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EFFECTS OF ENCLOSURE ON HOME RANGE AND RESOURCE SELECTION: A COMPARISON OF TWO AFRICAN ELEPHANT HERDS (*Loxodonta africana africana*)

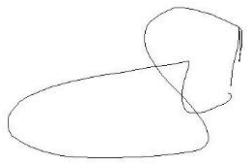
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A research report submitted to the Faculty of Science, University of the Witwatersrand, in partial fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 1 December 2013

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Masters of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



1 December 2013

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ABSTRACT

Enclosed game reserves are at risk of local vegetation over-utilization and homogenization by elephant. Understanding how the elephant spatial distribution is coupled to their seasonal resources use can aid future management given the threat of climate change.

A comparison of home ranges and core area sizes across seasons and years was made between an elephant herd outside in an open system, compared to the elephant inside Limpopo Lipadi Game and Wilderness Reserve (LLGWR). Location data, obtained by GPS-GSM technology, was used to determine seasonal home ranges and core areas by local convex hull (LoCoH) methods and to generate seasonal General Estimating Equations (GEE). Remote sensing data was used to determine habitat variables.

The home ranges of the elephant herd outside as expected, was twice as large during summers and a third larger during winters than the elephant herd inside the fenced reserve. The influence of seasonal rainfall on home range size was reflected at home range scale for the outside herd and for the core area scale for the herd inside the reserve. Increased rainfall overcomes the 'magnet effect' of artificial waterholes on elephant distribution in the landscape only in the open system. Inside the reserve, contrary to expectation the winter home ranges were non-significantly larger than summer home ranges due to space limitation induced by fencing and permanent artificial waterhole density.

Resource use was evaluated by using GEE models at a scale larger than established home ranges and therefore would reflect as home range determinants. The study confirms that elephant do not use resources randomly. A scale in resource selection of elephant cows exists, with distance to drainage lines at small scale preferred during winter, with aspect, slope, elevation, and NDVI at larger scales. Fencing furthermore, affects the scale at which selection occurs by limiting resource availability, especially during resource restrictive periods and limits range expansion during resource abundant periods. Elephant cows prefer gentle terrain, close to permanent water [<1.77km (SD$\pm$0.554) inside the reserve, and <2.33km (SD $\pm$ 2.13) outside the reserve], moderately high NDVI, riparian vegetation during late winter and early summer if available. Generally, during lower rainfall periods lower elevations are preferred along the elevation gradient, and during higher rainfall periods, higher elevations.

The elephant herd outside the reserve, furthermore prefer aspects in the landscape during hot summers that are cooling and cool winter aspects that are warming to facilitate energy saving and thermoregulation.

Key words: Elephant home range, core areas, fencing, seasonal, artificial waterholes, open system, NDVI, elevation gradient, distance to water, seasonal GEE modelling.

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1. INTRODUCTION

Elephants, as 'ecosystem-engineers', can alter their habitat (Jones *et al*. 2007; O'Connor *et al*. 2007). Understanding the seasonal distribution and resource use of a generalist, highly mobile and water dependant mega–herbivore species such as the African savanna elephant (*Loxodonta africana africana*, Blumenbach 1797) remains an adaptive management challenge in open areas and even more so in enclosed protected areas (Chamaillé-Jammes *et al*. 2008; Rogers 2003a, Rogers 2003b). Enclosed fenced areas can influence the seasonal resource variability and availability and furthermore limit elephant movement and distribution in the landscape.

The home range concept is used in this study to reflect the seasonal distribution at a spatial scale smaller than geographical scale (Johnson 1980; Senft *et al*. 1987). The size and shape or conformation of an elephants' home range reflects the movement and distribution patterns associated with its dynamic interaction with the biotic and abiotic environment, at various scales to meet nutritional, social, and physiological requirements (Osborn 2004; Kinahan *et al*. 2007; de Beer and Van Aarde 2008; De Knegt *et al*. 2010). Therefore, the dynamic relationship between the home range, space and resource use *per se* within the context of enclosure, needs to be given greater consideration given the vegetation management challenges (Reiss 1988; Morrison 2001; Osborne 2004; Mitchell and Powell 2004; Borger *et al.* 2008).

