agricultural fields (Hoare, 1999; Parker and Osborn, 2001; Sitati *et al*., 2003; Chiyo *et al*., 2005; Jackson *et al*., 2008; Graham *et al*., 2010; Ntumi, 2012), rainfall (Osborn, 2004), season (Stokke and du Toit, 2002; Leggett, 2006; Jackson *et al*., 2008; Chase and Griffin, 2009; Young *et al*., 2009a), the density (Wittemyer *et al*., 2007; Young *et al*., 2010), and population growth rates of elephant populations (Young *et al*., 2009b) and the size of the PPAs (Roux and Bernard, 2007). Furthermore, female and male elephants exhibit significant sexual body dimorphism and segregation in foraging and roaming behaviours (Stokke, 1999; Stokke and du Toit, 2000; Stokke and du Toit, 2002; Shannon *et al*., 2006; Woolley *et al*., 2009; de Knegt *et al*., 2011). Therefore, in this thesis I analysed the data for males and females separately.

AIMS OF THE STUDY

The aim of this study was to determine why elephants leave the PPAs in which they were collared. To accomplish this, I used Global Positioning System locations of collared elephants in PPAs within seven clusters of protected areas throughout southern Africa. I then divided the analyses into two parts based on scale. First, at the elephant location-scale I investigated differences in displacement rates within and beyond PPAs, spatial and temporal differences in the use of areas beyond PPAs and habitat selection by elephants beyond PPAs. Second, at the home range-scale, I measured the areas and proportions of the home ranges beyond PPAs and examined whether the variability in the areas and proportions was influenced by a range of intrinsic and extrinsic factors. The two different scales were chosen as these are relevant to the analyses as implied by the work of others.

WORKING HYPOTHESES

- Displacement rates will be larger beyond PPAs compared to within PPAs.
- The proportion of elephant telemetry locations beyond PPAs will be greater during the wet season than during the dry season.

- The proportion of elephant telemetry locations within the 50% isopleths of the home ranges will be larger within PPAs than beyond.
- Elephants leave PPAs to select areas close to water and people, or areas with high primary productivity, high herbaceous or tree cover, or low slopes.
- Elephants from more arid PPAs will have a larger area of their home range beyond the boundaries of the PPAs than elephants from wetter PPAs.
- The season-specific variability in the proportion of home ranges beyond PPAs can be accounted for by the density and population growth rates of elephant populations within PPAs, the size of the PPAs, and the size of the home ranges of elephants.

PREDICTIONS

To evaluate the hypotheses I considered and expected the following:

- When elephants leave the relative safety of PPAs and move through unprotected land they generally increase their displacement rates (Douglas-Hamilton *et al.*, 2005). I therefore expected that displacement rates will be larger beyond the PPAs than within the PPAs.
- The wet season home ranges of elephants are generally larger than their dry season ranges because elephants are not limited by the distribution of water during the wet season (Stokke and du Toit, 2002; Jackson *et al.*, 2008; Chase and Griffin, 2009). I therefore expected a larger proportion of wet season elephant telemetry locations to fall beyond PPAs than the proportion of dry season elephant telemetry locations.
- Elephants concentrate their activities within PPAs (Douglas-Hamilton *et al.*, 2005). I therefore expected a larger proportion of telemetry locations within the 50% isopleths of the home range to fall within PPAs and a smaller proportion to fall beyond PPAs.

- Elephants have been shown to move to areas with high primary productivity (Loarie *et al.*, 2009a; Young *et al.*, 2009b) and lower slopes (Wall *et al.*, 2006). They may select for areas close to humans where crops are grown (Hoare, 1999; Parker and Osborn, 2001; Sitati *et al.*, 2003; Chiyo *et al.*, 2005; Jackson *et al.*, 2008; Graham *et al.*, 2010; Ntumi, 2012) and select areas close to water (Harris *et al.*, 2008). Elephants are mixed feeders and therefore require both browse and graze (Codron *et al.*, 2006; Codron *et al.*, 2011; Owen-Smith and Chafota, 2012). Thus, I expected that elephants might leave the PPAs to select for these resources. To investigate this I first compared the landscapes that the elephants were using within and beyond the PPAs to determine whether they differed with regards to these variables. I then compared habitat selection models within and beyond the PPAs to examine selection for these resources beyond the PPAs.
- Elephants from more arid areas generally have larger home ranges to fulfil their needs than elephants from wetter areas (Osborn, 2004; Young *et al.*, 2009a). Therefore, I expected elephants from drier areas to have a larger area of their home range beyond PPAs than elephants from wetter areas.
- Elephants residing within PPAs with high elephant densities and fast growing populations will expand their range beyond the PPAs due to competition for scarce resources (Western and Maitumo, 2004; Wittermyer *et al.*, 2007). Therefore, I expected elephants living at high densities and in fast growing populations to have a greater proportion of their home range beyond PPAs.
- Roux and Bernard (2007) found that the upper limit of the home ranges of elephants they were studying in two small, fenced South African reserves was limited by the size of the reserves. Therefore, small PPAs may not meet the spatial requirements of elephants as well as larger PPAs and if elephants are able to, they will move beyond the boundaries of

small PPAs more often than larger PPAs. Therefore, I expected elephants in relatively small PPAs to have a greater proportion of their home range beyond the PPAs.

- For elephants, the size of their home ranges is influenced by the availability and distribution of resources (Grainger *et al*., 2005; Leggett, 2006; de Beer and van Aarde, 2008; Young *et al*., 2009a; Shannon *et al*., 2010). If the spatial needs of elephants are not being met within the PPAs, they will have to extend their home ranges beyond the PPAs. Consequently, I expected elephants with larger home ranges to have a greater proportion of their home range beyond PPAs.

CHAPTER 2

STUDY REGION

The study included seven clusters of protected areas across southern Africa (Figure 1 and Table 1). The clusters are based on van Aarde and Ferreira (2009) and were delineated on the basis of proximity. Each cluster comprised different types and numbers of PPAs (IUCN categories I to IV; IUCN, 1994) and SPAs (IUCN categories V to VI; IUCN, 1994). PPAs consisted of national parks, game parks, partial reserves, wildlife reserves, special reserves, and game reserves, while SPAs comprised game management areas (GMAs), safari areas, and communal conservancies. Within the seven clusters of protected areas my study sites comprised 12 PPAs. These PPAs included the Khaudum Game Reserve[4], Bwabwata National Park[5] and Mudumu National Park[6] in the Chobe cluster, Kafue National Park[7] in the Kafue cluster, Lower Zambezi National Park[8] in the Zambezi cluster, South Luangwa National Park[9], North Luangwa National Park[10], Vwaza Wildlife Marsh Reserve[11] and Kasungu National Park[12] in the Luangwa cluster, the Quirimbas National Park[13] in the Niassa cluster, the Limpopo National Park[14] in the Limpopo cluster, and Maputo National Reserve[15] in the Maputo cluster (Figure 1 and Table 1). The PPAs in my study could be divided into dry savannah PPAs and wet savannah PPAs based on rainfall (Sankaran *et al*., 2005). The PPAs

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[4] Khaudum Game Reserve will be referred to as Khaudum from here on

[5] Bwabwata National Park will be referred to as Bwabwata from here on

[6] Mudumu National Park will be referred to as Mudumu from here on

[7] Kafue National Park will be referred to as Kafue from here on

[8] Lower Zambezi National Park will be referred to as Lower Zambezi from here on

[9] South Luangwa National Park will be referred to as South Luangwa from here on

[10] North Luangwa National Park will be referred to as North Luangwa from here on

[11] Vwaza Wildlife Marsh Reserve will be referred to as Vwaza from here on

[12] Kasungu National Park will be referred to as Kasungu from here on

[13] Quirimbas National Park will be referred to as Quirimbas from here on

[14] Limpopo National Park will be referred to as Limpopo from here on

[15] Maputo National Reserve will be referred to as Maputo from here on

receiving < 650mm mean annual precipitation were located in dry savannahs and those receiving > 650mm mean annual precipitation were located in wet savannahs (Sankaran *et al*., 2005). All elephants included in the analyses were collared in these PPAs and hence assumed to reside within the parks where they were located when collaring took place.

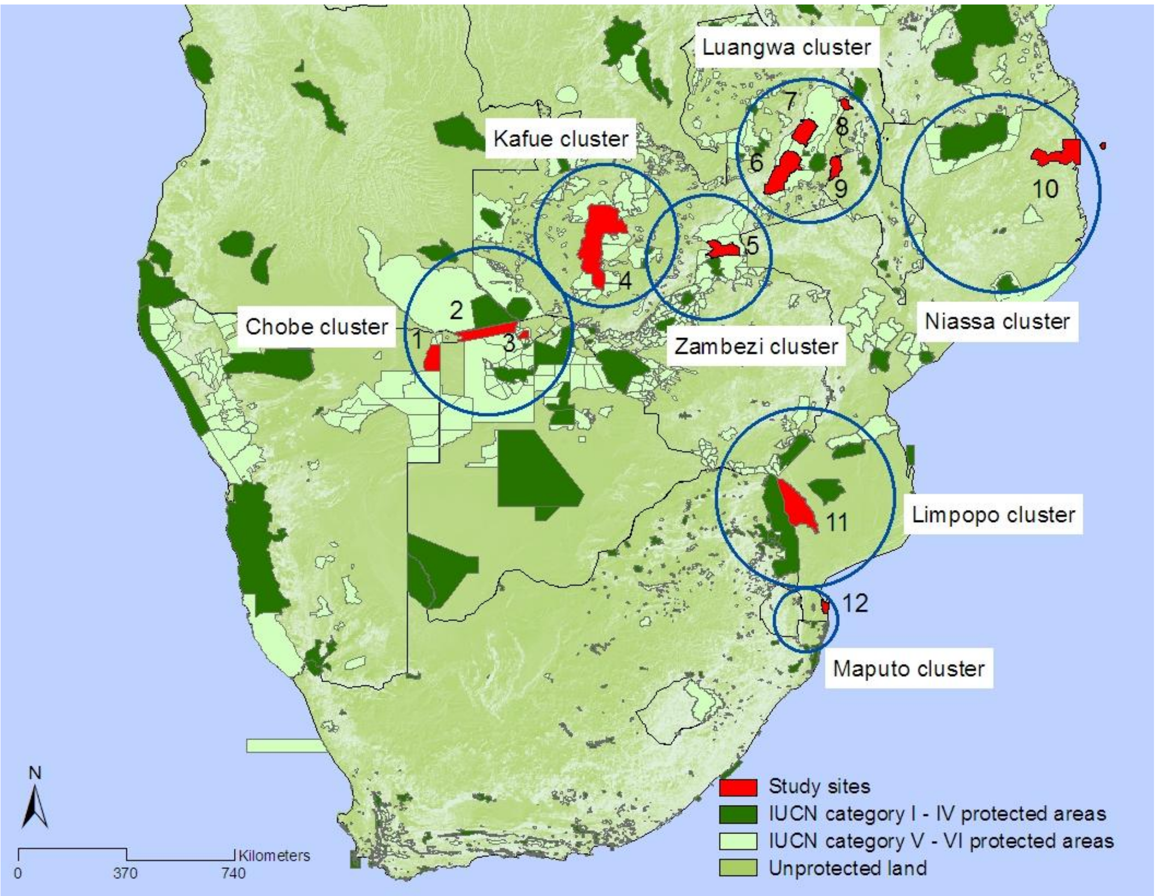

Figure 1. Locations of the 12 study sites within seven clusters of protected areas: (1) Khaudum; (2) Bwabwata; (3) Mudumu; (4) Kafue; (5) Lower Zambezi; (6) South Luangwa; (7) North Luangwa; (8) Vwaza; (9) Kasungu; (10) Quirimbas; (11) Limpopo; (12) Maputo.

The PPAs were managed primarily for biodiversity conservation (IUCN, 1994) and differed in the area covered, rainfall, water availability, and whether people resided within (Table 1). The PPAs fell within the IUCN categories of I to IV with the exceptions of Bwabwata and Quirimbas, which had not been assigned to an IUCN category at the time of the study (Table 1). The delineation of the primary and secondary protected areas was based on the dataset from the World Database on Protected Areas 2009 (http://www.wdpa.org). For Namibia additional community conservancies were downloaded from the Namibian Association of CBNRM Support Organisations website (http://www.nacso.org.na).

Table 2. The IUCN categories of the PPAs, the clusters of protected areas the PPAs were within, the mean annual precipitation, supplemented water, whether people resided within the PPA, the size of the PPAs, and the number and size of adjoining SPAs are presented.

PPA	IUCN category	Cluster of protected area	Mean annual rainfall ± standard deviation (mm)[a]	Rainfall collection period (years)	Supplemented water	People residing within	PPA area (km^2)	Number of adjoining SPAs	Adjoining SPAs area (km^2)
Khaudum	II	Chobe	524[b]	50	Yes - boreholes	No	3 658	3	10 093
Bwabwata	Unknown	Chobe	573[b]	50	No	Yes	6 333	5	20 276
Mudumu	II	Chobe	572[b]	50	No	No	726	5	3 286
Kafue	II	Kafue	783 ± 234	17	Yes - dam	No	22 400	9	39 754
Lower Zambezi	II	Zambezi	667 ± 204	10	No	No	4 092	5	15 972
South Luangwa	II	Luangwa	802 ± 145	21	No	No	9 050	4	14 170
North Luangwa	II	Luangwa	831 ± 141	7	No	No	4 636	3	25 150
Vwaza	IV	Luangwa	900 ± 324	17	Yes - lake	No	986	1	3 784
Kasungu	II	Luangwa	846[b]	50	Yes - dam	No	2 316	0	NA
Quirimbas	Unknown	Niassa	1050[b]	50	No	Yes	7 506	0	NA
Limpopo	II	Limpopo	471 ± 260	25	Yes - dam	Yes	12 000	0	NA
Maputo	IV	Maputo	756 ± 242	25	No	Yes	900	0	NA

[a] Mean annual rainfall was calculated from weather stations either within the protected areas or the closest stations to them (Jackson and Erasmus, 2005). For Khaudum, Bwabwata, Mudumu, Kasungu, and Quirimbas annual rainfall was calculated from interpolated monthly worldclim rainfall datasets (http://www.worldclim.org/).

[b] No standard deviations available.

The management and formation of the SPAs differed between the different countries in my study area. In Namibia, wildlife laws were amended in 1996, which allowed for the creation of community conservancies (Nelson and Agrawal, 2008), thereby giving limited rights of proprietorship over wildlife to conservancy residents and permitting them to benefit from the wildlife (Weaver and Skyer, 2005). The formation of the community conservancies has shifted the attitude of conservancy residents to wildlife, from one of resentment to one of viewing wildlife as a community asset, which has resulted in an increase in wildlife numbers (Weaver and Skyer, 2005).

In Zambia, community participation in wildlife policy began in the early 1980s with the establishment of the Luangwa Integrated Resources and Development Program (LIRDP), which operated within the Luangwa Valley, and the Administrative Management and Design for Game Management Areas (ADMADE), which operated at the national scale (Nelson and Agrawal, 2008). Even though the local residents gain financial benefits from utilisation of the wildlife, the management of the wildlife remains with the state, which has drawn criticism from some authors (see Nelson and Agrawal, 2008). Nevertheless, there has been a recorded positive change in the attitudes of local people to wildlife and a decrease in poaching (Lewis *et al*., 1990; Lewis and Alpert, 1997).

Between 1996 and 1999 legislation was introduced by the Malawian government to encourage community participation in the wildlife, fisheries and forestry sectors. However, due to the lack of wildlife and the high human populations beyond existing PPAs, the endorsed community participation in the wildlife sectors resulted in increased cooperation between PPAs and neighbouring communities instead of the formation of conservancies outside PPAs (Jones, 2007). Therefore, neighbouring communities were allowed controlled access to some natural resources within the PPAs as well as shared revenue from the PPAs (Jones, 2007).

Since the end of the civil war in Mozambique in 1992 community participation in wildlife management has been endorsed, thereby allowing the communities to apply for user rights and management authority for wildlife (Nelson and Agrawal, 2008). Wildlife numbers in Mozambique were depleted during the civil war, which has limited the growth of wildlife tourism in the country and inadequate published data are available on the economic benefits of hunting (Nelson and Agrawal, 2008). PPAs within Mozambique are inhabited by people and are therefore more similar to SPAs. However, in this thesis they will be regarded as PPAs.

DESCRIPTION OF CLUSTERS

CHOBE CLUSTER

Khaudum, Namibia

Khaudum was located on the north-eastern border of Namibia and Botswana. It was the only reserve that conserved the Namibian northern Kalahari sandveld biome (Wanke and Wanke, 2007) and was proclaimed in 1989. Along the eastern boundary of Khaudum was a veterinary control fence, which was constructed in the 1960s, thereby hampering wildlife migrations in the area (Martin, 2005). Otherwise Khaudum was unfenced thus enabling wildlife to roam beyond its boundaries and onto the surrounding land. Three springs in Khaudum supplied water naturally to the wildlife, which were supplemented with 13 artificial permanent waterholes (Wanke and Wanke, 2007). During the wet season additional water collected in pans and depressions. The annual rainfall was 400 – 450mm (Weaver and Skyer, 2005) and mainly fell in the wet season between November and April (de Beer and van Aarde, 2008). The vegetation in Khaudum consisted of woodlands dominated by *Burkea africana* and *Baikiaea plurijuga*, and shrublands dominated by *Terminalia sericea*, *Acacia* species and *Combretum* species (de Beer and van Aarde, 2008). The size of Khaudum was 3 658km^2.

Khaudum was adjoined by the Nyae-Nyae Conservancy to the south, communal lands to the west (Weaver and Skyer, 2005), and the George Mukoya and Muduva Nyangana Conservancies to the north. The areas surrounding Khaudum were sparsely populated (Wanke and Wanke, 2007). The Nyae-Nyae conservancy was registered in 1989 and covered an area of 8 992km^2. The elephant population of Khaudum comprised 3 400 elephants in 2004, which increased from about 80 elephants in 1976, probably due to war in Angola as well as water provisioning in Khaudum (van Aarde and Jackson, 2007). The Nyae-Nyae conservancy was home to the Ju/'hoansi San people who were a far-roaming hunter-gatherer society. The establishment of the conservancy and game reintroductions to the area helped them to benefit from the natural resources in the area through job creation and income from tourism and trophy hunting (Weaver and Skyer, 2005).

Information on the George Mukoya and Muduva Nyangana Conservancies was downloaded from Conservancy profiles on the Namibian Association of CBNRM Support Organisations website (http://www.nacso.org.na). The George Mukoya and Muduva Nyangana Conservancies were registered in 2005 and encompassed an area of 486km^2 and 615km^2, respectively. Approximately 2 000 people lived in each conservancy. Conservancy income in both conservancies was generated through trophy hunting.

The Caprivi region, Namibia

The Caprivi region was a long, thin piece of Namibia, which projected eastwards between Botswana, Angola, Zambia and Zimbabwe. The border between Botswana and Namibia was partially fenced with a veterinary fence. The Okavango River bordered the Caprivi region on the western side, the Zambezi and Chobe Rivers formed part of the eastern border and the Kwando River that flowed from north to south divided the Caprivi region into western and eastern halves. The average rainfall for the area was 650mm (Chase & Griffin, 2009), which along with the perennial rivers provided additional surface water in the wet season when it collected in dambos (seasonally flooded areas). The topography was relatively flat with an average altitude of 1000m ± 60m (Rodwell *et al*., 1995). The vegetation in the Caprivi region consisted of woodlands dominated by *Colophospermum mopane* and *Burkea africana*, mixed shrublands and grasslands (Chase and Griffin, 2009). More people live on the eastern than the western side of the Kwando River, with most of the settlements concentrated along rivers and roads.

Within the Caprivi region there were three national parks and a number of conservancies. This study concentrated on elephants collared within two of the national parks, namely Bwabwata (6 333km^2) on the western side of the Kwando River and Mudumu (726km^2) on the eastern side of the Kwando River. Bwabwata had people living within it, whereas Mudumu did not. Bwabwata was proclaimed a national park in 2007; however, the area it now mostly encompasses was previously the Caprivi Game Reserve. Mudumu was proclaimed in the 1990s. Bwabwata was bordered by two PPAs to the north, namely Sioma Ngwezi National Park (5 276km^2) in Zambia and Luiana Partial Reserve (8 400km^2) in Angola. Seven SPAs adjoined Bwabwata. Luengué Hunting Reserve (16 700km^2) in Angola adjoined Bwabwata to the north, the Ngamiland 13 Wildlife Management Area (2 938km^2) in Botswana adjoined Bwabwata to the south and three community conservancies within Namibia were on Bwabwata's eastern border. The community conservancies within Namibia were Kwandu, Mayuni and Mashi. Kwandu Conservancy was registered in 1999 and encompassed an area of 190km^2 with an approximate human population of 4 300 (http://www.nacso.org.na). To the south of Kwandu Conservancy was Mayuni Conservancy, which was registered in 1999, encompassed an area of 151km^2 and was inhabited by *c*. 2 400 people (http://www.nacso.org.na). Mashi Conservancy lay on the southern border of Mayuni Conservancy, it was registered in 2003, extended over an area of 297 km^2 and had an approximate population of 3 900 (http://www.nacso.org.na).

Mudumu was adjoined by five SPAs. Ngamiland 14 Wildlife Management Area (2 266km^2) in Botswana bordered Mudumu to the west, Sobbe Conservancy adjoined Mudumu to the north and east, Dzoti Conservancy to the east and Wuparo and Balyerwa Conservancies to the south. Sobbe Conservancy (404km^2) was registered in 2006 and had an approximate population of 2 000 (http://www.nacso.org.na). Dzoti Conservancy extended over an area of 245km^2 with an approximate population of 1 100 people. It was registered in 2009 (http://www.nacso.org.na). Balyerwa and Wuparo Conservancies were registered in 2006 and 1999, respectively. Balyerwa Conservancy encompassed an area of 223km^2 and had an approximate population of 1 500 people. Wuparo Conservancy extended over 148km^2 and was inhabited by *c*. 2 100 people (http://www.nacso.org.na).

KAFUE CLUSTER

Kafue, Zambia

Kafue was located in the south-central part of Zambia and covered an area of about 22 400km^2. It was officially gazetted as a national park in 1972 (Mwima, 2001). The Kafue River formed part of the eastern border of Kafue and along with its tributaries and the Itezhi-tezhi Dam, which was situated on the eastern border, provided water for wildlife. Rainfall ranged from 600mm in the south to 1200mm in the north (Mwima, 2001). The vegetation consisted of Kalahari woodlands, miombo woodlands, mopane woodlands, *Baikeaia* forests, termitaria vegetation, and grasslands (Guldemond *et al*., 2005). People did not reside within Kafue except for the park headquarters at Ngoma and Chunga in the southern and northern sectors of the park, respectively (Weyher *et al*., 2010). Kafue was unfenced and was adjoined by nine GMAs. Adjoining Kafue on the southern and south-western sides were Mulobezi GMA (3 420 km^2), Sichifula GMA (3 600km^2) and Kalomo Hills Forest Reserve (1 370km^2). Bilili Springs GMA bordered Kafue on the eastern side and covered an area of 3 080km^2. Adjoining Kafue on the eastern side and south of the Itezhi-tezhi Dam was the Nkala GMA, which encompassed an area of 194km^2. To the north of Nkala GMA and on the eastern border of Itezhi-tezhi Dam was Namwala GMA (3 600km^2), which was bordered on the north by Mumbwa GMA (3 370km^2). Adjoining the northern part of Kafue were Lunga-Luswishi GMA and Kansonso-Busanga GMA, which were 13 340km^2 and 7 780km^2, respectively. With the exception of Kalomo Hills Forest Reserve, which was created in 1970, all of the GMAs were created in 1971, but as Controlled Hunting Areas, which were converted to GMAs at a later date (Bandyopadhyay and Tembo, 2010).

ZAMBEZI CLUSTER

Lower Zambezi, Zambia

Lower Zambezi was situated on the southern border between Zambia and Zimbabwe and covered an area of 4 092km^2. It was on the northern bank of the Zambezi River and had an escarpment along its northern end. Here annual rainfall ranged from 800mm to 880mm (Chidumayo, 2002). The vegetation consisted of *Colophospermum mopane* woodlands, *Acacia albida* woodlands, and deciduous *Commiphora-Combretum* thicket (Dunham, 1988). Lower Zambezi was unfenced and adjoined the Chiawa GMA (2 344km^2) to the west, Luano GMA (8 930km^2) to the north, and Rufunsa GMA (3 179km^2) to the east. The three GMAs were created in different years, Chiawa GMA was created in 1989, Rufunsa GMA was created in 1980 and Luano GMA was created in 1971. Adjoining Lower Zambezi on the southern bank of the Zambezi River and within Zimbabwe was Mana Pools National Park (2 196km^2), which was a World Heritage Site, as well as Chewore and Sapi Safari Areas, which were 339km^2 and 1180km^2, respectively. A safari area in Zimbabwe is state land where consumptive use of wildlife is allowed but human habitation is not (Metcalfe, 2003). No human settlements were permitted in Lower Zambezi, however, Chidumayo (2002) noted that there had been a steady influx of settlers who were allocated land within the park by headmen from the surrounding GMAs.

LUANGWA CLUSTER

The Luangwa Valley, Zambia

The Luangwa Valley, in north-east Zambia, was a flat-bottomed trough some 700km long and with an average width of about 100km (Gerkmann *et al*., 2008). On the west it was bordered by the Muchinga Escarpment and on the eastern side it ascended to the mountain ranges of western Malawi (Gerkmann *et al*., 2008). The annual average rainfall ranged from 700mm to 900mm (Smith, 1997). The vegetation within the valley consisted of *Colophospermum mopane* and *Combretum/Terminalia* woodlands and grasslands, and miombo woodland on the escarpment and plateau areas (Jachmann, 1995).

Within the Luangwa Valley there were four national parks, which were adjoined by several GMAs. This study focussed on elephants collared in South Luangwa (9 050km^2) and North Luangwa (4 636km^2), which were separated by the Munyamadzi GMA. Both parks were bordered on their eastern sides by the perennial Luangwa River, one of the main tributaries of the Zambezi River (Gerkmann *et al*., 2008), which along with its many seasonal tributaries provided water for the wildlife. The Muchinga Escarpment formed the western boundary of South Luangwa and was incorporated into the western boundary of North Luangwa. No people lived beyond the tourist facilities within South and North Luangwa and both parks were unfenced.

On the south-eastern and eastern borders of South Luangwa were Sandwe GMA (1 530km^2) and Lupande GMA (4 840km^2), respectively. Lumimba GMA (4 500km^2) adjoined both South and North Luangwa on their eastern sides and Munyamadzi GMA separated the two parks and covered an area of 3 300km^2. Adjoining North Luangwa to the north and the north-west was Musalangu GMA, which covered an area of 17 350km^2. All of the GMAs adjoining South and North Luangwa were created in 1971.

Vwaza, Malawi

Vwaza was situated in northern Malawi on the Zambian border and was proclaimed in 1977 (Clarke and Bell, 1986; McShane, 1990). It covered an area of 986km^2. It received an annual average rainfall of 900mm and lay at an altitude of about 1000m above sea level (McShane, 1990). The South Rukuru River formed the southern boundary of Vwaza, which was joined by the Luwewe River flowing south through the reserve (McShane, 1990). Lake Kazuni covered part of the wetlands to the south-east of the reserve. The vegetation in the eastern part of the reserve consisted of *Brachystegia* woodlands on the slopes of the Nyika massif and *Combretum* woodlands in the valleys, and the vegetation in the western part of the reserve consisted of *Brachystegia* woodlands on the plateau and *Colophospermum mopane* on the clay flats (McShane, 1990). Vwaza was partially fenced. The Reserve was adjoined by the Lundazi Forest Reserve in Zambia on its western border; otherwise, it was surrounded by transformed land. Lundazi Forest Reserve (3 748km^2), which was created in 1978, was a component of Musalangu GMA thereby linking Vwaza to North and South Luangwa and together forming a single ecosystem (Hall-Martin and Modise, 2002).

Kasungu, Malawi

Kasungu was situated in central Malawi on the Zambian border, it was proclaimed in 1930 (Clarke and Bell, 1986) and covered an area of 2 316km^2. The altitude ranged from 1000 to 1500 metres above sea level and the average annual rainfall was 780mm (Bhima *et al*., 2003). The perennial Dwangwa, Lingadzi, and Liziwazi Rivers, their seasonal tributaries, and an artificial dam in the south of the park provided water. On the plateau areas of the Park the dominant vegetation was *Brachystegia/Julbernardia* woodland, in the valley areas there was open woodland with *Terminalia*, *Pericopsis*, and *Combretum* trees and *Hyparrhenia* grass (Jachmann and Bell, 1985). Kasungu was situated on Malawi's border with Zambia. It was not adjoined by any SPAs and on its Malawian borders was surrounded by people living at high densities and where the land was intensely transformed for agriculture. Even though there was no human habitation within Kasungu, local communities were allowed to practise bee-keeping and pick Saturniidae caterpillars within the Park (Munthali and Mkanda, 2002).

NIASSA CLUSTER

Quirimbas, Mozambique

Quirimbas was located in northern Mozambique, it was declared in 2002 and covered an area of 7 506km^2. It consisted of both terrestrial and marine habitats, with the marine habitats comprising 20% of its total area (Guerreiro *et al.*, 2011). The annual average rainfall ranged between 900 and 1000mm (Bandeira *et al.*, 2007). There was a topographic gradient in the composition of vegetation with coastal scrubs and mangroves at sea level in the east, transitioning through Acacia-grassland, mixed-woodland, and miombo woodland to miombo-velloziacea in the inselbergs in the west (Bandeira *et al.*, 2007). Quirimbas was unfenced and was not adjoined by any other PPAs or SPAs. At the time of the study, some 95 000 people lived within the Quirimbas (MITUR, 2012).

LIMPOPO CLUSTER

Limpopo, Mozambique

Limpopo was proclaimed in 2002 and was situated on the Mozambique border with the Kruger National Park in South Africa. It encompassed an area of 12 000km^2. The southern border was demarcated by the Olifants River and the Limpopo River formed the northern and eastern borders. The Massinger Dam was located in the south. The elevation ranged from 45 to 521 metres above sea level, and the average annual rainfall ranged from 450mm to 500mm (Stalmans *et al.*, 2004). The vegetation was dominated by *Colophospermum mopane* in the north, mixed bushveld varying from open savannah to woodland in the south, and sandveld areas with a diverse range of species (Hall-Martin and Modise, 2002). 30 000 people lived (MICOA, 2007) within Limpopo and were concentrated around the Limpopo and Shingwedzi

Rivers (Stalmans *et al*., 2004). Limpopo was not adjoined by any SPAs. The Limpopo National Park has been occupied by people even before its declared conservation status. In the strictest sense of the word its prior existence as a hunting area (Cautada 16) renders it an SPA, rather than a PPA.

MAPUTO CLUSTER

Maputo, Mozambique

Maputo was located in the south-eastern border of Mozambique and was bordered on the east by the Indian Ocean. Maputo was established in 1932 (de Boer *et al*., 2007) and covered an area of 800km^2. The average annual rainfall ranged from 690 to 1000mm (de Boer *et al*., 2007). The Futi and Maputo Rivers flowed through the western part of the reserve. There were six vegetation communities: riverine vegetation; open woodlands; dry sublittoral forest thicket; grasslands, dune thicket and forest; and mangroves (de Boer *et al*., 2000). People lived within the boundaries of the reserve. At the time of the study the reserve was unfenced with the exception of a 38km electric fence constructed between the Futi and Maputo Rivers, which enclosed agricultural fields protecting them from crop damage by elephants (de Boer and Ntumi, 2001). Maputo was not adjoined by any SPAs at the time of the study, however, the Futi Corridor linking Maputo and Tembe National Park in South Africa was proclaimed a protected area in June 2011 (http://www.peaceparks.org/).

CHAPTER 3

MATERIALS AND METHODS

DATA COMPILATION

LOCATION-SCALE ANALYSES

Elephant location data

I used data collected from 35 female and 14 male elephants fitted with satellite telemetry collars within the study sites across southern Africa. The collaring procedures adhered to the conditions set by the Animal Ethics Committee of the University of Pretoria. The three elephants in Maputo were fitted with ST-14 Platform Transmitter Terminals (Telonics, Arizona, U.S.A.). The location accuracy of these collars ranged from 0 – 1 000m. However, I only used locations with accuracy of 0 - 150m in this study. The elephants from the rest of the study sites were fitted with Africa Wildlife Tracking collars (model SM 2000E; Pretoria, South Africa), which used a Garmin Global Positioning System (GPS) unit to relay the locations to a satellite. From there they were downloaded to the Conservation Ecology Research Unit (CERU) at the University of Pretoria via Startrack (Australia) and Skygistics (South Africa). A controlled assessment of the collars suggested that 95% of locations fell within a 37 ± 26m radius of the true location (Ott and van Aarde, 2010). Elephants were tracked for a varying number of years between 2000 and 2010 (Table 3). With the exception of the displacement rates analysis, the locations for the analyses in this thesis were divided into core wet and core dry seasons.

The core wet season was defined as the sequential months during which more than 70% of the annual rainfall was received (December - March) and the core dry season was the sequential months during which less than 2% of the annual rainfall was received (June - September) (Young *et al*., 2009a). The intervals between the locations from the collars generally ranged from 12 to 24 hours. There was a small sub-set of locations with approximately 1 hour intervals during a maximum of one month. For the estimates of displacement rates, I used the approximate 1 hour locations. Loarie *et al*. (2009b) used location data with a minimum of 15 minute and a maximum of 105 minute intervals to investigate within-day movements of elephants. However, Dai *et al*. (2007) found that elephant movements were auto correlated at 15 minute intervals, therefore I only included locations with a minimum of 30 minute and a maximum of 90 minute intervals. I only included elephants that had hourly locations both while roaming in and beyond the PPAs, which resulted in analyses for 10 females and 5 males. The majority of these locations fell within the core wet season. However, for some of the elephants the locations fell within the core dry season and for the Khaudum female the locations included were from November. The number of hourly locations ranged from 18 to 684 (Table 3). For the seasonal and core range analyses, I filtered the data to one location per day (24 hour intervals), which resulted in a range of 44 to 122 seasonal locations and 0 to 61 seasonal core locations (Table 3). The wet season location data were incomplete for the Kafue 3 female and therefore were excluded from the wet season analyses. For the core locations analyses, I only included locations that fell within the 50% isopleths of the home ranges (see next section). For the habitat selection analyses, I filtered the data to two locations per day (12 hour intervals) to minimise the disparities between the coarse-scale habitat variables and the fine-scale location data (see Friar *et al*., 2010). For each elephant the season-specific locations were summed across years. The number of locations per elephant per core wet and core dry season ranged from 78 to 890 and 112 to 943, respectively (Table 3). Each collared female represented a separate breeding herd and only elephants collared within the boundary of a PPA were included in my study.

Table 3. The period over which each elephant was tracked and the number of locations per season and tracking interval for each of them. The number of locations are grouped according to the time intervals between the locations.

Females									
Elephant	Years tracked	Total number of locations						1 hour data	
		24 hour data				12 hour data			
		Wet season		Dry season		Wet season	Dry season	Number of locations	Season/Month
		All locations	Core locations	All locations	Core locations				
Khaudum 1	2004 – 2006	75	34	85	35	146	266	-[a]	-
Khaudum 2	2004 – 2006	93	45	109	54	266	338	-	-
Khaudum 3	2004 – 2006	87	42	113	54	264	343	-	-
Khaudum 4	2004 – 2006	88	44	77	26	264	307	-	-
Khaudum 5	2004 – 2006	87	33	99	37	259	324	-	-
Khaudum 6	2004 – 2006	93	46	114	57	274	349	268	November
Bwabwata 1	2007 – 2010	115	21	122	13	679	703	-	Wet
Mudumu 1	2006 – 2010	70	35	117	53	420	512	-	-
Kafue 1	2003 – 2005	116	45	122	56	208	230	-	-
Kafue 2	2003 – 2005	116	58	121	44	168	219	-	-
Kafue 3	2003 – 2005	-	-	122	54	115	175	18	Dry
Kafue 4	2003 – 2005	117	49	121	60	207	226	-	-
Lower Zambezi 1	2004 – 2006	72	23	94	25	243	267	-	-
Lower Zambezi 2	2004 – 2006	78	26	95	47	255	278	-	-
Lower Zambezi 3	2004 – 2006	89	44	102	49	268	282	73	Dry
Lower Zambezi 4	2004 – 2006	93	38	93	46	263	287	-	-
Lower Zambezi 5	2004 - 2006	85	42	101	50	259	293	61	Dry
South Luangwa 1	2004 – 2008	89	44	97	40	649	604	555	Wet
South Luangwa 2	2004 – 2008	86	36	101	39	661	744	-	-
South Luangwa 3	2006 – 2009	96	26	109	48	525	666	-	-
South Luangwa 4	2006 – 2010	120	52	122	59	734	943	111	Wet
South Luangwa 5	2006 – 2008	122	56	122	61	358	478	-	-
North Luangwa 1	2004 – 2007	44	15	65	32	105	329	-	-
North Luangwa 2	2004 – 2007	98	22	100	39	423	540	678	Wet
North Luangwa 3	2004 – 2007	102	36	88	24	419	530	-	-
Vwaza 1	2004 – 2008	80	38	100	50	575	518	384	Wet

Table 3. Continued

Vwaza 2	2004 – 2007	83	28	98	48	450	553	684	Wet
Kasungu 1	2004 – 2008	77	38	107	53	517	571	-	-
Kasungu 2	2004 – 2008	81	40	98	48	611	702	-	-
Quirimbas 1	2008 – 2010	121	61	122	52	455	435	-	-
Quirimbas 2	2008 – 2010	121	61	122	61	451	449	-	-
Limpopo 1	2003 – 2006	118	53	108	42	366	445	-	-
Limpopo 2	2003 – 2006	114	51	113	50	225	217	-	-
Maputo 1	2000 – 2002	62	0	48	24	78	112	-	-
Maputo 2	2000 – 2002	112	28	94	46	233	171	-	-
				Males					
Bwabwata 1	2007 – 2009	115	44	122	12	491	688	108	Wet
Mudumu 1	2006 – 2010	121	39	122	61	890	695	-	-
Mudumu 2	2006 – 2009	120	41	121	29	681	665	-	-
Mudumu 3	2006 – 2009	119	56	122	58	570	468	-	-
Kafue 1	2003 – 2004	116	59	123	45	126	228	-	-
Kafue 2	2003 – 2004	117	44	121	47	119	239	65	Dry
Kafue 3	2003 – 2005	113	56	123	50	180	232	56	Dry
Kafue 4	2003 – 2005	115	44	121	55	199	228	-	-
Vwaza 1	2004 – 2008	69	23	103	51	529	559	661	Wet
Kasungu 1	2004 – 2008	87	42	109	54	660	731	-	-
Quirimbas 1	2008 – 2010	118	60	122	61	383	462	145	Wet
Limpopo 1	2003 – 2007	118	59	107	46	498	388	-	-
Limpopo 2	2003 – 2006	119	49	118	36	390	486	-	-
Maputo 1	2000 – 2002	46	22	44	0	90	115	-	-

[a] – represent missing values

Elephant home ranges

For each elephant I calculated a seasonal home range in R version 2.14.1 (R Development Core Team, 2011) using the adaptive local convex hull method (*a*-LoCoH) (Getz *et al*., 2007). Home ranges were defined using the 100% isopleths and core home ranges were defined using the 50% isopleths. The core home ranges were used to calculate the number of telemetry locations falling within the 50% isopleths, which I then defined as core locations. The telemetry locations used in this analysis were not always complete for the four months of the core wet or core dry season. However, because the core home ranges were generated using the same location data as the core locations, missing days would have been accounted for. Within the 100% home range I generated random points to compare the landscapes the elephants were using within the PPAs to the landscapes that the elephants were using beyond the PPAs, and to estimate availability for the habitat selection analysis. The *a*-LoCoH method is a nonparametric kernel method that produces bounded home ranges by constructing kernels within the radius *a* so that the sum of the distances of all points within the radius to a root point was less than or equal to *a*. I used the maximum distance between locations for an individual as the value for *a* (Getz *et al*., 2007). The *a*-LoCoH method was used in preference to the kernel density estimator (Worton, 1989) because of its superior convergence properties as sample sizes increase and its ability to detect either topographical or anthropogenic boundaries (Getz *et al*., 2007).

Explanatory variables

NDVI

NDVI is an index that measures primary productivity of the landscape (Pettorelli *et al*., 2005). I used 10-day, 1km^2 resolution NDVI *Satellite Pour l'Observation de le Terre Vegetation* (SPOT-VGT) composites (http://free.vgt.vito.be/). Within ArcMAP 9.3 (ESRI, 2008), the composites were converted to a –1 to +1 scale and negative and zero values, which may have been erroneous, were deleted.

Slope

Merged Digital elevation model (DEM) tiles for southern Africa (http://srtm.csi.cgiar.org) were used to calculate slope. The tiles were based on data from the NASA Shuttle Radar Topographic Mission (SRTM) and then processed to fill data voids (Jarvis *et al.*, 2006).

Vegetation Cover

The tree and herbaceous cover datasets were downloaded from www.landcover.org (Hansen *et al.*, 2006). The rasters were products of the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor onboard NASA's Terra satellite and contained percentage estimates for vegetation types. The data were reprojected in Arcmap 9.3. The percentages were used for the landscape comparisons and were then converted to proportions for the elephant habitat selection analyses.

Water

To create a water layer several Tracks 4 Africa (Tracks4Africa (Pty) Ltd; http://tracks4africa.co.za) polygon and linear layers, namely data from the "swamps", "features" and "rivers" layers, were merged. I then used Google Earth and a LandSat Mosaic from the Fundisa disk as references to hand digitize permanent water that was not captured in the Tracks 4 Africa datasets. Datasets containing the locations of boreholes and springs in Khaudum and Kruger National Park were then merged with this new water layer. The borehole and spring datasets were cross-referenced with information on the availability and quality of the water (Wanke and Wanke, 2007), and the water points that were not fit for animal consumption or had been closed down, were deleted. The merged water layer was divided into wet and dry seasonal layers. Data for pans, swamps and minor rivers were included in the wet season layer but excluded from the dry seasonal layer as these features were more likely to only contain water in the wet season. The layers were then converted into rasters and the Euclidean distance from each cell to the nearest water source was calculated. My wet season mapping of water was conservative because there were many pans and depressions across the landscape that would have contained water from the rains but were not included in my maps.

Human use

Tracks 4 Africa layers containing locations of human use were merged and then used to calculate the Euclidean distance from each cell to the nearest area of human use across the study sites. This layer included tourist camps within the PPAs and settlements beyond the PPAs.

HOME RANGE-SCALE ANALYSES

Elephant location data

I used data collected from 34 female and 14 male elephants collared within the study sites across southern Africa. The data were divided into the core wet (December – March) and core dry (June – September) seasons as defined by Young *et al*. (2009a). The data were filtered to one location per day (24 hour intervals). I only included core seasons that had locations for each month within the four month period. The wet season location data were incomplete for the Kafue 3 female and therefore were excluded from the wet season analyses. The number of locations per elephant per core wet and core dry season ranged from 44 to 122 and 44 to 122, respectively (Table 3). Each collared female represented a separate breeding herd and only elephants collared within the boundary of a PPA were included in my study.