Poole (1996) defined a ‘family unit’ as the basic unit of elephant society which consists of an individual female and her dependent offspring. In this study, the elephant family unit and their spatial and temporal patterns of resource use will be identified to determine present and future areas of vegetation impact. Secondly, quantifying, important seasonal biotic and abiotic home range determinants for elephant. Both these broad factors could be influenced by fencing and contribute to the seasonal home range conformation. The trend in the literature is that home range size relates non-linearly to time, increased vegetation heterogeneity and vegetation productivity (McLoughlin and Ferguson 2000; Osborn 2004; Ntumi *et al*. 2005; Grainger *et al.* 2005, Murwira and Skidmore, 2005; De Beer and Van Aarde 2008). In addition, resource availability, sex, body size, and disturbance also influence home range size and shape (Harestad and Bunnel 1979; Reiss 1988; Swihart *et al*. 1988; Osborne 2004; Stokke and Du Toit, 2004). Furthermore, range expansion of the home range is determined by available space, rainfall, and forage quality and quantity (Osborne 2004; Murwira and Skidmore 2005; Young *et al*. 2009). Generally, therefore, increased home range sizes can be expected in open, drier savannas.

Core areas are areas within the home range which are not used with equal intensity (Powell 2000). Furthermore, elephants spend proportionately more time in these more productive areas within their home range and therefore potentially can affect the vegetation adversely, even extirpation of some species close to water (O’Connor *et al*. 2007; Kerley *et al*. 2008). These effects on vegetation are potentially exacerbated in smaller enclosed areas due to the absence of refugia

areas for vegetation (Johnson 1980; Gaylard *et al*. 2003; Douglas-Hamilton *et al*. 2005; O'Connor *et al*. 2007; Kerley *et al*. 2008). Many authors recognize the importance of the concentration and distribution of water points, artificial or natural, in shaping the seasonal distribution of elephants in the landscape; and influencing the core area and home range size (Stokke and Du Toit 2002; Gaylard *et al*. 2003; Shannon *et al*. 2006; Chamaillé-Jammes *et al*. 2007; Smit *et al*. 2007; De Beer and Van Aarde 2008; Harris *et al*. 2008; Roux and Bernard 2009; Loarie *et al*. 2009; De Knegt *et al*. 2010).

Large herbivores in semi-arid savannas are dependent on resource distribution which varies in space and time. Therefore, resource use cannot be random and is dependent on selection of areas which give the highest return in nutrients per unit of foraging time or alternatively energy expenditure constraints. However, patterns of resource selection are complex, and not only dependant on scale and seasonal availability of resources but also on social factors, disturbance, and density dependence factors (Mitchell and Powell 2004; McLoughlin *et al*. 2010). My definition of resources is similar to Morrison (2010) which is; any biotic or abiotic factor that would influence the fitness of the organism. Furthermore, use of a resource is defined as the quantity of resources utilized in a fixed period of time, and availability is defined in terms of accessibility in the study area to the elephant cow (Johnson 1980). Because of the consistent relationship between body size and metabolism, this predicts that larger areas with low and fragmented resource concentrations are required to fulfil the metabolic needs of larger mammals (Du Toit 1990; Haskell *et al*. 2002). Furthermore, according to Ritchie

and Olff (1999) resource density and distribution is scale dependant, and their spatial distribution can be described with fractal geometry or simple scaling laws. Due to this rule, larger species like elephant would detect the larger patches of resources, but lower resource concentrations within their food will be tolerated. Resource selection by elephants therefore is a hierarchy of choices (Johnson 1980; Senft *et al.* 1987; Wu and Loucks 1995, Ritchie and Olff 1999; Haskell *et al.* 2002). Space limited areas therefore are expected to show differences in selection of resources due to the effect on resource distribution and availability, in comparison to open systems. Enhanced understanding of how elephants utilize available space with fluctuating resources to secure sufficient nutrition in time and space can aid improved management inside and outside protected areas.