Elephant home ranges

I calculated the area of the home ranges for each elephant in R version 2.14.1using the *a*-LoCoH method (Getz *et al*., 2007). For each elephant, I calculated one core wet and one core dry season home range. I used the maximum distance between locations for an individual as the value for a (Getz *et al*., 2007). Home ranges were defined using the 100% isopleths. Using ArcMAP 9.3 and the Geospatial Modelling Environment I then measured the proportions and areas of the seasonal a-LoCoH ranges beyond the PPAs.

Explanatory variables

Mean annual rainfall

Mean annual rainfall was calculated from weather stations either within the PPAs or the closest stations to them (Jackson and Erasmus, 2005). When these data were not available mean annual rainfall was calculated from interpolated monthly rainfall datasets (http://www.worldclim.org/).

Population growth and density of elephants

To calculate exponential population growth rates, population estimates for each PPA were extracted from the CERU database, which was augmented from the African Elephant Databases (Said *et al*., 1995; Barnes *et al*., 1998), Status Reports (Blanc *et al*., 2003; Blanc *et al*., 2007), volumes 1 to 41 of the *Pachyderm* series, as well as other published and unpublished sources as described by Junker *et al*. (2008). For the elephant population of each PPA I developed time series for the period 1980 to 2006, which included at least four estimates. The estimates were converted to natural logs and then regressed against time to calculate the exponential growth rate and 95% confidence intervals (Caughley, 1977). The time series included population estimates concurrent with the years for which the study elephants were collared. If the years were not concurrent then population estimates were calculated using $N_t = N_0e^{rt}$, where N_t = the population estimate at time t, N_0 = the initial population estimate, r = the exponential growth rate, and t = time between estimates (Caughley, 1977).

Density was calculated as the population estimate divided by the size of the PPA. I used population estimates and the size of the corresponding surveyed areas from unpublished aerial surveys found in Blanc *et al*. (2007) for years that were concurrent with those of my study. For Kafue I used the population estimate from Guldemond *et al*. (2005). When the population estimates were not for the same years, I calculated the population estimates using the same techniques as described for the exponential population growth rate.

PPA area

The area in km^2 of each PPA was determined from the World Database on Protected Areas 2009, which collated the sizes from governmental declarations or management plans (UNEP-WCMC, 2009).

DATA ANALYSIS

LOCATION-SCALE ANALYSES

All statistical analyses were performed in R version 2.14.1.

Displacement rates analysis

I calculated the minimum distanced travelled per hour by ten females and five males as suggested by the straight lines between consecutive hourly locations. The females included in the analyses were from Khaudum, Bwabwata, Kafue, Lower Zambezi, South Luangwa, North Luangwa, and Vwaza. The males were from Bwabwata, Kafue, Vwaza, and Quirimbas. Within the Geospatial Modelling Environment version 0.3.4 (Beyer, 2011), I calculated the steplengths between consecutive locations and divided by time to get the displacement rates (kilometres per hour). I calculated the mean displacement rate each elephant was travelling at within and beyond the PPAs and performed a sign test to determine whether the mean rates significantly differed within and beyond the PPAs (Sokal and Rohlf, 1995).

Differences between the proportions of locations beyond PPAs during the wet season and the dry season

To establish if there was a difference in the proportion of elephant locations beyond PPAs during the core wet and dry seasons, I used a chi-square test of independence (Sokal and Rohlf, 1995). Analyses were first conducted for each individual elephant and then for the pooled females' locations and the pooled males' locations.

Differences between the proportions of core locations within and beyond PPAs

I used goodness-of-fit tests with an expected ratio of 1:1 (Sokal and Rohlf, 1995) and a null hypothesis that the number of core locations within and beyond PPAs will be equal. I first analysed each elephant's core locations separately using an exact test of goodness-of-fit. I then pooled the females' core locations and the males' core locations and analysed the data using chi-square goodness-of-fit tests.

Habitat selection analyses

To determine whether elephants leave PPAs to select areas close to water and humans, or with high residual primary productivity, herbaceous or tree cover, or low slopes, I first compared the landscapes within and beyond the PPAs and then compared elephant habitat selection within and beyond the PPAs.

Comparison of landscapes within and beyond PPAs

I compared the landscapes the elephants were using within and beyond the PPAs by generating and comparing random points between the two locations. Random points were generated at a density of three random points per km^2 within each home range. I then used a Mann-Whitney U-test to compare each variable at the random points beyond PPAs to random points within. During both seasons the females in Limpopo did not leave the PPA and during the dry season the females in Maputo did not leave the PPA. These PPAs therefore were excluded from the analysis. To remove the variability caused by differences in landscapes residual NDVI values were calculated for each random point *j* as:

$$rP_j = P_j - \sum_{j=1}^{m} P_j \,/m$$

where P_j is the NDVI value of the random point *j* and *m* is the mean NDVI value of all the random points either within or beyond each PPA (Young *et al.*, 2009b).

Comparison of elephant habitat selection within and beyond PPAs

Resource selection function (RSF) models were used to model elephant habitat selection within and beyond each PPA by comparing the elephant locations (1) to the random points (0). The RSF models had the structure:

$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_n x_n)$,

where $w(x)$ is the resource selection function, and β_n is the selection coefficient for covariate x_n (Manly *et al.*, 2002). To remove the variability caused by differences in landscapes residual NDVI values were calculated for each location j as:

$$rP_j = P_j - \sum_{j=1}^{m} P_j / m$$

where P_j is the NDVI value of the location j and m is the mean NDVI value of all the locations points either within or beyond each PPA (Young *et al.*, 2009b). The predictor variables were examined for collinearity using Pearson's correlations (r) using a threshold of $r > |0.6|$. If two variables exceeded this threshold they were not included in the same model. The global model was assessed to determine which of the correlated variables to include, and whether quadratic terms were needed due to nonlinearity. The proportion of herbaceous cover and proportion of tree cover were correlated in the majority of the models, and therefore only one was included in each model. I assessed the global models for the inclusion of correlated variables and quadratic terms as well as the other three candidate models (Table 4) using Akaike's information criteria (AIC) corrected for small sample sizes ($\mathrm{AIC_c}$) (Burnham and Anderson, 2002). The support for each candidate model was then measured using $\mathrm{AIC_c}$ differences (Δ_i) ($\mathrm{AIC_{c(\Delta i)}}$) where the best model has $\Delta_i = 0$; values from 0-2 signify substantial support; values from 4-7 signify considerably less support and values > 10 no support (Burnham and Anderson, 2002). $\mathrm{AIC_c}$ weights ($\mathrm{AIC}_{(Wi)}$) were also calculated, which represent the probability of each model as being the best model in the candidate group. If there was substantial support as well as similar AIC_c weights for two models, then the more parsimonious model was chosen as the best model. Finally, I assessed the predictive performance of the best model using k-fold cross validation ($k = 5$) and Spearman's rank correlation (r_s) to assess the relationship between elephant occurrence frequency and ranked RSF-availability bins (Boyce *et a*l., 2002).

It is recommended that at least ten samples are needed for each parameter included in the model and that this is based on the frequency of the least frequent outcome (Hosmer and Lemeshow, 2000). Therefore, I had to exclude the elephants that did not fulfil this criterion and had less than ten locations either within or beyond the PPAs for each parameter included in the final models. During the wet season this resulted in the inclusion of 20 females within and 19 females beyond the PPAs, and seven males within and seven males beyond the PPAs. During the dry season I included 26 females within and 15 females beyond the PPAs, and six males within and nine males beyond the PPAs. I then qualitatively compared selection for high NDVI, herbaceous and tree cover, low slopes, and areas close to water and humans beyond the PPAs to within the PPAs.

Table 4. A priori candidate models used in the location-scale logistic regression analyses to compare elephant habitat selection within and beyond PPAs.

Model	Model structure
Null	Intercept only
1	NDVI[a] + proportion herb cover[b] or proportion tree cover + distance to water (km)
2	NDVI + proportion herb cover or proportion tree cover + distance to water (km) + distance to humans (km)
Global	NDVI + proportion herb cover or proportion tree cover + slope (^{0}) + distance to water (km) + distance to humans (km)

[a] NDVI is an abbreviation of residual NDVI.
[b] Proportion herb cover is an abbreviation of proportion of herbaceous cover.

HOME RANGE-SCALE ANALYSES

The relationship between mean annual rainfall and area of home ranges beyond PPAs

I used linear regression to determine whether the area of the females' and males' seasonal home ranges beyond the boundaries of the PPAs decreased with increasing mean annual rainfall. I did this to test whether differences in rainfall across the study sites was the underlying variable responsible for differences in home range size and consequently in the area of the home ranges beyond PPAs. The areas of the home ranges beyond the PPAs were $\log_{10}$ transformed in the wet and dry season female models and the dry season male models, to account for outliers (Zuur *et al*., 2010). When the areas of home ranges beyond the boundaries of the PPAs were $\log_{10}$ transformed any values equal to 0 would have transformed into $-\infty$. Therefore, I used the transformation $\log_{10}(Y + 1)$ as the transformation (Sokal and Rohlf, 1995). The residuals of the dry season male analysis displayed heterogeneity of variance and I consequently used a generalised least squares model for analysis instead of linear regression (Zuur *et al*., 2009).

The contribution of extrinsic and intrinsic variables to the variability in the proportion of home ranges beyond PPAs

To determine if the season-specific variability in the proportion of home ranges of elephants beyond PPAs could be explained by the density and population growth rates of elephant populations within PPAs, the area of the PPAs, and the size of their home ranges, I used regression analysis. For each core season the males and females were modelled separately, and the seasonal female data were further divided into wet and dry savannahs. I did not divide the male data set because of the small sample size. I followed the methods in Zuur *et al*. (2009), which allowed me to determine if a random effect was needed to account for within-PPA correlation. Consequently, I fitted a linear regression model and a mixed effects model with the PPAs as the random intercept and applied a likelihood ratio test with a correction for testing on the boundary to determine the optimal model. The mixed effects linear multiple regression model was the optimal model for the females during the wet season ($L = 9.79$, $df = 1$, $p = 0.001$) and for the females from wet savannahs during the wet season ($L = 9.29$, $df = 1$, $p = 0.001$). For the remaining analyses linear multiple regression was used. Population growth rates could not be calculated for either Limpopo or Quirimbas as time series were not available for these PPAs. Furthermore, density was not known for Quirimbas and these sites were excluded from this part of the analyses. The predictor variables were all tested for collinearity using Pearson's correlations (r) using a threshold of $r > |0.6|$. I then used AIC corrected for small sample sizes (AIC_c) (Burnham and Anderson, 2002) to determine which of the variables best explained the proportion of the home ranges beyond the PPAs. The support for each candidate model was then measured using AIC_c differences (Δ_i) ($AIC_{c(\Delta i)}$), and AIC_c weights ($AIC_{(Wi)}$) were calculated. Furthermore, I calculated the relative variable importance by summing the $AIC_{(Wi)}$ of all the models in which the variable appeared (Burnham and Anderson, 2002). This was done only for analyses where each variable appeared in the same number of models (see Anderson, 2008). The set of candidate models included the global model and all combinations of uncorrelated variables (Table 5). When needed, the proportions of the home ranges falling beyond the boundaries of the PPAs were logit transformed using the car package (Fox and Weisberg, 2011) to meet the assumptions of linear modelling (Warton and Hui, 2011). When the proportions of home ranges beyond the boundaries of the PPAs were logit transformed any values equal to 0 or 1 would have transformed into -∞ and ∞, respectively. Therefore, the smallest non-zero proportion y for values equal to 0, or the smallest non-zero proportion $1 - y$ for values equal to 1 were added to the logit function (Warton and Hui, 2011). Size of home range was $\log_{10}$ transformed for all the analyses with the exception of the males during the wet season, and the size of the PPAs were $\log_{10}$ transformed for all the analyses with the exception of the females from the dry savannahs during the wet season.

Table 5. The candidate models used in the regression analyses to determine if the variability in the proportion of seasonal elephant home ranges beyond PPAs could be explained by the density and population growth rate of the elephant populations within the PPAs, the size of the home ranges of elephants, or the size of the PPAs.

Model number	Model structure
1	Density[a]
2	Exponential *r*
3	Size of home range[b]
4	Size of PPA[b]
5	Density + exponential *r*
6	Density + size of home range
7	Density + size of PPA
8	Exponential *r* + size of home range
9	Exponential *r* + size of PPA
10	Size of home range + size of PPA
11	Density + exponential *r* + size of home range
12	Density + exponential *r* + size of PPA
13	Density + size of home range + size of PPA
14	Exponential *r* + size of home range + size of PPA
15 (Global)	Density + exponential *r* + size of home range + size of PPA

These are the candidate models for analyses without correlated variables. When variables were correlated they could not appear in the same model, and therefore the models were adjusted accordingly. Variables were correlated for females from dry savannahs in the wet and dry season and for the males during both seasons.

[a] Density was measured as elephants per km^2

[b] Size of home range and size of PPAs were measured in km^2

CHAPTER 4

RESULTS

LOCATION-SCALE ANALYSES

Displacement rates

The displacements rates for 8 of 10 females were larger within the PPAs, with the exception of the Khaudum female and South Luangwa 1 (Table 6). Mean displacement rates (± standard error) within the PPAs varied between 0.25 ± 0.03 km h^{-1} (n = 54) to 1.21 ± 0.08 km h^{-1} (n = 191), while rates beyond the PPAs varied between 0.17 ± 0.01 km h^{-1} (n = 106) to 1.86 ± 0.14 km h^{-1} (n = 77). Statistically the values were similar (p = 0.29, sign test). The mean rates of the two males from Kafue and the Bwabwata male were faster beyond the PPAs than within the PPAs. Contrastingly, the Vwaza male and the Quirimbas male averaged faster rates within the PPAs than beyond the PPAs (Table 6). The males' displacement rates within the PPAs varied from 0.23 ± 0.04 km h^{-1} (n = 16) to 0.66 ± 0.03 km h^{-1} (n = 505), and beyond the PPAs varied from 0.25 ± 0.05 km h^{-1} (n = 24) to 0.81 ± 0.11 km h^{-1} (n = 50). There was not a significant difference between the mean displacement rates within and beyond the PPAs (p = 1.00, sign test).

Table 6. The displacement rates of elephants within and beyond PPAs. The means and standard errors of the means are presented for each elephant. Values within brackets represent the number of consecutive hourly telemetry locations used to calculate the mean displacement rates.

Elephant	Displacement rates within PPA (km h^{-1}) Mean ± standard error	Displacement rates beyond PPA (km h^{-1}) Mean ± standard error
Females		
Khaudum 6	1.21 ± 0.08 (191)	1.86 ± 0.14 (77)
Bwabwata 1	0.87 ± 0.29 (9)	0.86 ± 0.07 (103)
Kafue 3	0.84 ± 0.25 (8)	0.32 ± 0.20 (10)
Lower Zambezi 3	0.34 ± 0.03 (68)	0.18 ± 0.04 (5)
Lower Zambezi 5	0.25 ± 0.03 (54)	0.21 ± 0.04 (5)
South Luangwa 1	0.44 ± 0.05 (50)	0.53 ± 0.02 (505)
South Luangwa 4	0.48 ± 0.05 (99)	0.23 ± 0.05 (12)
North Luangwa 2	0.39 ± 0.01 (572)	0.17 ± 0.01 (106)
Vwaza 1	0.57 ± 0.03 (370)	0.39 ± 0.15 (14)
Vwaza 2	0.60 ± 0.02 (591)	0.38 ± 0.04 (93)
Males		
Bwabwata 1	0.58 ± 0.05 (100)	0.65 ± 0.25 (8)
Kafue 2	0.23 ± 0.04 (16)	0.65 ± 0.10 (49)
Kafue 3	0.39 ± 0.15 (6)	0.81 ± 0.11 (50)
Vwaza 1	0.66 ± 0.03 (505)	0.53 ± 0.05 (156)
Quirimbas 1	0.49 ± 0.05 (121)	0.25 ± 0.05 (24)

Differences between the proportions of locations beyond PPAs during the wet season and the dry season

More individual females had a significantly larger proportion of locations beyond PPAs during the wet season than during the dry season (14 of 34; Figure 2a). Furthermore, when the females were pooled, there was a significantly larger proportion of wet season locations beyond PPAs ($\chi^2 = 54.62$, $df = 1$, $p < 0.001$). Contrastingly, both for the individual males (4 of 14; Figure 2b) and the pooled males ($\chi^2 = 0.41$, $df = 1$, $p = 0.52$), there were no significant differences in the proportion of locations beyond the PPAs during the wet and dry seasons.

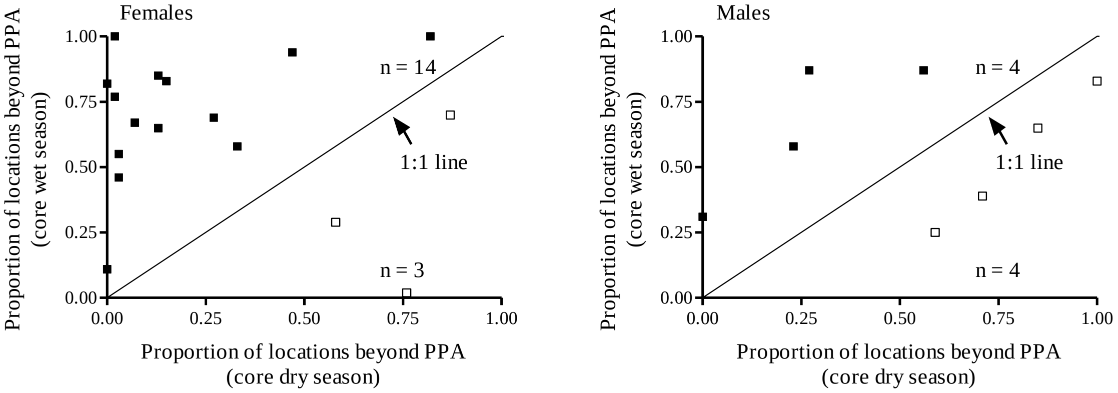

Figure 2. The proportions of locations beyond the boundaries of PPAs for the core wet season (December – March) plotted against those for the core dry season (June – September) for females and males. The filled symbols above the 1:1 line represent the elephants with a significantly larger proportion of their locations beyond a PPA during the core wet season and the open symbols below the 1:1 line represent those with a significantly larger proportion of their locations beyond a PPA during the core dry season.

Differences between the proportions of core locations within and beyond PPAs

During the wet season, the same number of individual females had a significantly larger proportion of their core locations within PPAs and beyond PPAs (14 of 33). Similarly, when the females were pooled, there were equal proportions of core locations within and beyond the PPAs ($\chi^2 = 0.88$, $df = 1$, $p = 0.35$). When the individual females were divided into dry and wet savannahs, more females from dry savannahs had a significantly larger proportion of core locations within PPAs (6 of 10), and more females from wet savannahs had a significantly larger proportion of core locations beyond PPAs (10 of 23). More individual males had a significantly larger proportion of core locations beyond PPAs (8 of 14). This result remained significant when the males were pooled ($\chi^2 = 16.95$, $df = 1$, $p < 0.001$). Similarly, when the males were divided into dry and wet savannahs, more males from dry savannahs had a significantly larger proportion of core locations beyond PPAs (5 of 6). However, an equal number of males from wet savannahs had a significantly larger proportion of core locations within and beyond PPAs (3 of 8).

During the dry season, both the individual females (24 of 33) and pooled females ($\chi^2 = 547.51$, $df = 1$, $p < 0.001$) had a significantly larger proportion of core locations within PPAs. When the females were divided into dry and wet savannahs, more females from both savannahs had a significantly larger proportion of core locations within PPAs. Contrastingly, more individual males (8 of 13) and pooled males ($\chi^2 = 10.32$, $df = 1$, $p = 0.001$) had a larger proportion of core locations beyond PPAs. Furthermore, more males from dry savannahs had a significantly larger proportion of core locations beyond PPAs (5 of 6). However, more males from wet savannahs had a larger proportion of core locations within PPAs (4 of 7).

Comparison of landscapes within and beyond PPAs

The landscapes that the elephants were using within and beyond the PPAs were generally significantly different (Tables 7 and 8; Appendices I-IV). However, residual NDVI was significantly similar for the majority of the areas the females were using within and beyond the PPAs, especially during the dry season.

Table 7. Table showing the similarities and differences in the variables between the areas used by elephants within and beyond PPAs during the wet season. The results are based on Mann-Whitney U-tests. = represents significant similarities between the two locations ($p < 0.05$). + represents significantly greater mean values beyond the PPAs ($p < 0.05$). – represents significantly smaller mean values beyond the PPAs ($p < 0.05$). Only results for PPAs that had elephants included in the RSF modelling are presented.

PPA	Females					
	Residual NDVI	Percentage herb cover	Percentage tree cover	Slope (°)	Distance to water (km)	Distance to humans (km)
Khaudum	-	-	+	-	+	+
Mudumu	=	-	+	+	+	+
Kafue	=	=	-	-	=	-
Lower Zambezi	+	-	-	+	+	-
South Luangwa	=	-	+	+	+	+
Vwaza	-	-	=	+	=	=
Quirimbas	-	+	-	+	+	-
	Males					
	Residual NDVI	Percentage herb cover	Percentage tree cover	Slope (°)	Distance to water (km)	Distance to humans (km)
Mudumu	=	-	+	+	+	+
Kafue	=	-	+	-	+	-
Vwaza	+	=	=	+	-	+
Quirimbas	+	-	+	+	+	+
Limpopo	+	+	-	+	-	+

Table 8. Table showing the similarities and differences in the variables between the areas used by elephants within and beyond PPAs during the dry season. The results are based on Mann-Whitney U-tests. = represents significant similarities between the two locations ($p < 0.05$). + represents significantly greater mean values beyond the PPAs ($p < 0.05$). – represents significantly smaller mean values beyond the PPAs ($p < 0.05$). Only results for PPAs that had elephants included in the RSF modelling are presented.

PPA	Females					
	Residual NDVI	Percentage herb cover	Percentage tree cover	Slope (°)	Distance to water (km)	Distance to humans (km)
Khaudum	=	+	+	-	+	+
Mudumu	=	-	+	=	+	-
Kafue	=	+	-	-	+	-
Lower Zambezi	=	-	+	+	+	=
South Luangwa	=	-	+	+	+	+
North Luangwa	=	+	-	-	-	-
Vwaza	=	+	-	-	-	-
Quirimbas	=	+	-	-	+	-
	Males					
	Residual NDVI	Percentage herb cover	Percentage tree cover	Slope (°)	Distance to water (km)	Distance to humans (km)
Mudumu	-	=	+	+	-	-
Kafue	-	+	-	-	-	-
Vwaza	=	+	-	=	-	+
Limpopo	+	+	-	-	-	+

Comparison of elephant habitat selection within and beyond PPAs

When the habitat selection patterns of elephants within PPAs were compared to those beyond PPAs, the following general patterns emerged. During the wet season, females and males selected for similar variables when within and beyond the PPAs (Table 9; Figure 3a). During the dry season, the selection patterns of females for high NDVI, herbaceous and tree cover and low slopes were similar within and beyond the PPAs (Table 9; Figure 3b). However, eight of fifteen for areas close to humans when beyond the PPAs (Table 9; Figure 3b). The dry season selection patterns of males were similar for high herbaceous cover, low slopes and areas close to water within and beyond the PPAs (Table 9; Figure 3d). Six of nine males selected for high tree cover, and seven of nine males selected for areas close to humans when beyond the PPAs (Table 9; Figure 3d).

Table 9. The number of females and males that selected for high residual NDVI, high herbaceous and tree cover, low slope and areas close to water and humans when within and beyond the PPAs. n = sample size

	Females				Males			
	Wet season		Dry season		Wet season		Dry season	
	Within PPA (n = 20)	Beyond PPA (n = 19)	Within PPA (n = 27)	Beyond PPA (n = 15)	Within PPA (n = 7)	Beyond PPA (n = 7)	Within PPA (n = 6)	Beyond PPA (n = 9)
NDVI[a]	4	6	5	7	3	2	1	2
Proportion of herb cover[b]	5	6	6	3	1	1	0	0
Proportion of tree cover	7	8	7	5	3	2	3	6
Slope (°)	4	3	5	3	0	2	3	3
Distance to water (km)	7	8	13	6	3	3	3	4
Distance to humans (km)	8	7	9	8	4	3	3	7

[a] NDVI is an abbreviation of residual NDVI.

[b] Proportion herb cover is an abbreviation of proportion of herbaceous cover.

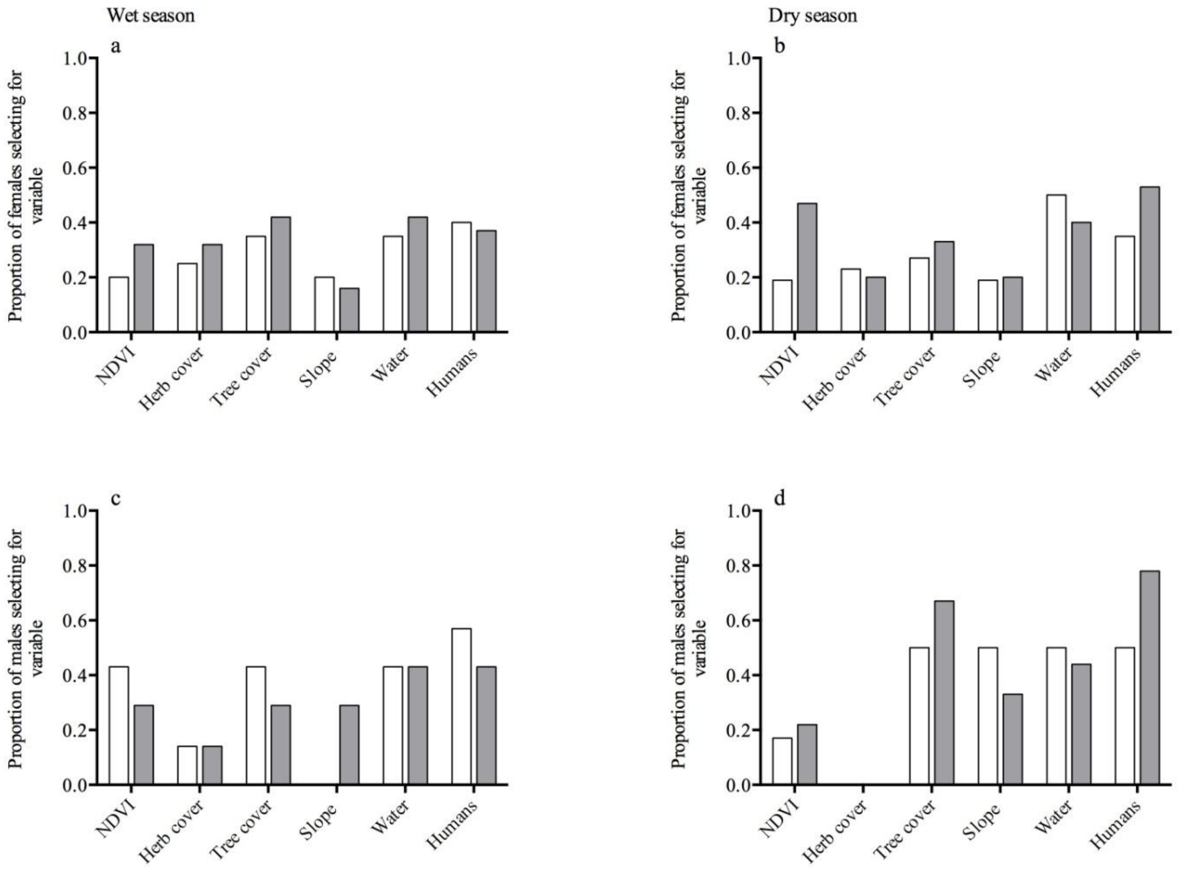

Figure 3. The proportion of elephants that selected for an explanatory variable within PPAs (clear bars) and beyond PPAs (shaded bars). Results are shown for females during the wet season (a) and the dry season (c), and males during the wet season (b) and the dry season (d).

I then divided the results into dry and wet savannahs. During the wet season, the habitat selection patterns of females and males from dry savannahs were similar within and beyond PPAs (Table 10; Figure 4). In the wet savannahs, habitat selection patterns were similar within and beyond the PPAs (Table 10; Figure 4).

During the dry season and in the dry savannahs, the habitat selection patterns for females and males within and beyond the PPAs were similar, but for all of the males that selected for areas close to humans when beyond the PPAs (Table 10; Figure 4). In the wet savannahs, habitat selection patterns for females within and beyond PPAs were similar (Table 10; Figure 4). For males, habitat selection patterns were similar for high NDVI, high herb cover, low slope, and areas close to humans. Three of five males selected for high tree cover and areas close to water when beyond the PPAs (Table 10; Figure 4).

Table 10. The number of females and males in wet and dry savannahs that selected for high residual NDVI, high herbaceous and tree cover, low slope and areas close to water and humans when within and beyond the PPAs.

	Dry savannahs							
	Females				Males			
	Wet season		Dry season		Wet season		Dry season	
	Within PPA (n = 6)	Beyond PPA (n = 4)	Within PPA (n = 7)	Beyond PPA (n = 2)	Within PPA (n = 2)	Beyond PPA (n = 4)	Within PPA (n = 3)	Beyond PPA (n = 4)
NDVI[a]	1	1	2	1	2	1	0	0
Proportion of herb cover[b]	3	2	3	0	1	1	0	0
Proportion of tree cover	1	1	2	1	1	2	2	3
Slope (°)	0	0	0	1	0	2	1	2
Distance to water (km)	1	1	5	0	2	2	2	1
Distance to humans (km)	1	2	1	1	1	1	1	4

	Wet savannahs							
	Females				Males			
	Wet season		Dry season		Wet season		Dry season	
	Within PPA (n = 14)	Beyond PPA (n = 15)	Within PPA (n = 20)	Beyond PPA (n = 13)	Within PPA (n = 5)	Beyond PPA (n = 3)	Within PPA (n = 3)	Beyond PPA (n = 5)
NDVI[a]	3	5	3	6	1	1	1	2
Proportion of herb cover[b]	2	4	3	3	1	0	0	0
Proportion of tree cover	6	7	5	4	2	0	1	3
Slope (°)	4	3	5	2	0	0	2	1
Distance to water (km)	6	7	9	6	1	1	1	3
Distance to humans (km)	6	5	8	7	3	1	2	3

[a] NDVI is an abbreviation of residual NDVI.

[b] Proportion herb cover is an abbreviation of proportion of herbaceous cover.

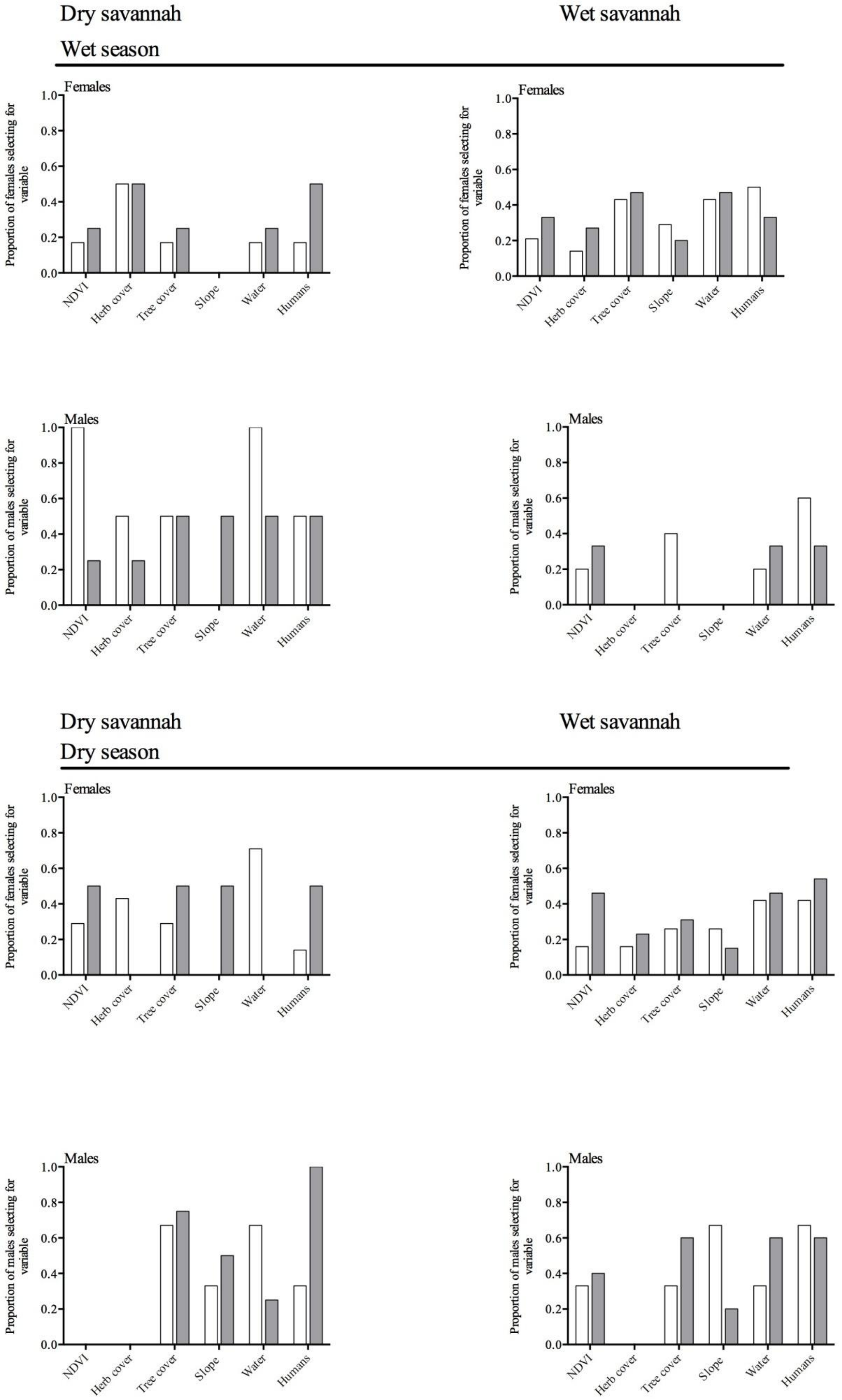

Figure 4. The proportion of elephants from dry and wet savannahs that selected for an explanatory variable within PPAs (clear bars) and beyond PPAs (shaded bars).

HOME RANGE-SCALE ANALYSES

When the merged seasonal home ranges were overlaid onto maps of the clusters of protected areas, it was apparent that the study elephants were generally remaining within the boundaries of the clusters (Appendices V-XI).

The relationship between mean annual rainfall and area of home ranges beyond PPAs

The area of the wet season female home ranges did not significantly decrease with increasing mean annual rainfall ($F_{1,32} = 0.03$, $R^2 = 0.001$, $p = 0.87$; Figure 5a). In contrast to my expectations the area of the dry season female home ranges significantly increased with increasing mean annual rainfall ($F_{1,33} = 9.47$, $R^2 = 0.22$, $p = 0.004$; Figure 5b). The area of the wet season male home ranges decreased with increasing mean annual rainfall (Figure 5c). However, this relationship was not significant ($F_{1,12} = 1.88$, $R^2 = 0.14$, $p = 0.20$). When a generalized least square model was used, the area of the dry season male home ranges significantly decreased with increasing mean annual rainfall ($p = 0.001$; Figure 5d).

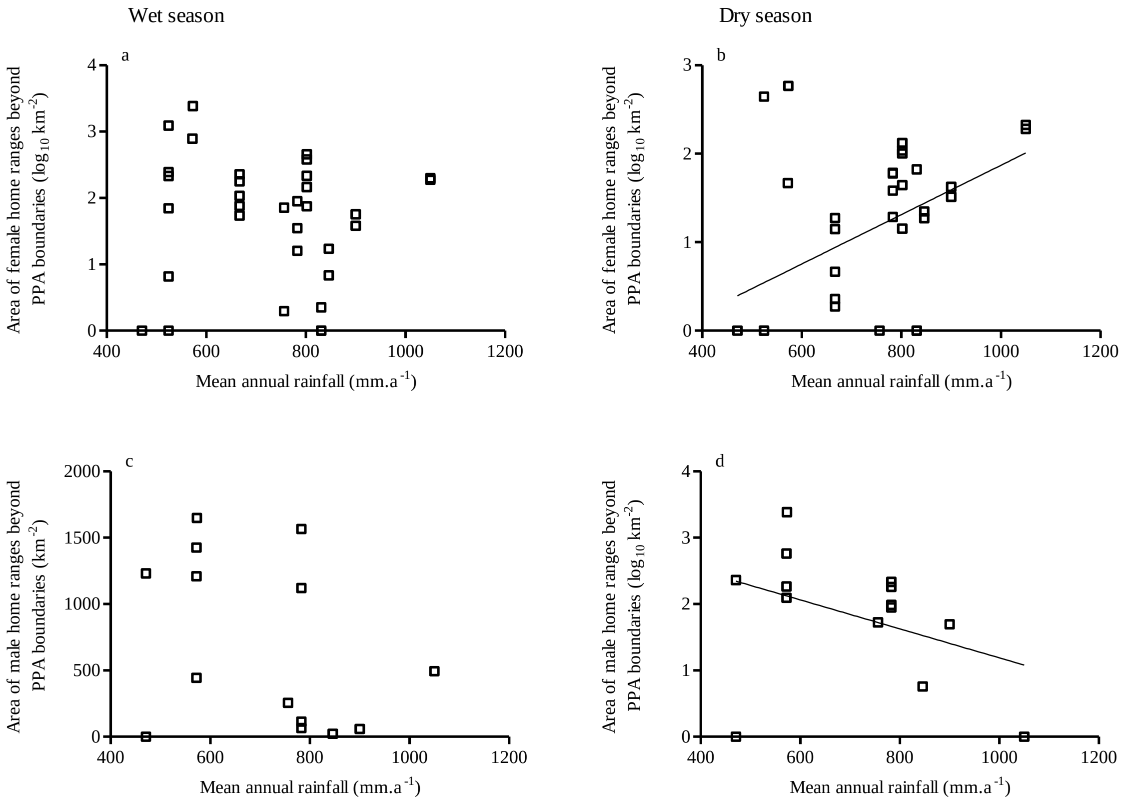

Figure 5. The area of home ranges beyond PPAs as a function of mean annual rainfall for females during the wet season (a) and the dry season (b), and males during the wet season (c) and the dry season (d). Lines were fitted only when there was a significant relationship ($p < 0.05$).

The contribution of extrinsic and intrinsic variables to the variability in the proportion of home ranges beyond PPAs

A single variable model was selected as the best model for all of the female analyses with the exception of the females from dry savannahs during the dry season when a model containing two variables was the best (Table 11). During the wet season, the model containing size of home range was selected as the best for the female mixed model, and the females from dry savannahs ($R^2 = 0.71$; Table 12). The proportion of home ranges beyond PPAs increased with increasing size of home ranges for all females and for females from dry savannahs. When the mixed model was used to analyse the female data from wet savannahs, the model including population growth rate was selected as the best, where the proportion of female home ranges beyond PPAs increased with increasing population growth rate, however, the standard errors were large (Table 12). During the dry season, a model containing population growth rate was selected as the best for all the females (R^2 = 0.18; Table 12), where the proportion of home ranges beyond PPA’s increased with decreasing population growth rate. A model including the size of the PPAs was selected as the best for females from wet savannahs (R^2 = 0.13; Table 12), where the proportion of home ranges beyond PPAs increased with increasing PPA size. For females from dry savannahs a model including both population growth rate and size of the home ranges was ranked the best (R^2 = 0.88; Table 12). The proportion of these home ranges beyond PPAs increased with decreasing population growth rate and increasing size of home ranges. When the relative variable importance could be calculated population growth rate scored 2.14 higher than the second most important variable in the dry season female model but only 1.03 times higher than the second most important variable in the model for females from wet savannahs during the wet season. The size of the home range scored 1.80 times higher than the second most important variable in the wet season female model, and the size of the PPAs scored 1.33 times higher in the model for females from wet savannahs during the dry season (Table 11).

Population growth rate was the only variable included in the best model for the males during the wet season (R^2 = 0.58; Table 11 and Table 12) and during the dry season (R^2 = 0.42; Table 11 and Table 12). The proportion of the male home ranges beyond PPAs increased with increasing population growth rate (Table 12). Relative variable importance could not be calculated due to correlated variables not appearing in the same number of candidate models.

Table 11. This table presents the results of the model selection for the regression analyses determining whether the season-specific variability in the proportion of home ranges beyond the boundaries of PPAs could be explained by extrinsic and intrinsic variables. The variables included in the models were density of the elephant populations within the PPAs (1), the population growth rate of the elephant populations within the PPAs (2), the size of the home ranges of elephants (3), and the size of the PPAs (4).The sample size, the number of the top ranked model, the number of parameters, the AICc values and weights (*W*i), the model number of other plausible models, and the relative variable importance are reported. Missing values (-) occur when variables were correlated and therefore relative variable importance could not be calculated.

Females	Sample size	Best model	K	AIC$_c$	AIC$_{(Wi)}$	Other possible models (ΔAIC$_c$ between 0 and 2)	Relative variable importance			
							1	2	3	4
Wet season	30	3	4	139.39	0.29	1, 2	0.30	0.28	0.54	0.27
Dry savannah	8	3	3	41.42	0.60	2	-	-	-	-
Wet savannah	22	2	4	100.45	0.20	4, 3, 1	0.32	0.35	0.33	0.34
Dry season	31	2	3	126.55	0.21	9, 8, 11, 5	0.34	0.92	0.40	0.43
Dry savannah	8	7	4	1.54	0.49	2	-	-	-	-
Wet savannah	23	4	3	92.33	0.25	9, 2	0.23	0.51	0.24	0.68
Males										
Wet season	11	2	3	43.69	0.53	1	-	-	-	-
Dry season	11	2	3	52.80	0.39	7	-	-	-	-

Table 12. The beta coefficients (β), standard errors (S.E.) and R^2 values from the top ranked linear and mixed effects regression models examining the relationship between the proportion of season-specific home ranges of elephants beyond PPAs, the density (elephants per km^2) and population growth rate (*r*) of elephant populations within PPAs, the size of their home ranges (km^2), and the size of the PPAs (km^2). Missing values (-) occur when mixed effects regression was used to analyse the data and therefore R^2 values are not reported.

Females	Variable included in best model	β	S.E.	R^2
Wet season	Size of home range (km^2)[a]	1.81	1.26	-
Dry savannah	Size of home range (km^2)[a]	13.49	3.54	0.71
Wet savannah	Exponential *r*	4.80	11.49	-
Dry season	Exponential *r*	-8.14	3.27	0.18
Dry savannah	Exponential *r*	-4.10	0.80	0.88
	Size of home range (km^2)[a]	0.47	0.13	
Wet savannah	Size of PPA (km^2)[a]	1.34	0.77	0.13
Males				
Wet season	Exponential *r*	14.74	4.21	0.58
Dry season	Exponential *r*	16.22	6.37	0.42

[a] Size of home range and size of PPA were log$_{10}$ transformed

CHAPTER 5

DISCUSSION

In this thesis, I investigated a number of environmental and population variables that may explain why elephants cross the boundaries of PPAs. I tested six hypotheses, four at the location-scale and the remaining two at the home range-scale. My study took place in 12 different PPAs across southern Africa, which differed in size, shape, rainfall, vegetation, topography, provision of water, management categories, human disturbance, and number of elephants. 45 out of 49 elephants moved beyond the boundaries of the PPAs in which they were collared.