The original 'functional response' definition of Hollings (1959) is when the consumption rate of prey (resource) by a predator (herbivore) is described in relation to prey density (Spalinger and Hobbs 1992). More recently, this definition has evolved into use by explaining herbivore-vegetation interactions, where changes in preference of resources occur as a function of resource availability (Mysterud and Ims 1999; Noy-Meir 1975; Rowcliffe et *al*. 1999; Owen-Smith 2002; Roever *et al*. 2012).

Given the challenges of understanding the seasonal distribution of elephant herds related to their resource distribution, in context of the effect of enclosure, the study was undertaken. The first objective in the study is determining the influence of enclosure on space use by elephant. To achieve this objective, I compared

seasonal home range sizes, core area sizes, and resource selection of two elephant herds in different environmental conditions. One herd enclosed inside a reserve (Limpopo-Lipadi Game and Wilderness Reserve) and another outside the reserve (that previously had been in the reserve). My prediction, in this semi-arid savanna, is the summer home ranges and core areas will be larger than winter home ranges since ephemeral rivers and pans might allow breeding herds to roam in search of better quality forage. Furthermore, the second prediction is that the home range size inside the reserve is smaller comparing similar seasons, than the home ranges of the herd outside, without movement constraints imposed by fencing. The second objective is to quantify specific resources used based on Generalized Estimating Equations (GEE) and to highlight seasonal resource utilization differences inside and outside the reserve based on availability differences due to fencing.

2. METHODS

2.1 Study area. The study area is part of the Greater Limpopo Basin. The study areas' (-22^0 33'S; 28^0 90'E and -22^0 11' S; $28^0$55'E) southern boundary is the Limpopo River and northern border, the Motloutse River in South Eastern Botswana (Figure 2.1). The study inside the new Limpopo-Lipadi Game and Wilderness Reserve (LLGWR; 295.50 km^2) and adjacent area (955.23 km^2), was from April 2008-September 2010. The ecoregion is part of the Southern African Bushveld and occurs on an undulating interior plateau, at an elevation of 380 – 1100m. Cowling *et al.* (1997) divides the general vegetation into a generalized 'mixed savanna' and 'mopane savanna'. The summer, being the

wet season, is from November to March, with an annual average rainfall of 360 mm $year^{-1}$ (Table 2.1, 2008); with day-time ambient temperatures from 38^{o}C to 46^{o}C with night temperatures that seldom fall below 15^{0}C. The dry season, in winter, occurs from April to September with the general temperature ranging from – 3^{0}C to 45^{0}C with a 21^{0}C average. The mopane, *Colophospermum mopane*, shows plasticity in growth form from shrub to trees, with the coppicing shrubland having its origins from elephant over browsing (R. Scholes *pers. comm.*, Figure 2.2) and covers an estimated 30% of the size of the reserve (29550 ha). The soils are generally coarse, sandy and shallow (luvisols and regosols), overlying granite, quartzite, sandstone, or shale. Like in most small to medium sized reserves, the elephant density and effect on localized vegetation around water sources remains a concern for reserve management.

*2.2 Elephant location data***.** Space and habitat use by elephants in the LLGWR was inferred from locations obtained by geographic positioning system (GPS) tracking collars (Hawk 105, Africa Wildlife Tracking, Pretoria, South Africa) having an estimated accuracy of <8m. Furthermore, GPS fixes were transmitted via a cellular phone (GSM) system to a website, from which this data was retrieved after permission was obtained from reserve management. Locations were recorded at 3 hourly intervals. Two elephant cows were collared, one with a calf and another matriarchal cow of a different herd. A veterinarian immobilized the elephants with M99 (etorphine hydrochloride) at 14mg, 40mg azaperone (sedative) and 3000 i.u. of hyalase on

the 6th April 2008. Both herds were in the protected area for eighteen months prior to capture. However during the end of November 2008, one collared cow and family unit escaped the reserve and has been roaming in communal-, wildlife management areas and Tuli River Lodge.