My first hypothesis that displacement rates of elephants will be larger beyond PPAs compared to within PPAs was rejected, both for the females and the males. Other studies have shown that elephants will increase their displacement rates when beyond protected areas (Douglas-Hamilton *et al.*, 2005) or in human-dominated areas where elephants are less tolerated by the human occupants (Graham *et al.*, 2009). Three of the five males averaged greater speeds beyond the PPAs than within. Two of these males were from Kafue where the males travelled through a game management area and beyond into unprotected land. Perhaps these males did increase their speed when they moved into unprotected land where they would have been less tolerated. The third male was from Bwabwata where humans resided both within and beyond the PPAs. Therefore, for this male I would not expect a difference in the average displacement rates within and beyond the PPA. The hourly data were limited and for the females there were generally more hourly telemetry locations within the PPAs, which may have biased the results. However, when I only included the four females with at least 24 one-hour telemetry data (one day’s worth of data) either within or beyond the PPAs, the same number of females had a larger displacement rate within the PPAs as beyond the PPAs.

My second hypothesis that the proportion of elephant telemetry locations beyond PPAs would be greater in the wet season than the dry season was accepted for females, but rejected for males. Females are more restricted in movements than males (Stokke and du Toit, 2002; Smit *et al.*, 2007). Other studies have found that this intensifies during the dry season, when water is limited, as the herds need to remain within a relatively short distance to water (Stokke and du Toit, 2002). Therefore, females' dry season home ranges are generally smaller than wet season home ranges. My results suggest that the females were constricting their dry season home ranges to within the PPAs, where water provided by boreholes, rivers or dams, was available, and then expanding their wet season home ranges beyond the PPAs when water across the landscape increased in availability. Contrastingly, there was not a seasonal difference in the proportion of male locations beyond PPAs. Males are not restricted by group living and can tolerate lower quality food than females (Stokke and du Toit, 2000; Woolley *et al.*, 2009). Consequently they are able to vary their roaming behaviour (Shannon *et al.*, 2010) and roam greater distances, even when resources are limited (Stokke and du Toit, 2002; Smit *et al.*, 2007).

I expected elephants to have a greater proportion of core telemetry locations within the relative safety of PPAs. During the wet season, this expectation only held for females from dry savannahs. The females from dry savannahs were predominately from Khaudum, where drinking water was supplied within the PPA. This has led to the elephant population increasing within the PPA and remaining within the PPA during both the wet and the dry seasons (Loarie *et al.*, 2009b). Even though the result for the wet savannah females is contrary to my expectations, it is not surprising, as females expanded their wet season home ranges beyond PPAs. When this occurred they apparently simultaneously intensified their activities beyond PPAs. Similarly, the pooled males and the individual males from dry savannahs concentrated their activities beyond PPAs. Elephants in Kenya concentrate their activities within protected areas, which were usually separated by relatively dangerous unprotected areas (Douglas-Hamilton *et al*., 2005). Presumably elephants were harassed by the human inhabitants within these unprotected areas. The majority of the PPAs in my study were adjoined by the SPAs, and therefore the elephants could easily move between the protected areas without crossing unprotected land, which may explain the contrasting results. An equal number of males from wet savannahs concentrated their wet season activities within and beyond the PPAs, implying that they were utilising both the PPAs and the SPAs.

During the dry season, and in line with my expectations, the females had a greater proportion of core telemetry locations within PPAs. Because the females' dry season home ranges were generally more restricted to the PPAs than their wet season home ranges, it follows that their core locations would also be concentrated within PPAs. Only the males from the wet savannahs had a greater proportion of locations within PPAs, and then it was only one more male than the number that had a greater proportion of core locations beyond PPAs. This result again suggests that the males were utilising both the PPAs and the adjoining SPAs. Males may roam over larger distances than females to avoid other males in musth (Stokke and du Toit, 2002), or to search for females when they are in musth (Whitehouse and Schoeman, 2003).

The landscapes that the elephants were using within and beyond the PPAs were generally different. This result was unsurprising because savannahs are heterogeneous (e.g. Belsky, 1995). The selection patterns for females and males within and beyond the PPAs during the wet season were similar.

During the dry season, habitat selection patterns for the variables within and beyond the PPAs were similar for females and males. One of the notable exceptions to this was the selection for areas close to people beyond the PPAs by both females and males. Elephants also selected for areas close to people within the PPAs. I acknowledge that this was probably a result of the presence of waterholes at many of the tourist camps, which were included in this layer. Beyond the PPAs, people frequently build settlements close to water (Jackson *et al*., 2008), which are bordered by small-scale crop plantations. Elephants may leave PPAs to raid crops from these plantations (Parker and Osborn, 2001; Osborn, 2004; Chiyo *et al*., 2005). Therefore, the strong selection for areas close to people beyond the PPAs may be indicative of the elephants selecting these areas to meet their water requirements, or to raid crops. To determine whether the elephants were leaving the PPAs to raid crops, much finer-scale analyses would have to be performed and interpolated with known crop raiding incidents. Additionally, six of the nine males studied, and three of the five males from wet savannahs selected for high tree cover when beyond the PPAs during the dry season. Roever *et al*. (2012) showed a functional response for tree cover across southern Africa, with it being a more important predictor of elephant use in more arid areas with less vegetation. Similarly, my results suggest that tree cover was a more important predictor beyond PPAs because there was less tree cover available within these areas.

My study showed that habitat selection patterns for elephants were similar within and beyond the PPAs for most of the variables considered, which suggests that elephants did not leave the PPAs to select for these variables beyond. However, during the dry season, the elephants selected for human settlements when beyond the PPAs. There were more settlements present beyond the PPAs than within. Because these settlements were probably built close to water, the elephants may have selected these areas to meet their water requirements or to raid crops.

My hypothesis that elephants from more arid PPAs will have a larger area of their home range beyond the boundaries of the PPAs than elephants from wetter PPAs was only accepted for the males during the dry season. In contrast to my expectations, females from

PPAs with higher mean annual rainfall had larger areas of their home ranges beyond the PPAs than females from more arid PPAs. This result was only significant for females during the dry season. Water is a key determinant of elephant spatial utilisation during the dry season (e.g. Young *et al*., 2009a) and therefore when water was available within the PPAs the females did not have to leave the PPAs to find water. In my study Khaudum was the most arid PPA and drinking water, in the form of boreholes, was provided throughout the dry season. Indeed, de Beer and van Aarde (2008) showed that the area of home ranges in arid areas decreased with increasing water point density. Furthermore, elephants from Mudumu have been shown to constrict their range to within the PPA boundaries during the dry season and expand their ranges into southern Zambia in the wet season when surface water across the landscape increases (Chase and Griffin, 2009). In the wetter savannahs, the females in this study may have been less restricted by the availability of water beyond the PPAs. Many of the PPAs in the wetter savannahs were bordered by rivers, allowing the females to utilise the areas both within and beyond the PPAs.

In line with my expectations, males from PPAs with lower mean annual rainfall had larger areas of their home ranges beyond the PPAs than males from wetter PPAs. This result was significant during the dry season, suggesting that males from more arid areas then were roaming greater distances to fulfil their needs than males from wetter areas. Inter-annual variability in rainfall may have played a role in the unaccounted variability in the area of home ranges beyond PPAs, and therefore these analyses could have been improved by using daily rainfall data that coincided with the elephant location data.

A single variable model was ranked the best for most of the female analyses. During the wet season, females with larger home ranges had a greater proportion of their home ranges beyond the PPAs, this also applied to females from dry savannahs. The top-ranked model containing population growth rate was only marginally better than the other single variable models tested for the females from the wet savannahs. Additionally, the standard errors of the co-efficient were large suggesting that the model did not fit very well. During the dry season, the proportion of female home ranges beyond PPAs increased with decreasing population growth rate. However, only a small amount of the variance was explained by this variable suggesting that other important variables were excluded. In the dry savannah PPAs with higher population growth rate the size of the females' home ranges were smaller and were more constricted to within the boundaries of the PPAs. The three dry savannah PPAs were Khaudum, Bwabwata, and Mudumu. The population growth rate was highest in Khaudum, where the majority of the females remained within the PPA and close to the water points (de Beer and van Aarde, 2008). For the wet savannahs my results, which were contrary to my expectations, suggest that the size of the PPAs does not influence the proportion of the home range, however, a lot of the variance was unexplained indicating that other variables would also influence the response variable.

Population growth rate was the only variable included in the best male models. My results suggest that in PPAs with higher population growth rate intraspecific competition for limited dry season resources between males was greater, thereby forcing males beyond the PPAs (Wittemyer *et al*., 2007). During the wet season when resources were more abundant and widely distributed, males from PPAs with higher population growth rates may have increased the area of their home range beyond PPAs to avoid other males in musth or to search for females in oestrus (Stokke and du Toit, 2002; Whitehouse and Schoeman, 2003). However, only a few males were included in this study. This may have consequences for the modelling approach that I followed and reduce the predictability of the model (Bissonette, 1999).

The majority of the PPAs in this study were surrounded by areas of low human density (Mittermeier *et al*., 2003). Indeed, people lived within Bwabwata, Quirimbas, Limpopo and Maputo, which probably resulted in similar amounts of land transformation within and beyond the PPAs. The two exceptions to this rule were Vwaza and Kasungu, both of which were in Malawi and were adjoined by densely populated areas (McShane, 1990; Munthali and Mkanda, 2002), which had impeded elephant movements. The low human densities beyond the PPAs possibly allowed the elephants to utilise the land (Hoare and Du Toit, 1999). Adjoining many PPAs in this study were SPAs, into which the elephants often roamed when they left the PPAs. Collectively, these PPAs and SPAs formed clusters of protected areas (van Aarde and Ferreira, 2009). The home ranges of the elephants were generally within the boundaries of these clusters of protected areas. Therefore, the clusters of protected areas were extremely important in adding to the amount of space available to the elephants. Conservation incentives for elephants need to include spatial use patterns of elephants and the reality that elephants do not distinguish between different categories of protected land. My study suggests that PPAs and SPAs can form protected area networks that cater for the spatial needs of savannah elephants. A few of these networks already exist and some of these in the form of transfrontier conservation areas (TFCAs).

As human populations grow, the challenge of how to increase food production while simultaneously conserving biodiversity is under debate. Two different approaches have been proposed, namely land sharing and land sparing (Godfray, 2011; Phalan *et al*., 2011). The former is when land is used for both conservation and less intensive food production, and the latter is when protected areas, set aside purely for conservation, and land for intensive farming are separated. Land sparing appeared to be the best strategy for the protection of bird and tree species in Ghana and northern India (Phalan *et al*., 2011). However, the authors do acknowledge that a more sophisticated method of land sparing needs to be implemented than the one where islands of protected areas are set aside in a sea of large-scale intensive farming. They suggest that conservation can occur in community concessions and indigenous reserves

(Phalan *et al*., 2011). Tscharntke *et al*., (2012) argue that the land sharing versus land sparing debate is simplified, and that increased crop yields through land sparing will not reduce global hunger levels. They argue that generally hungry people do not have access to large-scale, intensive farming practices but instead employ more eco-efficient farming methods for which the conservation of biodiversity plays an important role (Tscharntke *et al*., 2012). In relation to my study, land sparing occurred in the majority of the PPAs included, where people did not reside or utilize the land set aside for wildlife protection. Land sharing took place in the SPAs, where people and wildlife shared the land and only small-scale pastoral activities and crop farming occurred. The elephants in my study used both the PPAs and the SPAs, therefore highlighting the importance of both land sparing and land sharing, and implying that a more integrated approach is needed when considering the spatial requirements of elephants.

In conclusion, the reasons for elephants leaving PPAs varied seasonally and between the sexes. However, the displacement rates of both females and males were similar within and beyond the PPAs. During the wet season, females expanded their home ranges beyond the PPAs and concentrated their activities both within and beyond the PPAs. The habitat selection patterns of females were similar within and beyond the PPAs. During the dry season, females constricted their home ranges to within the PPAs and concentrated their activities within the PPAs. Females from more arid areas had a smaller area of their home ranges beyond the PPAs, which increased with decreasing population growth rate and increasing size of the home ranges, than females from wetter areas. The proportion of home ranges of females from wet savannahs increased with increasing size of the PPAs. When the females were beyond the PPAs during the dry season, more females selected for areas close to people. There were no significant differences in the proportion of male locations beyond PPAs in the wet and dry seasons, and males concentrated their activities beyond PPAs during both seasons. Furthermore, the proportion of dry and wet season home ranges of males increased with increasing population growth rate. However, this result was inconclusive. During the wet season, more males selected for areas with low slopes beyond PPAs, whereas during the dry season more males selected for areas close to people and with high tree cover. Additionally, the area of the dry season home ranges of males beyond wetter PPAs was larger than the area of home ranges beyond more arid PPAs. When the elephants in this study left the PPAs they roamed within the boundaries of the clusters of protected areas.

This study shows that elephants are utilising both the PPAs and the SPAs, and that both are therefore important for elephant conservation. The males appeared to utilise the SPAs adjoining the PPAs during both seasons, but females utilised the SPAs more during the wet season when resources were not limiting. Generally, high numbers of elephants within the PPAs did not influence the proportion of their home ranges beyond the PPAs. Other variables that may have influenced the roaming of elephants beyond the boundaries of PPAs, such as social factors (Wittemyer *et al*., 2007; Wittemyer *et al*., 2008) and migrations were not tested for in this study. Some elephant herds are dominant over others and this may influence the amount of time that a herd spends within the relative protection afforded by a PPA (Wittemyer *et al*., 2007; Wittemyer *et al*., 2008). We also need to consider that current PPAs may not encompass migration routes of elephants and therefore elephants may leave PPAs to follow these ancient routes.

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Appendix I. The mean ± standard errors of the explanatory variables measured at random points within and beyond the PPAs. The random points were generated within the wet season pooled female home ranges for each PPA and therefore represent the areas the females were using within and beyond PPAs. Values in brackets represent the number of random points either within or beyond the PPAs. Only results for PPAs that had elephants included in the RSF modelling are presented.

Females								
	Khaudum		Mudumu		Kafue		Lower Zambezi	
Explanatory variable	In (13 460)	Out (7 630)	In (955)	Out (6 486)	In (5 327)	Out (578)	In (877)	Out (6 466)
NDVI	<0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.01 ± 0.0
Percentage herb cover	80.8 ± 0.0	79.6 ± 0.1	83.0 ± 0.1	78.5 ± 0.1	79.7 ± 0.1	79.8 ± 0.3	75.4 ± 0.5	73.9 ± 0.3
Percentage tree cover	1.6 ± 0.0	3.1 ± 0.01	8.6 ± 0.2	19.5 ± 0.1	19.7 ± 0.1	18.2 ± 0.4	21.2 ± 0.4	18.2 ± 0.1
Slope (^{0})	0.6 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	1.1 ± 0.0	0.9 ± 0.1	1.0 ± 0.0	1.4 ± 0.0
Distance to water^a (km)	0.5 ± 0.0	1.8 ± 0.0	0.5 ± 0.0	1.7 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.2 ± 0.0
Distance to humans^a (km)	2.5 ± 0.0	3.3 ± 0.0	1.1 ± 0.0	1.7 ± 0.0	1.8 ± 0.0	0.6 ± 0.0	2.4 ± 0.0	1.5 ± 0.0

	South Luangwa		Vwaza		Quirimbas	
Explanatory variable	In (6 299)	Out (7 140)	In (2 934)	Out (626)	In (669)	Out (1 475)
NDVI	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0
Percentage herb cover	87.6 ± 0.1	81.2 ± 0.1	72.5 ± 0.2	71.2 ± 0.5	68.0 ± 0.4	71.6 ± 0.2
Percentage tree cover	11.3 ± 0.1	18.3 ± 0.1	27.4 ± 0.2	28.1 ± 0.6	32.0 ± 0.4	28.4 ± 0.2
Slope (^{0})	0.6 ± 0.0	1.1 ± 0.0	1.4 ± 0.1	4.1 ± 0.02	2.4 ± 0.1	2.8 ± 0.1
Distance to water^a (km)	0.4 ± 0.0	0.5 ± 0.0	1.1 ± 0.0	1.0 ± 0.0	0.4 ± 0.0	1.1 ± 0.0
Distance to humans^a (km)	1.2 ± 0.0	1.3 ± 0.0	2.6 ± 0.0	2.6 ± 0.0	2.1 ± 0.0	1.8 ± 0.0

^{a} Distance variables were multiplied by 0.1

Appendix II. The mean ± standard errors of the explanatory variables measured at random points within and beyond the PPAs. The random points were generated within the wet season pooled male home ranges for each PPA and therefore represent the areas the males were using within and beyond PPAs. Values in brackets represent the number of random points either within or beyond the PPAs. Only results for PPAs that had elephants included in the RSF modelling are presented.

	Males									
	Mudumu		Kafue		Vwaza		Quirimbas		Limpopo	
Explanatory variable	In (1 861)	Out (20 882)	In (13 038)	Out (10 361)	In (1 968)	Out (275)	In (2 002)	Out (1 372)	In (12 519)	Out (6 413)
NDVI	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0
Percentage herb cover	83.2 ± 0.1	81.0 ± 0.1	81.9 ± 0.1	80.9 ± 0.1	71.2 ± 0.2	70.9 ± 0.9	68.0 ± 0.3	65.9 ± 0.3	76.6 ± 0.1	84.0 ± 0.1
Percentage tree cover	8.9 ± 0.1	15.5 ± 0.1	17.3 ± 0.1	17.9 ± 0.1	28.8 ± 0.2	28.3 ± 0.9	31.9 ± 0.3	34.1 ± 0.3	21.6 ± 0.1	12.0 ± 0.1
Slope (^{0})	0.4 ± 0.0	0.5 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.4 ± 0.1	4.7 ± 0.4	1.8 ± 0.0	2.6 ± 0.1	1.4 ± 0.0	1.6 ± 0.0
Distance to water[a] (km)	0.4 ± 0.0	1.2 ± 0.0	0.8 ± 0.0	1.2 ± 0.0	1.1 ± 0.0	0.9 ± 0.1	1.3 ± 0.0	2.9 ± 0.0	0.6 ± 0.0	0.3 ± 0.0
Distance to humans[a] (km)	1.2 ± 0.0	1.6 ± 0.0	2.6 ± 0.0	2.1 ± 0.0	2.4 ± 0.0	2.8 ± 0.0	1.2 ± 0.0	1.4 ± 0.0	1.0 ± 0.0	1.2 ± 0.0

[a] Distance variables were multiplied by 0.1

Appendix III. The mean ± standard errors of the explanatory variables measured at random points within and beyond the PPAs. The random points were generated within the dry season pooled female home ranges for each PPA and therefore represent the areas the females were using within and beyond PPAs. Values in brackets represent the number of random points either within or beyond the PPAs. Only results for PPAs that had elephants included in the RSF modelling are presented.

Females								
	Khaudum		Mudumu		Kafue		Lower Zambezi	
Explanatory variable	In (11 294)	Out (3 493)	In (1 464)	Out (363)	In (2 851)	Out (502)	In (1 516)	Out (418)
NDVI	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0
Percentage herb cover	80.9 ± 0.0	81.0 ± 0.1	83.2 ± 0.1	82.3 ± 0.3	78.1 ± 0.2	81.1 ± 0.3	76.8 ± 0.4	65.4 ± 1.2
Percentage tree cover	1.6 ± 0.0	3.6 ± 0.1	8.9 ± 0.2	13.9 ± 0.3	21.4 ± 0.2	16.7 ± 0.3	19.5 ± 0.3	25.7 ± 0.7
Slope (^{0})	0.6 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	1.1 ± 0.0	0.8 ± 0.0	1.0 ± 0.0	1.7 ± 0.2
Distance to water^{a} (km)	0.4 ± 0.0	2.5 ± 0.0	1.8 ± 0.0	2.3 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
Distance to humans^{a} (km)	2.1 ± 0.0	3.3 ± 0.0	1.2 ± 0.0	0.9 ± 0.0	1.6 ± 0.0	0.6 ± 0.0	1.7 ± 0.0	1.7 ± 0.0

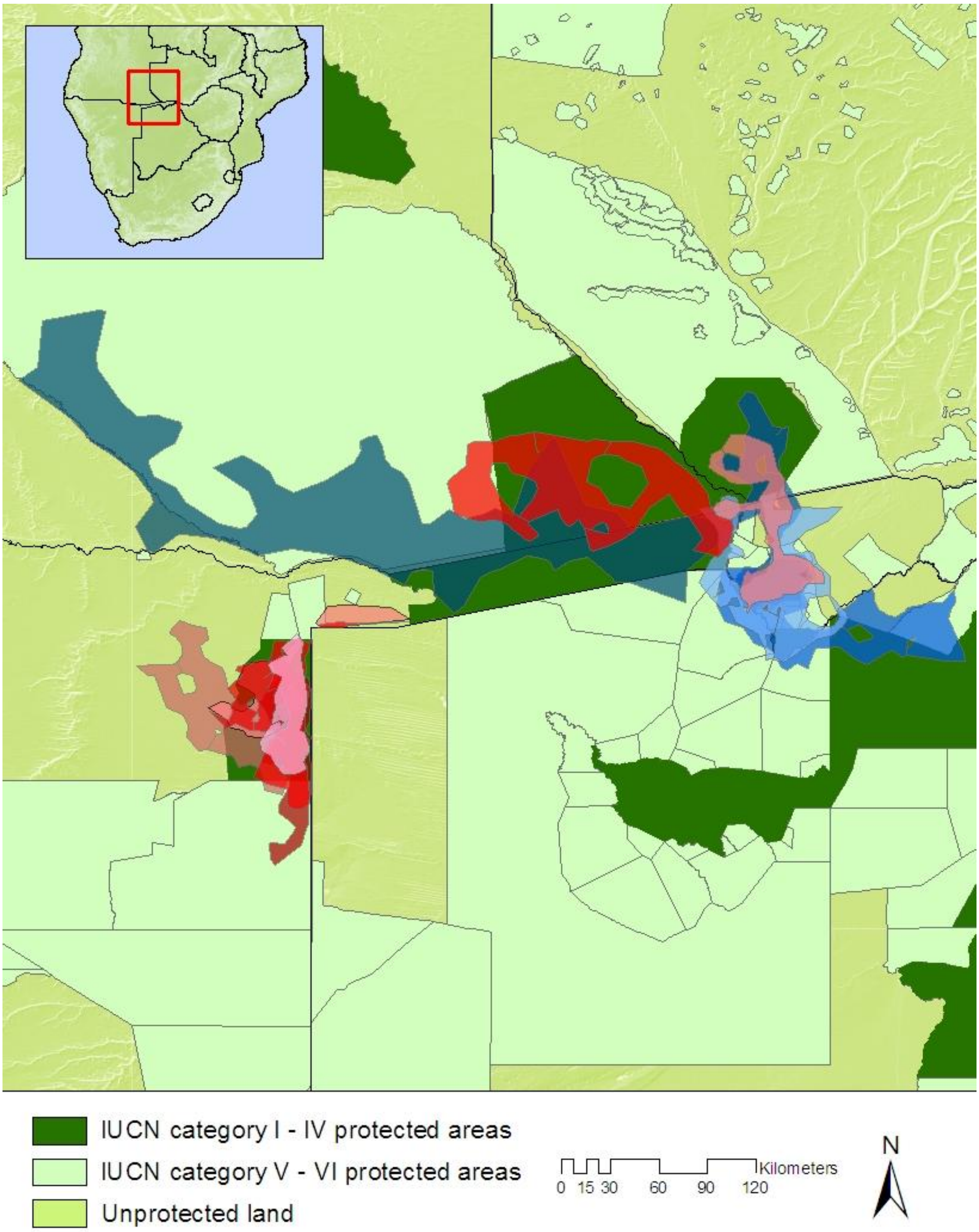
	South Luangwa		North Luangwa		Vwaza		Quirimbas	
Explanatory variable	In (3 175)	Out (4 192)	In (1 732)	Out (243)	In (1 279)	Out (250)	In (127)	Out (1 654)
NDVI	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0	<-0.1 ± 0.0
Percentage herb cover	86.5 ± 0.1	80.2 ± 0.1	79.5 ± 0.2	86.8 ± 0.2	72.9 ± 0.3	82.0 ± 0.6	69.5 ± 0.7	72.5 ± 0.2
Percentage tree cover	12.7 ± 0.1	19.4 ± 0.2	20.2 ± 0.2	12.3 ± 0.7	27.0 ± 0.3	16.4 ± 0.6	30.5 ± 0.7	27.4 ± 0.2
Slope (^{0})	0.7 ± 0.0	1.3 ± 0.0	1.6 ± 0.1	0.9 ± 0.0	2.0 ± 0.1	1.8 ± 0.1	3.7 ± 0.7	2.6 ± 0.1
Distance to water^{a} (km)	0.3 ± 0.0	0.6 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	1.0 ± 0.0	0.1 ± 0.0	0.5 ± 0.0	1.4 ± 0.0
Distance to humans^{a} (km)	1.0 ± 0.0	1.1 ± 0.0	1.7 ± 0.0	1.1 ± 0.0	2.8 ± 0.0	2.7 ± 0.0	2.2 ± 0.0	1.6 ± 0.0

[a] Distance variables were multiplied by 0.1

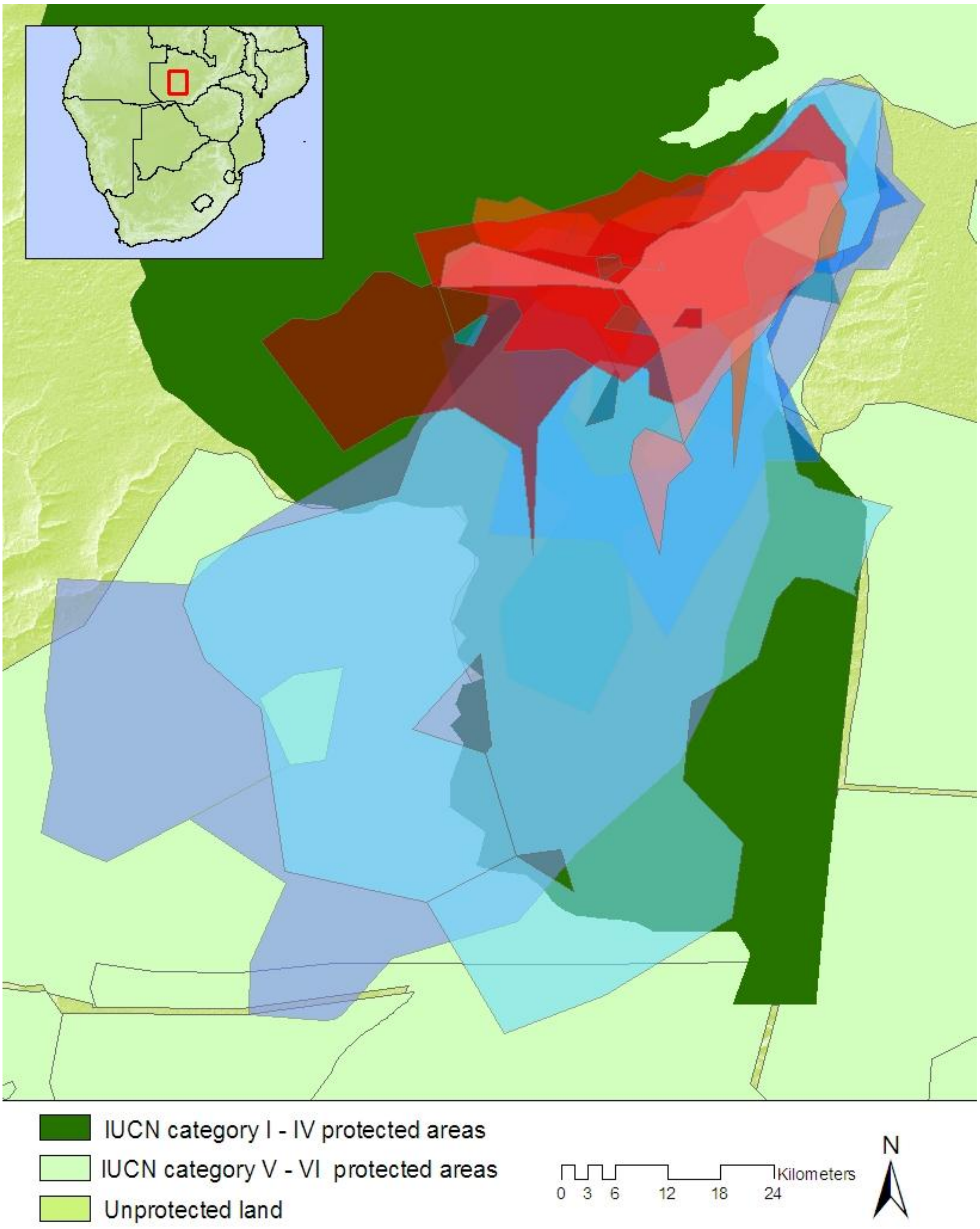
Appendix IV. The mean ± standard errors of the explanatory variables measured at random points within and beyond the PPAs. The random points were generated within the dry season pooled male home ranges for each PPA and therefore represent the areas the males were using within and beyond PPAs. Values in brackets represent the number of random points either within or beyond the PPAs. Only results for PPAs that had elephants included in the RSF modelling are presented.

	Males							
	Mudumu		Kafue		Vwaza		Limpopo	
Explanatory variable	In (1 920)	Out (5 672)	In (3 082)	Out (2 041)	In (1 127)	Out (184)	In (6 039)	Out (4 410)
NDVI	<-0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0	<0.1 ± 0.0	<-0.1 ± 0.0	<0.1 ± 0.0
Percentage herb cover	83.1 ± 0.1	82.5 ± 0.1	78.9 ± 0.2	81.0 ± 0.2	71.1 ± 0.3	79.7 ± 0.8	78.2 ± 0.1	84.9 ± 0.1
Percentage tree cover	8.2 ± 0.1	12.6 ± 0.1	20.5 ± 0.2	17.2 ± 0.2	28.8 ± 0.3	19.9 ± 0.8	19.6 ± 0.1	10.6 ± 0.1
Slope (^{0})	0.5 ± 0.0	0.6 ± 0.0	0.9 ± 0.0	0.8 ± 0.0	2.5 ± 0.1	1.5 ± 0.1	1.5 ± 0.0	0.8 ± 0.0
Distance to water[a] (km)	1.2 ± 0.0	0.4 ± 0.0	0.7 ± 0.0	0.3 ± 0.0	1.3 ± 0.0	0.2 ± 0.0	0.5 ± 0.0	0.3 ± 0.0
Distance to humans[a] (km)	1.1 ± 0.0	0.9 ± 0.0	1.6 ± 0.0	0.6 ± 0.0	2.5 ± 0.0	2.9 ± 0.0	0.9 ± 0.0	1.1 ± 0.0

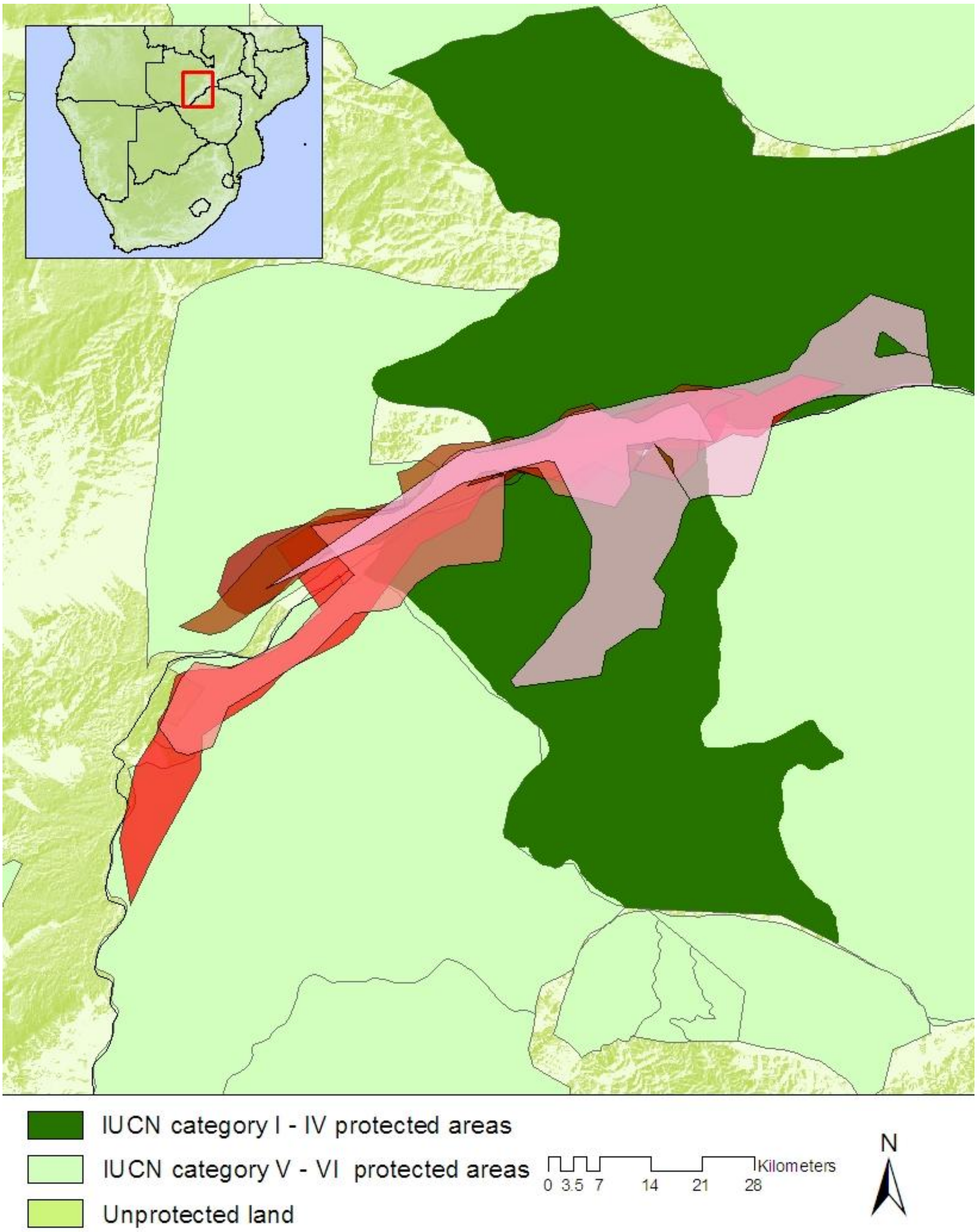
[a] Distance variables were multiplied by 0.1



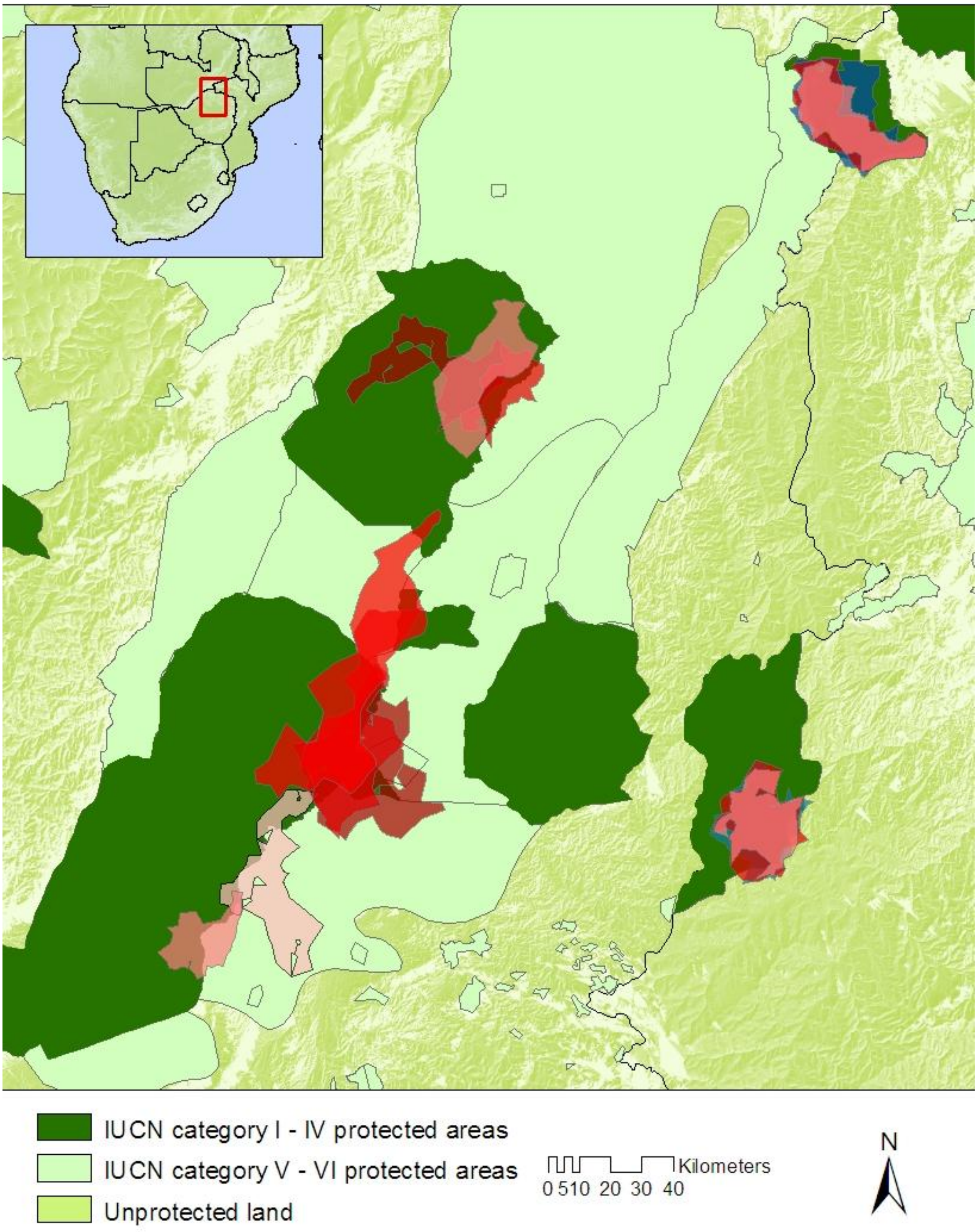
Appendix V. The elephant home ranges within the Chobe cluster of protected areas. The varying shades of red and pink represent the female home ranges and the varying shades of blue represent the male home ranges. The home ranges for each elephant were calculated using all the available elephant locations.



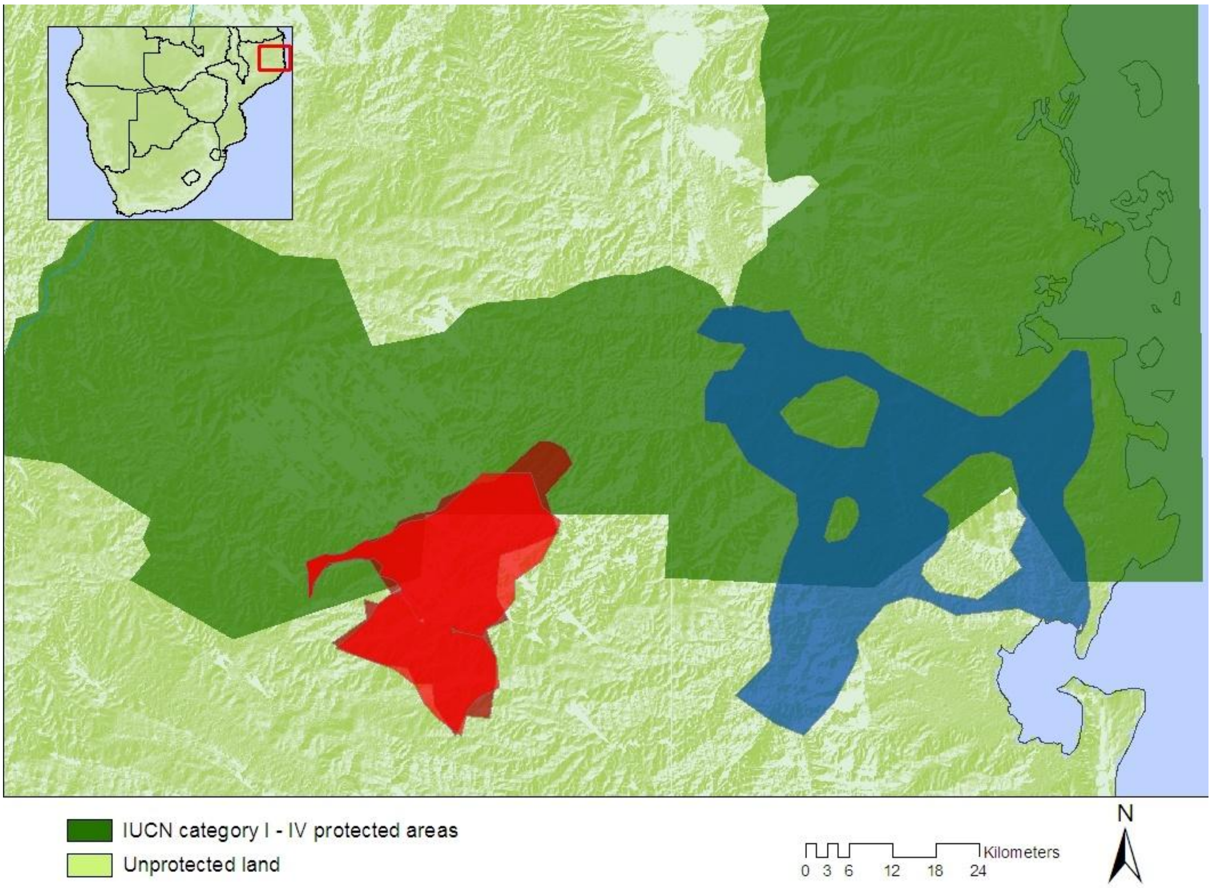
Appendix VI. The elephant home ranges within the Kafue cluster of protected areas. The varying shades of red and pink represent the female home ranges and the varying shades of blue represent the male home ranges. The home ranges for each elephant were calculated using all the available elephant locations. Note that the map is focused in on the study site and elephant home ranges within the Kafue cluster of protected areas.



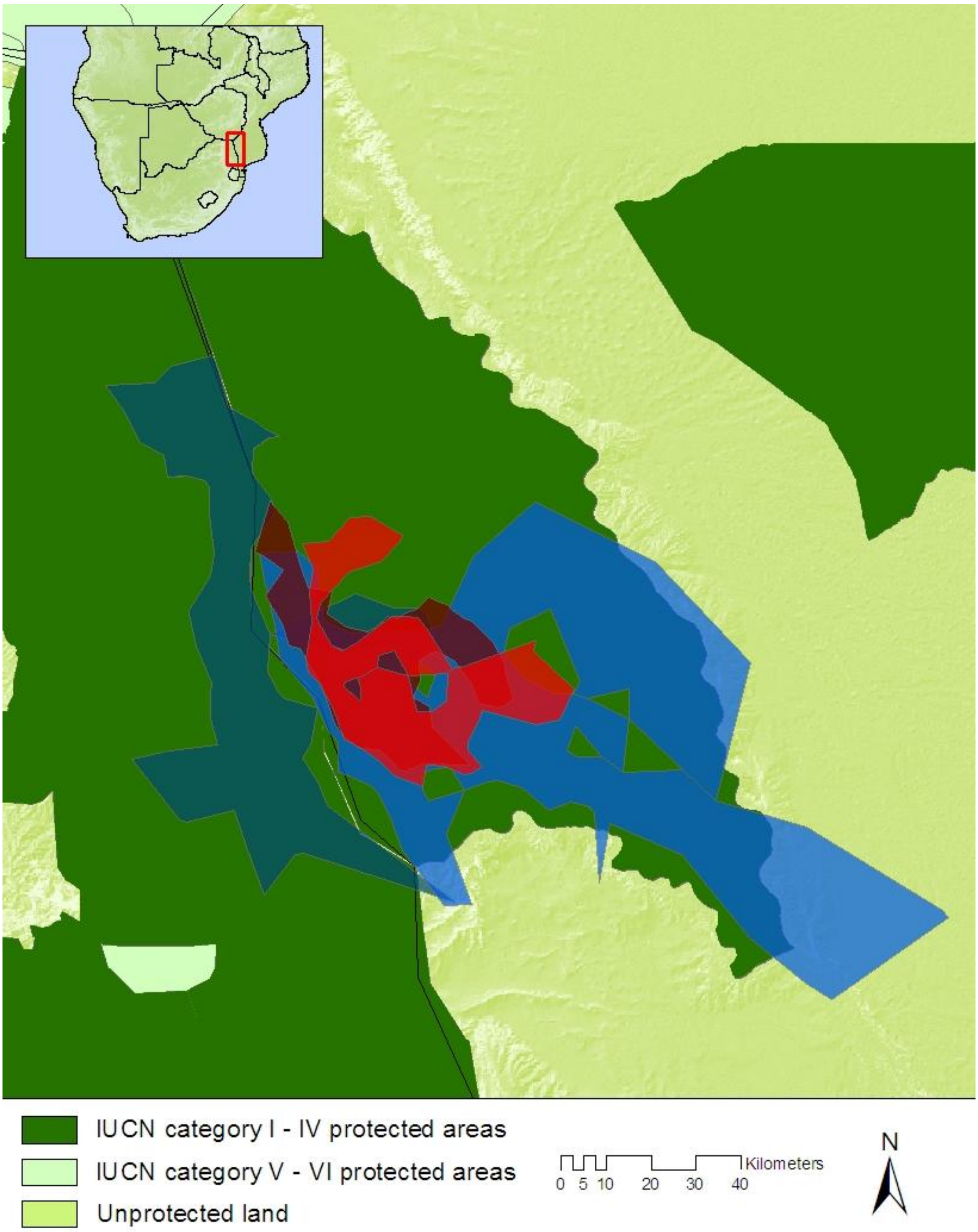
Appendix VII. The elephant home ranges within the Zambezi cluster of protected areas. The varying shades of red and pink represent the female home ranges. The home ranges for each elephant were calculated using all the available elephant locations. Note that the map is focused in on the study site and elephant home ranges within the Zambezi cluster of protected areas.



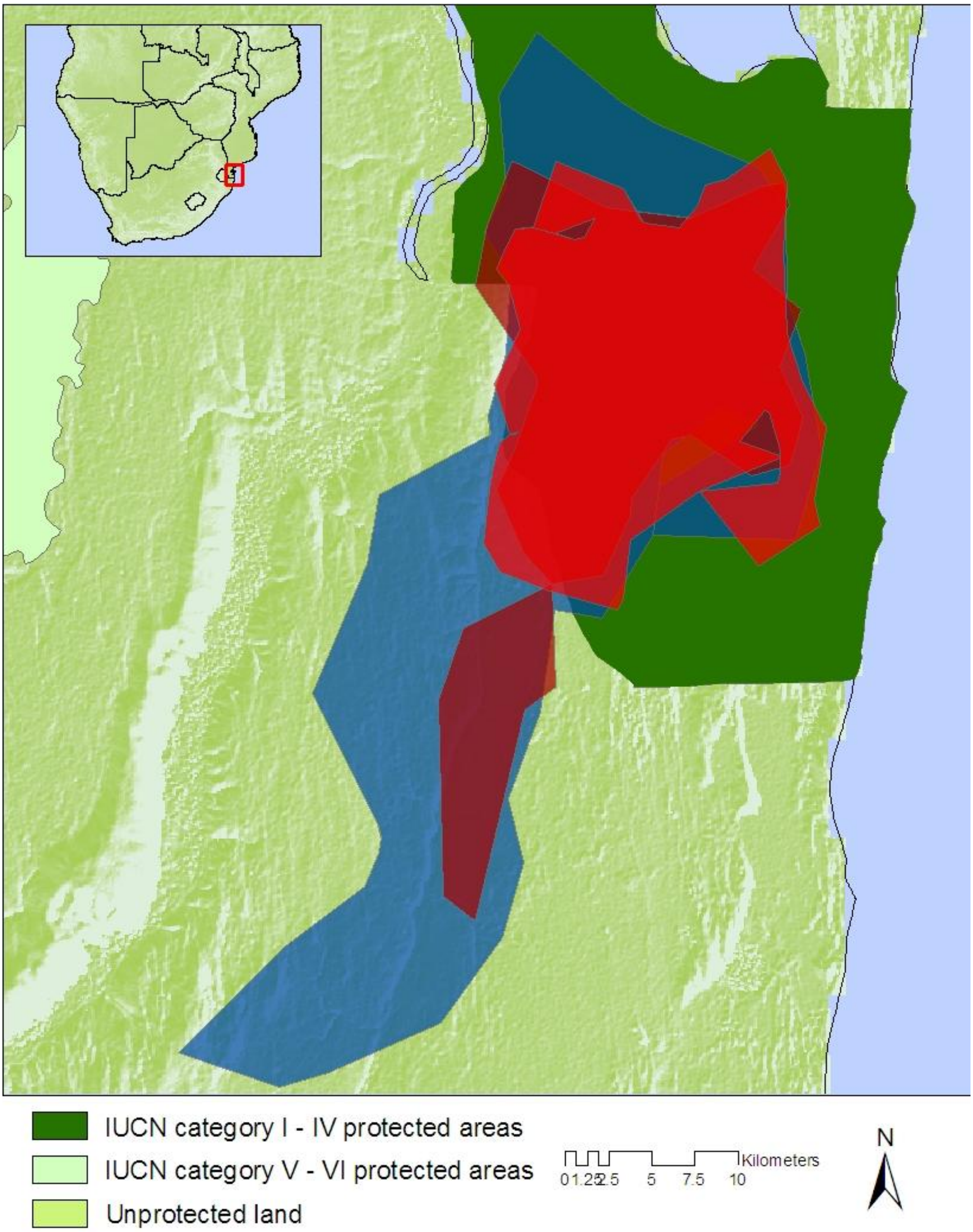
Appendix VIII. The elephant home ranges within the Luangwa cluster of protected areas. The varying shades of red and pink represent the female home ranges and the varying shades of blue represent the male home ranges. The home ranges for each elephant were calculated using all the available elephant locations.



Appendix IX. The elephant home ranges within the Niassa cluster of protected areas. The varying shades of red represent the female home ranges and blue represents the male home range. The home ranges for each elephant were calculated using all the available elephant locations. Note that the map is focused in on the study site and elephant home ranges within the Niassa cluster of protected areas.



Appendix X. The elephant home ranges within the Limpopo cluster of protected areas. The varying shades of red and pink represent the female home ranges and the varying shades of blue represent the male home ranges. The home ranges for each elephant were calculated using all the available elephant locations. Note that the map is focused in on the study site and elephant home ranges within the Limpopo cluster of protected areas.



Appendix XI. The elephant home ranges within the Maputo cluster of protected areas. The varying shades of red represent the female home ranges and blue represents the male home range. The home ranges for each elephant were calculated using all the available elephant locations. Note that the map is focused in on the study site and elephant home ranges within the Maputo cluster of protected areas.

Appendix XII. The top ranked AIC models for the habitat selection analyses for female and male elephants during the wet season. Four candidate a priori models consisting of landscape and anthropogenic variables were ranked using AIC and the AIC weights (AIC($_{Wi}$)) were calculated. The name of the top ranked model, number of parameters (K), Akaike weights (AIC($_{Wi}$)), Spearman rank correlation coefficient (r_s) are reported. * indicates significance ($p < 0.05$) for the model fit. Only PPAs that had at least one female or male elephant with enough locations either within or beyond the PPA were included.

Wet season									
Within PPA									
Females					Males				
Elephant	Model[a]	K	AIC$_{(Wi)}$	r_s	Elephant	Model	K	AIC$_{(Wi)}$	r_s
Khaudum 1	Global	8	1.00	0.91*	Mudumu 1	2	8	1.00	0.77*
Khaudum 2	Global	9	0.99	0.83*	Kafue 1	2	6	0.64	0.71*
Khaudum 3	Global	9	1.00	0.93*	Kafue 2	2	7	0.73	0.74*
Khaudum 4	2	6	0.61	0.85*	Kafue 3	2	5	0.72	0.90*
Khaudum 5	Global	10	0.58	0.98*	Vwaza 1	Global	9	1.00	0.92*
Mudumu 1	1	5	0.48	0.64*	Quirimbas 1	2	5	0.63	0.82*
Kafue 1	2	7	0.73	0.80*	Limpopo 1	2	7	1.00	0.81*
Kafue 2	2	7	0.62	0.91*					
Kafue 3	Global	6	0.55	0.81*					
Kafue 4	2	7	0.72	0.96*					
Lower Zambezi 2	Global	6	0.79	0.89*					
South Luangwa 1	2	8	0.64	0.87*					
South Luangwa 2	2	8	0.48	0.84*					
South Luangwa 3	Global	7	0.52	0.82*					
South Luangwa 4	2	5	0.71	0.88*					
South Luangwa 5	Global	8	1.00	0.85*					
Vwaza 1	Global	9	0.83	0.93*					
Vwaza 2	2	7	0.73	0.64*					
Quirimbas 1	2	7	0.65	0.92*					

[a] The global model consisted of NDVI, percentage of herbaceous or tree cover, the slope of the terrain (º), the distance to water (km), and distance to humans (km). Model 1 consisted of NDVI, percentage of herbaceous or tree cover, and the distance to water (km). Model 2 consisted of NDVI, percentage of herbaceous or tree cover, the distance to water (km), and distance to humans (km).

Appendix XII. Continued

Quirimbas 2	2	5	0.51	0.78*

Beyond PPA

Females					Males				
Elephant	Model	K	$AIC_{(Wi)}$	r_s	Elephant	Model	K	$AIC_{(Wi)}$	r_s
Khaudum 2	Global	7	0.96	0.97*	Mudumu 1	2	5	0.65	0.70*
Khaudum 4	1	5	0.63	0.78*	Mudumu 2	Global	9	0.91	0.94*
Khaudum 6	Global	9	0.98	0.92*	Mudumu 3	2	6	0.51	0.98*
Mudumu 1	2	5	0.51	0.95*	Kafue 4	Global	10	0.89	0.68*
Kafue 1	2	6	1.00	0.90*	Vwaza 1	Global	6	1.00	0.90*
Lower Zambezi 1	2	6	0.46	0.87*	Quirimbas 1	2	7	0.73	0.87*
Lower Zambezi 2	1	3	0.73	0.82*	Limpopo 1	Global	8	1.00	0.98*
Lower Zambezi 3	2	7	0.53	0.70*					
Lower Zambezi 4	Global	5	0.97	0.87*					
Lower Zambezi 5	2	8	0.72	0.76*					
South Luangwa 1	2	6	0.65	0.92*					
South Luangwa 2	2	5	0.60	0.96*					
South Luangwa 3	1	5	0.55	0.78*					
South Luangwa 4	2	6	0.45	0.92*					
South Luangwa 5	2	7	1.00	0.94*					
Vwaza 1	2	6	0.56	0.75*					
Vwaza 2	2	6	0.63	0.93*					
Quirimbas 1	1	3	0.53	0.88*					
Quirimbas 2	2	5	0.87	0.98*					

Appendix XIII. The top ranked AIC models for the habitat selection analyses for female and male elephants during the dry season. Four candidate a priori models consisting of landscape and anthropogenic variables were ranked using AIC and the AIC weights (AIC($_{Wi}$)) were calculated. The name of the top ranked model, number of parameters (K), Akaike weights (AIC($_{Wi}$)), Spearman rank correlation coefficient (r_s) are reported. * indicates significance ($p < 0.05$) for the model fit. Only PPAs that had at least one female or male elephant with enough locations either within or beyond the PPA were included.

Dry season									
Within PPA									
Females					Males				
Elephant	Model[a]	K	AIC$_{(Wi)}$	r_s	Elephant	Model	K	AIC$_{(Wi)}$	r_s
Khaudum 1	Global	9	0.95	0.93*	Mudumu 1	Global	9	1.00	0.82*
Khaudum 2	Global	9	1.00	0.98*	Mudumu 2	Global	7	0.62	0.94*
Khaudum 3	2	7	0.63	0.85*	Kafue 1	Global	8	0.64	0.84*
Khaudum 4	2	6	0.67	0.95*	Kafue 3	Global	9	0.64	0.87*
Khaudum 5	1	9	1.00	0.87*	Vwaza 1	Global	9	0.79	0.82*
Khaudum 6	2	7	0.49	0.97*	Limpopo 1	Global	9	1.00	0.92*
Mudumu 1	2	5	0.67	0.93*					
Kafue 1	2	8	0.54	0.85*					
Kafue 2	Global	7	0.68	0.88*					
Kafue 3	Global	10	0.47	0.98*					
Kafue 4	2	6	0.72	0.84*					
Lower Zambezi 1	2	5	0.73	0.81*					
Lower Zambezi 2	Global	8	0.99	0.80*					
Lower Zambezi 3	2	7	0.72	0.96*					
Lower Zambezi 5	2	7	0.72	0.71*					
South Luangwa 1	Global	7	0.64	0.92*					
South Luangwa 2	Global	8	0.98	1.00*					
South Luangwa 3	2	6	0.66	0.78*					

[a] The global model consisted of NDVI, percentage of herbaceous or tree cover, the slope of the terrain (°), the distance to water (km), and distance to humans (km). Model 1 consisted of NDVI, percentage of herbaceous or tree cover, and the distance to water (km). Model 2 consisted of NDVI, percentage of herbaceous or tree cover, the distance to water (km), and distance to humans (km).

Appendix XIII. Continued

South Luangwa 4	Global	4	0.91	0.93*
South Luangwa 5	1	4	0.56	0.82*
North Luangwa 1	Global	7	0.60	0.89*
North Luangwa 2	2	8	0.61	0.64*
North Luangwa 3	2	7	0.63	0.95*
Vwaza 1	Global	9	0.78	0.98*
Vwaza 2	Global	10	0.86	0.95*
Quirimbas 1	Global	6	0.83	0.90*

Beyond PPA

Females					Males				
Elephant	Model	K	$AIC_{(Wi)}$	r_s	Elephant	Model	K	$AIC_{(Wi)}$	r_s
Khaudum 5	2	6	0.52	0.87*	Mudumu 1	Global	10	1.00	0.98*
Mudumu 1	2	7	0.48	0.98*	Mudumu 2	Global	10	0.92	0.94*
Kafue 1	Global	6	0.99	0.70*	Mudumu 2	Global	6	0.53	0.94*
Lower Zambezi 2	Global	7	0.53	0.65*	Kafue 1	Global	6	0.86	0.90*
Lower Zambezi 4	2	6	0.73	0.81*	Kafue 2	2	7	0.66	0.98*
Quirimbas 2	2	6	0.64	0.82*					
South Luangwa 1	2	6	0.72	0.92*	Kafue 3	Global	7	0.80	0.73*
South Luangwa 2	2	6	0.80	0.98*	Kafue 4	Global	9	0.53	0.88*
South Luangwa 3	Global	7	0.62	0.98*	Vwaza 1	2	6	0.73	0.98*
South Luangwa 4	1	6	0.72	0.78*	Limpopo 1	Global	8	0.51	0.92*
South Luangwa 5	Global	6	1.00	0.88*					
North Luangwa 2	2	6	1.00	0.94*					
Vwaza 1	Global	8	0.67	0.97*					
Vwaza 2	2	6	0.70	0.87*					
Quirimbas 1	2	6	0.99	0.81*					

Appendix XIV**.** The beta coefficients (β) and standard errors (S.E.) from the top ranked wet season female habitat selection models comparing selection within and beyond PPAs. The explanatory variables included in the models were primary productivity (NDVI), the proportion of herbaceous cover (herb cover), the proportion of tree cover (tree cover), the slope of the terrain (slope), the distance to water (distance to water), and the distance to humans (distance to humans). Missing values (-) occur when the variable was not included in the top ranked model. Distance variables were multiplied by 0.1.

Within PPA

	Khaudum 1		Khaudum 2		Khaudum 3		Khaudum 4		Khaudum 5		Mudumu 1		Kafue 1	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-4.62	3.61	-6.48	2.81	-5.81	2.56	-12.98	3.85	4.04	2.64	-	-	-19.05	4.26
NDVI^2	-255.73	89,92	-	-	140.61	57.54	-	-	219.16	58.43	-	-	-	-
Herb cover	0.84	2.56	-101.83	52.79	-93.00	50.46	-	-	-124.13	50.22	-148.79	63.32	-	-
Herb cover^2	-	-	66.85	33.44	62.38	31.47	-	-	80.04	31.29	92.83	38.47	-	-
Tree cover	-	-	-	-	-	-	6.26	2.91	-	-	-	-	4.91	1.28
Tree cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	0.52	0.11	1.43	0.42	0.72	0.17	-	-	0.26	0.15	-	-	-	-
Slope^2 (°)	-	-	-0.48	0.17	-	-	-	-	-	-	-	-	-	-
Distance to water (km)	-2.83	0.78	0.83	0.19	-0.76	0.31	-0.73	0.86	-3.71	0.92	-2.23	1.08	3.20	1.62
Distance to water^2 (km)	1.82	0.59	-	-	1.96	0.65	1.20	0.49	2.95	1.05	2.11	0.78	-2.82	1.56
Distance to humans (km)	0.07	0.14	3.32	1.26	-0.45	0.15	-0.44	0.20	-3.34	0.79	-	-	-4.06	0.70
Distance to humans^2 (km)	-	-	-0.75	0.26	-	-	-	-	0.73	0.17	-	-	0.96	0.28

Within PPA

	Kafue 2		Kafue 3		Kafue 4		Lower Zambezi 2		South Luangwa 1`		South Luangwa 2		South Luangwa 3	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-18.80	3.06	-14.81	3.59	-28.73	3.66	-	-	8.99	3.14	-4.05	3.60	-	-
NDVI^2	-67.69	16.59	-	-	156.13	50.56	-	-	101.36	48.95	-132.95	48.86	-	-
Herb cover	-	-	-	-	-	-	-	-	-60.97	26.44	0.00	1.03	-	-
Herb cover^2	-	-	-	-	-	-	-	-	38.12	16.03	-	-	-	-
Tree cover	5.82	1.04	7.02	1.19	6.62	0.98	4.26	1.07	-	-	-	-	9.39	2.73
Tree cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-23.26	9.95
Slope (°)	-	-	-0.24	0.16	-	-	0.92	0.38	-	-	-	-	-0.27	0.18
Slope^2 (°)	-	-	-	-	-	-	-0.17	0.09	-	-	-	-	-	-
Distance to water (km)	1.64	0.72	-	-	4.71	1.34	-3.32	1.78	-2.22	2.05	0.93	1.03	-1.04	0.26
Distance to water^2 (km)	-	-	-	-	-5.92	1.56	-	-	-	-	-2.75	1.02	-	-
Distance to humans (km)	-4.54	0.55	-1.22	0.39	-1.92	0.26	1.18	0.30	-7.36	2.61	3.41	1.33	1.81	0.76
Distance to humans^2 (km)	1.09	0.20	0.15	0.08	-	-	-	-	6.19	2.00	-0.90	0.39	-0.78	0.35

Appendix XIV. Continued

	Within PPA											
	South Luangwa 4		South Luangwa 5		Vwaza 1		Vwaza 2		Quirimbas 1		Quirimbas 2	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	2.42	1.14	6.18	2.41	-14.68	3.35	-6.67	3.36	-25.02	9.40	19.21	12.29
NDVI^2	-	-	59.82	28.24	-	-	-	-	-772.81	307.15	716.82	385.98
Herb cover (%)	-3.81	1.38	4.46	2.02	-	-	-15.47	6.15	-	-	-	-
Herb cover^2 (%)	2.76	1.12	-	-	-	-	9.80	4.15	-	-	-	-
Tree cover (%)	-	-	-	-	10.77	3.77	-	-	-0.45	1.20	0.05	1.33
Tree cover^2 (%)	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	-1.15	0.31	0.06	0.02	-	-	-0.08	0.05	-	-
Slope^2 (°)	-	-	-	-	-	-	-	-	-	-	-	-
Distance to water (km)	-	-	-0.48	1.69	-5.00	0.49	-3.54	0.50	9.54	2.15	-	-
Distance to water^2 (km)	-	-	-	-	1.97	0.22	1.52	0.23	-9.90	2.49	-	-
Distance to humans (km)	-0.75	0.14	-6.46	1.66	5.65	2.01	-0.55	0.14	-	-	1.13	0.43
Distance to humans^2 (km)	-	-	3.42	1.23	-1.24	0.40	-	-	-	-	-	-

	Beyond PPA													
	Khaudum 2		Khaudum 4		Khaudum 6		Mudumu 1		Kafue 1		Lower Zambezi 1		Lower Zambezi 2	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	46.83	6.64	-0.29	4.56	-3.27	1.58	-15.85	2.17	-9.29	3.37	-	-	-	-
NDVI^2	-	-	-214.84	130.38	46.47	22.79	-293.21	37.46	-	-	-	-	-	-
Herb cover (%)	-	-	5.98	2.50	-150.03	36.72	-	-	-	-	-	-	-	-
Herb cover^2 (%)	-	-	-	-	97.58	23.49	-	-	-	-	-	-	-	-
Tree cover (%)	-10.89	4.56	-	-	-	-	4.45	0.70	6.69	2.00	2.71	0.66	2.31	0.70
Tree cover^2 (%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	1.00	0.33	-	-	0.50	0.22	-	-	3.97	0.97	-	-	-	-
Slope^2 (°)	-	-	-	-	-	-	-	-	-1.35	0.42	-	-	-	-
Distance to water (km)	13.36	3.15	-0.76	0.28	0.50	0.12	-	-	-1.59	0.48	2.59	1.63	-1.19	0.39
Distance to water^2 (km)	-2.40	0.65	-	-	-	-	-	-	-	-	-	-	-	-
Distance to humans (km)	-3.69	0.44	-	-	2.27	0.58	-0.13	0.07	-	-	-0.91	0.42	-	-
Distance to humans^2 (km)	-	-	-	-	-0.33	0.09	-	-	-	-	0.25	0.13	-	-

Appendix XIV. Continued

	Beyond PPA													
	Lower Zambezi 3		Lower Zambezi 4		Lower Zambezi 5		South Luangwa 1		South Luangwa 2		South Luangwa 3		South Luangwa 4	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-1.61	1.28	-	-	0.73	2.58	7.28	2.61	-6.77	1.64	-5.44	2.19	2.18	1.81
NDVI^2	-	-	-	-	-124.59	40.19	-21.80	33.29	-	-	-	-	-	-
Herb cover (%)	4.86	1.77	-	-	1.24	0.87	-1.08	0.96	-	-	-	-	1.40	0.81
Herb cover^2 (%)	-3.17	1.49	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover (%)	-	-	1.53	0.68	-	-	-	-	2.89	0.80	4.14	1.07	-	-
Tree cover^2 (%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	-0.06	0.02	-	-	-	-	-	-	-	-	-	-
Slope^2 (°)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Distance to water (km)	-0.34	0.55	-	-	-1.37	1.04	-2.58	0.49	-	-	3.93	1.33	4.00	0.81
Distance to water^2 (km)	-	-	-	-	2.69	1.16	-	-	-		-4.02	1.61	-4.11	0.74
Distance to humans (km)	2.80	0.66	4.28	0.55	-1.18	0.45	-2.01	0.29	7.33	0.99	-	-	-0.22	0.11
Distance to humans^2 (km)	-1.29	0.33	-1.44	0.20	0.34	0.11	-	-	-2.00	0.31	-	-	-	-

	Beyond PPA									
	South Luangwa 5		Vwaza 1		Vwaza 2		Quirimbas 1		Quirimbas 2	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	41.03	3.01	41.86	5.67	34.89	3.96	-	-	-	-
NDVI^2	156.25	16.69	166.40	25.67	145.15	20.18	-	-	-	-
Herb cover (%)	-	-	-	-	2.11	1.28	-	-	-1.12	0.84
Herb cover^2 (%)	-	-	-	-	-	-	-	-	-	-
Tree cover (%)	-9.30	1.19	8.66	4.81	-	-	1.48	0.90	-	-
Tree cover^2 (%)	-	-	-30.94	9.24	-	-	-	-	-	-
Slope (°)	-0.15	0.04	-	-	-	-	-	-	-0.14	0.05
Slope^2 (°)	-	-	-	-	-	-	-	-	0.00	0.00
Distance to water (km)	-5.62	0.60	-	-	-1.58	0.24	-0.58	0.13	-0.57	0.12
Distance to water^2 (km)	1.35	0.28	-	-	-	-	-	-	-	-
Distance to humans (km)	-	-	-5.10	0.67	-3.04	0.40	-		-	-
Distance to humans^2 (km)	-	-	-	-	-	-	-	-	-	-

Appendix XV**.** The beta coefficients (β) and standard errors (S.E.) from the top ranked wet season male habitat selection models comparing selection within and beyond PPAs. The explanatory variables included in the models were primary productivity (NDVI), the proportion of herbaceous cover (herb cover), the proportion of tree cover (tree cover), the slope of the terrain (slope), the distance to water (distance to water), and the distance to humans (distance to humans). Missing values (-) occur when the variable was not included in the top ranked model. Distance variables were multiplied by 0.1.

	Within PPA													
	Mudumu 1		Kafue 1		Kafue 2		Kafue 3		Vwaza 1		Quirimbas 1		Limpopo 1	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	28.48	6.07	9.91	4.29	-26.77	5.20	-28.50	3.58	-13.79	3.26	-6.75	3.37	4.18	1.48
NDVI^2	-	-	209.24	119.08	-	-	-	-	-	-	-	-	-	-
Herb cover	-	-	-	-	-	-	-	-	-1.20	0.54	-2.04	0.57	1.46	0.50
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	-10.58	5.70	-2.41	1.67	4.82	1.54	8.50	1.10	-	-	-	-	-	-
Tree cover^2	50.22	20.11	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	-	-	-	-	-	-	0.27	0.07	-	-	-	-
Slope^2 (°)	-	-	-	-	-	-	-	-	-0.02	0.01	-	-	-	-
Distance to water (km)	-6.49	1.34	0.54	0.15	2.50	1.36	-	-	0.69	0.51	0.64	0.10	1.17	0.44
Distance to water^2 (km)	2.61	0.87	-	-	-2.51	1.12	-	-	-0.82	0.25	-	-	-1.41	0.33
Distance to humans (km)	-8.34	2.07	0.27	0.12	-3.64	0.62	-2.31	0.33	4.23	1.00	-0.48	0.16	-0.28	0.49
Distance to humans^2 (km)	2.65	0.91	-	-	0.62	0.17	0.38	0.08	-0.92	0.21	-	-	0.54	0.22

	Beyond PPA													
	Mudumu 1		Mudumu 2		Mudumu 3		Kafue 4		Vwaza 1`		Quirimbas 1		Limpopo 2	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-	-	3.49	1.11	-14.95	2.42	-10.84	3.92	29.73	4.83	-21.67	6.53	7.45	2.59
NDVI^2	-	-	44.33	21.35	-420.59	50.19	-325.10	99.03	106.55	22.87	-604.94	190.15	-258.61	70.98
Herb cover	-	-	3.48	0.73	-	-	-24.05	8.21	-	-	31.39	10.60	-	-
Herb cover^2	-	-	-	-	-	-	13.18	5.46	-	-	-24.17	8.16	-	-
Tree cover	0.19	0.46	-	-	2.05	0.52	-	-	-5.81	1.26	-	-	2.84	0.97
Tree cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	0.06	0.06	-0.18	0.13	-0.67	0.23	-0.27	0.09	-	-	-0.57	0.10
Slope^2 (°)	-	-	-	-	-	-	0.12	0.05	-	-	-	-	0.02	0.01
Distance to water (km)	-1.61	0.19	-0.77	0.22	-0.29	0.05	-0.40	0.14	-	-	-	-	0.14	0.34
Distance to water^2 (km)	0.75	0.08	0.26	0.12	-	-	-	-	-	-	-	-	-	-
Distance to humans (km)	-0.60	0.07	-0.75	0.22	-	-	1.80	0.56	-2.10	0.42	4.55	1.17	-0.54	0.12
Distance to humans^2 (km)	-	-	0.22	0.07	-	-	-0.28	0.11	-	-	-2.41	0.49	-	-

Appendix XVI**.** The beta coefficients (β) and standard errors (S.E.) from the top ranked dry season female habitat selection models comparing selection within and beyond PPAs. The explanatory variables included in the models were primary productivity (NDVI), the proportion of herbaceous cover (herb cover), the proportion of tree cover (tree cover), the slope of the terrain (slope), the distance to water (distance to water), and the distance to humans (distance to humans). Missing values (-) occur when the variable was not included in the top ranked model. Distance variables were multiplied by 0.1.

	Within PPA													
	Khaudum 1		Khaudum 2		Khaudum 3		Khaudum 4		Khaudum 5		Khaudum 6		Mudumu 1	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	21.26	5.47	11.02	3.42	-0.02	4.75	3.13	4.13	-5.94	5.35	-1.92	4.88	-16.22	2.93
NDVI^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herb cover	-	-	-62.61	34.91	-	-	4.66	2.10	3.71	1.95	-	-	-	-
Herb cover^2	-	-	41.73	22.06	-	-	-	-	-	-	-	-	-	-
Tree cover	11.26	5.03	-	-	5.80	3.31	-	-	-	-	3.58	1.19	22.04	4.44
Tree cover^2	-79.83	30.93	-	-	-	-	-	-	-	-	-	-	-72.56	19.70
Slope (°)	0.85	0.31	1.00	0.26	-	-	-	-	-	-	0.87	0.27	-	-
Slope^2 (°)	-0.21	0.10	-0.23	0.08	-	-	-	-	-	-	-0.19	0.09	-	-
Distance to water (km)	-2.83	0.47	-5.73	0.77	-4.16	1.02	-2.13	0.72	-6.22	1.17	-0.69	0.35	-	-
Distance to water^2 (km)	-	-	4.28	0.76	3.03	1.22	1.75	0.55	6.27	1.62	-	-	-	-
Distance to humans (km)	2.33	0.60	0.04	0.08	1.12	0.34	0.76	0.12	-	-	2.36	0.57	-1.60	0.19
Distance to humans^2 (km)	-0.62	0.15	-	-	-0.30	0.10	-	-	-	-	-0.71	0.15	-	-

	Within PPA													
	Kafue 1		Kafue 2		Kafue 3		Kafue 4		Lower Zambezi 1`		Lower Zambezi 2		Lower Zambezi 3	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	19.22	5.29	4.05	3.28	4.51	3.41	-5.17	3.12	-2.79	2.93	-2.58	2.37	-7.86	2.43
NDVI^2	-418.93	114.90	-159.15	77.97	-190.11	92.74	-	-	-	-	-	-	-	-
Herb cover	-1.78	1.34	-	-	-	-	-2.53	0.85	-0.65	0.77	-	-	-	-
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	-	-	1.42	0.64	2.42	0.87	-	-	-	-	0.26	0.89	2.63	1.10
Tree cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	0.16	0.09	0.85	0.43	-	-	-	-	-0.60	0.28	-	-
Slope^2 (°)	-	-	-	-	-0.25	0.14	-	-	-	-	0.12	0.05	-	-
Distance to water (km)	-7.53	3.87	1.27	0.85	-3.54	1.03	-0.14	0.64	-4.46	1.02	-5.53	1.37	-16.17	3.67
Distance to water^2 (km)	17.57	8.44	-	-	2.17	0.82	-	-	-	-	-	-	21.55	10.35
Distance to humans (km)	-9.44	1.80	-1.70	0.35	-0.68	0.36	1.63	0.62	-1.32	0.32	11.67	1.90	2.63	0.79
Distance to humans^2 (km)	6.15	1.42	-	-	0.13	0.07	-0.88	0.29	-	-	-2.83	0.43	-1.07	0.25

Appendix XVI. Continued

	Within PPA													
	Lower Zambezi 4		South Luangwa 1		South Luangwa 2		South Luangwa 3		South Luangwa 4		South Luangwa 5		North Luangwa 1	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-1.52	1.99	10.39	2.67	-14.42	2.74	13.22	3.55	-	-	-	-	-10.36	4.11
NDVI^2	-	-	293.72	68.42	-324.65	54.15	-174.55	98.67	-	-	-	-	-	-
Herb cover	-2.50	0.82	2.09	0.94	-	-	-	-	-	-	0.55	1.85	2.24	0.83
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	-	-	-	-	6.52	0.90	-	-	-	-	-	-	-	-
Tree cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	-	-	-0.22	0.12	0.48	0.16	1.14	0.52	0.35	0.13	-	-	-0.17	0.10
Slope^2 (°)	-	-	-	-	-	-	-0.54	0.25	-	-	-	-	-	-
Distance to water (km)	-7.99	2.29	0.67	0.38	1.03	0.44	-2.23	0.34	1.59	0.22	-14.99	4.72	-1.61	0.33
Distance to water^2 (km)	15.71	5.72	-	-	-	-	-	-	-	-	38.54	15.26	-	-
Distance to humans (km)	-2.89	0.82	-2.53	0.29	-1.29	0.67	-	-	-0.47	0.19	-	-	3.81	0.77
Distance to humans^2 (km)	1.58	0.45	-	-	0.96	0.28	-	-	-	-	-	-	-0.63	0.16

	Within PPA									
	North Luangwa 2		North Luangwa 3		Vwaza 1		Vwaza 2		Quirimbas 1`	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-6.90	3.96	-	-	41.71	4.54	-15.39	2.66	4.91	9.86
NDVI^2	-441.09	112.88	-	-	-99.71	43.81	-	-	-	-
Herb cover	-	-	-	-	-	-	-34.98	8.16	-	-
Herb cover^2	-	-	-	-	-	-	22.78	5.51	-	-
Tree cover	0.88	1.41	12.29	3.09	-1.45	0.86	-	-	6.32	2.64
Tree cover^2	-	-	-24.65	6.97	-	-	-	-	-	-
Slope (°)	-	-	-	-	-0.06	0.03	0.12	0.08	-0.07	0.04
Slope^2 (°)	-	-	-	-	-	-	-0.01	0.01	-	-
Distance to water (km)	17.63	5.37	4.27	1.35	-9.80	1.57	1.70	0.73	-	-
Distance to water^2 (km)	-39.31	16.47	-13.50	2.39	5.40	0.98	-1.42	0.37	-	-
Distance to humans (km)	23.62	8.03	-12.38	2.10	45.52	5.02	-15.34	1.98	41.50	17.40
Distance to humans^2 (km)	-9.46	3.36	4.53	0.87	-8.99	0.95	3.04	0.39	-10.89	4.10

Appendix XVI. Continued

Beyond PPA

	Khaudum 5		Mudumu 1		Kafue 1		Lower Zambezi 2		Lower Zambezi 4		South Luangwa 1		South Luangwa 2		South Luangwa 3	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	23.03	8.58	-6.65	5.28	-11.84	10.98	24.66	7.87	6.02	3.82	18.69	6.21	-12.19	2.61	7.14	4.35
NDVI^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herb cover	-	-	-	-	-	-	1.50	0.78	0.64	0.54	-2.91	1.56	-	-	-	-
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	8.81	2.00	29.39	10.27	7.39	2.05	-	-	-	-	-	-	1.77	1.00	13.96	3.58
Tree cover^2	-	-	-76.25	29.93	-	-	-	-	-	-	-	-	-	-	-31.09	8.38
Slope (°)	-0.49	0.34	-	-	4.49	1.42	0.30	0.20	-	-	-	-	1.42	0.58	0.17	0.15
Slope^2 (°)	-	-	-	-	-1.89	0.70	-	-	-	-	-	-	-0.74	0.35	-	-
Distance to water (km)	32.80	5.64	2.25	0.86	-	-	-10.35	3.14	-1.46	1.01	1.70	0.57	1.92	0.22	-	-
Distance to water^2 (km)	-6.80	1.19	-0.71	0.21	-	-	-	-	-	-	-	-	-	-	-	-
Distance to humans (km)	-	-	-1.13	0.58	-1.91	0.79	50.55	12.92	2.46	1.30	-8.47	1.82	-	-	-2.56	0.64
Distance to humans^2 (km)	-	-	-	-	-	-	-15.32	3.94	-1.24	0.48	3.64	1.63	-	-	0.94	0.32

Beyond PPA

	South Luangwa 4		South Luangwa 5		North Luangwa 2		Vwaza 1`		Vwaza 2		Quirimbas 1		Quirimbas 2	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-5.73	3.62	6.28	2.75	2.42	5.22	21.61	6.24	-	-	-7.69	2.34	-7.04	2.23
NDVI^2	-	-	176.97	46.89	-	-	-	-	-	-	-	-	167.07	50.53
Herb cover	-	-	-	-	-	-	-51.10	27.15	-	-	-24.67	8.74	-2.17	0.78
Herb cover^2	-	-	-	-	-	-	33.38	16.51	-	-	15.29	6.20	-	-
Tree cover	-4.43	2.78	-1.80	1.05	7.28	3.40	-	-	1.85	1.53	-	-	-	-
Tree cover^2	16.69	6.25	-	-	-33.97	10.99	-	-	-	-	-	-	-	-
Slope (°)	-	-	-0.13	0.03	-	-	0.35	0.23	-	-	0.05	0.02	0.03	0.02
Slope^2 (°)	-	-	-	-	-	-	-0.05	0.03	-	-	-	-	-	-
Distance to water (km)	-11.85	0.81	-	-	-8.45	1.67	-7.90	5.02	-13.14	5.86	-0.44	0.13	-0.55	0.12
Distance to water^2 (km)	9.53	0.89	-	-	-	-	-	-	53.45	20.67	-	-	-	-
Distance to humans (km)	-	-	-1.08	0.19	3.40	0.81	-2.29	0.52	-22.20	3.58	-	-	-	-
Distance to humans^2 (km)		-	-	-	-	-	-	-	3.94	0.66	-	-	-	-

Appendix XVII. The beta coefficients (β) and standard errors (S.E.) from the top ranked dry season male habitat selection models comparing selection within and beyond PPAs. The explanatory variables included in the models were primary productivity (NDVI), the proportion of herbaceous cover (herb cover), the proportion of tree cover (tree cover), the slope of the terrain (slope), the distance to water (distance to water), and the distance to humans (distance to humans). Missing values (-) occur when the variable was not included in the top ranked model. Distance variables were multiplied by 0.1.

Within PPA

	Mudumu 1		Mudumu 3		Kafue 1		Kafue 3		Vwaza 1		Limpopo 1	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-64.96	7.78	-	-	2.80	3.12	18.78	4.27	0.63	2.02	-17.30	1.54
NDVI^2	195.76	52.13	-	-	-165.30	67.06	-140.69	63.60	-84.38	34.75	-87.22	17.74
Herb cover	-	-	-	-	-	-	-0.63	1.05	-	-	-	-
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	19.81	3.14	14.91	4.66	2.33	0.89	-	-	-0.56	0.52	-1.04	2.07
Tree cover^2	-	-	-46.98	22.42	-	-	-	-	-	-	13.42	3.78
Slope (°)	1.96	0.44	-0.15	0.27	-0.26	0.15	-0.70	0.38	0.09	0.05	-0.28	0.05
Slope^2 (°)	-	-	-	-	-	-	0.23	0.10	-0.01	0.00	-	-
Distance to water (km)	-12.53	1.79	-0.12	0.09	-0.01	0.24	-0.99	1.00	1.08	0.51	-4.89	0.64
Distance to water^2 (km)	4.36	0.65	-	-	-	-	-	-	-0.58	0.21	1.80	0.62
Distance to humans (km)	-10.99	4.62	5.13	1.91	-1.36	0.51	-9.59	1.10	-0.12	0.13	-0.27	0.17
Distance to humans^2 (km)	5.40	2.13	-3.22	0.92	0.27	0.13	4.32	0.69	-	-	-	-

Beyond PPA

	Mudumu 1		Mudumu 2		Mudumu 3		Kafue 1		Kafue 2`		Kafue 3		Kafue 4	
Explanatory variable	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.	β	S.E.
NDVI	-5.91	0.80	-17.62	1.40	-	-	1.08	3.39	8.45	4.43	-19.84	10.22	-1.14	3.62
NDVI^2	68.30	8.40	-91.02	12.95	-	-	-	-	-	-	-	-	-351.38	101.92
Herb cover	-0.48	0.71	-	-	-	-	-	-	-	-	-	-	-	-
Herb cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tree cover	-	-	24.36	2.12	2.49	1.23	6.48	1.27	4.46	1.13	2.23	1.91	11.68	3.04
Tree cover^2	-	-	-24.94	4.49	-	-	-	-	-	-	-	-	-16.05	5.96
Slope (°)	1.04	0.23	-1.29	0.54	-0.62	0.34	1.03	0.45	-	-	0.74	0.26	-0.14	0.10
Slope^2 (°)	-0.31	0.09	0.97	0.35	-	-	-0.25	0.12	-	-	-	-	-	-
Distance to water (km)	-2.80	0.42	-0.87	0.49	3.17	0.67	-	-	2.77	1.88	-4.67	2.63	-1.10	0.69
Distance to water^2 (km)	2.18	0.32	-	-	-1.17	0.27	-	-	-6.69	3.17	7.53	3.15	-	-
Distance to humans (km)	-3.46	0.49	0.16	0.67	-0.67	0.39	-1.79	0.48	11.59	3.37	-1.16	0.98	9.41	2.44
Distance to humans^2 (km)	1.12	0.29	-0.78	0.32	-	-	-	-	-9.73	3.21	-	-	-8.04	2.24

Appendix XVII. Continued

Beyond PPA				
	Vwaza 1		Limpopo 2	
Explanatory variable	β	S.E.	β	S.E.
NDVI	36.00	8.52	-10.98	2.22
NDVI^2	293.89	81.47	248.20	45.37
Herb cover	-	-	-	-
Herb cover^2	-	-	-	-
Tree cover	-6.34	1.70	2.84	0.91
Tree cover^2	-	-	-	-
Slope (°)	-	-	-0.12	0.08
Slope^2 (°)	-	-	-	-
Distance to water (km)	-3.70	1.28	-5.60	0.94
Distance to water^2 (km)	-	-	6.16	1.32
Distance to humans (km)	-1.89	0.51	-1.32	0.13
Distance to humans^2 (km)	-	-	-	-