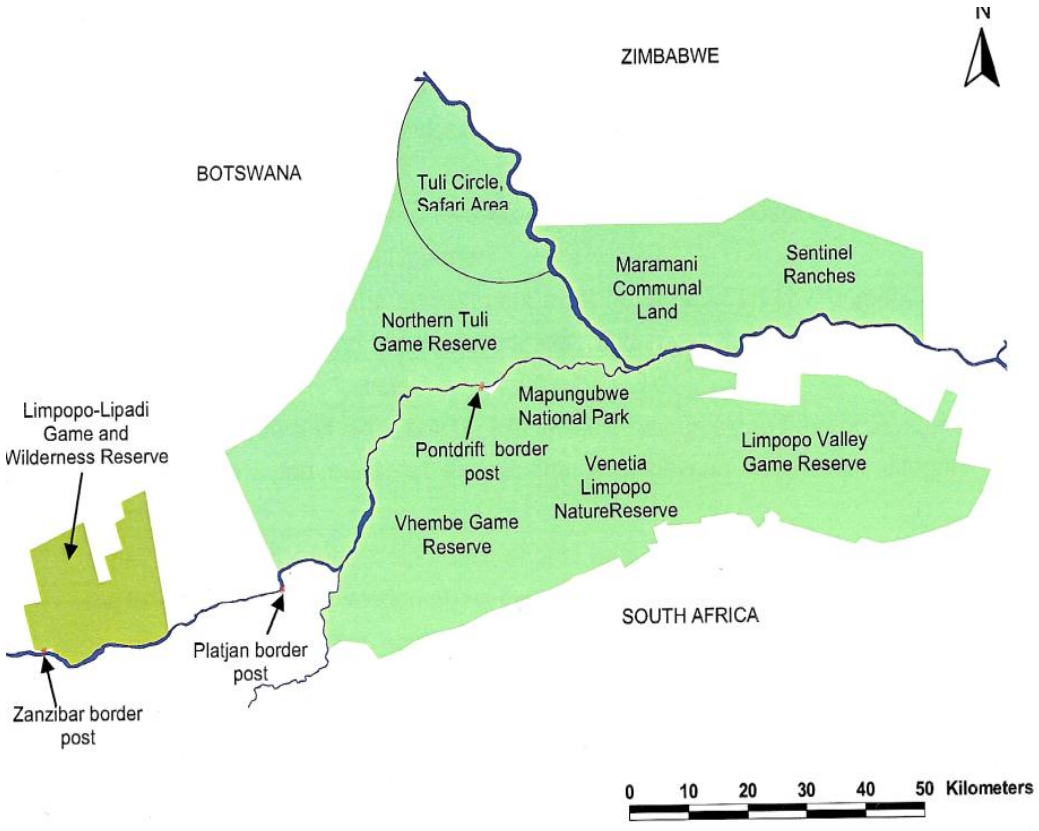


Figure 2.1: Location of the Limpopo-Lipadi Game and Wilderness Reserve in relation to other protected Trans Frontier Conservation Areas in Botswana, South Africa and Zimbabwe (From: Environmental Management Plan Limpopo – Lipadi, 2006).

The herd that escaped (collar identification 313) outside, although contributing to only one season data inside the reserve (winter 2008), will be compared to the herd that remained inside the reserve during the study period (collar identification 312). In addition, the riparian corridor was fenced off to limit westward movement along the Limpopo River during end of September 2009

at the Saambou Bridge. Although only two individual mature cow elephants were marked, their movements were expected to resemble those of a family unit due to the social nature and structure of elephant (Galanti *et al*. 2000; Polansky and Wittermeyer 2011).

Table 2.1: Mean monthly rainfall figures in the study area from 2008-2010

Month	Mean Rainfall (mm) 2008	Mean Rainfall (mm) 2009	Mean Rainfall (mm) 2010
January	136	221	66.75
February	55	32.6	30.25
March	7	56	*84*
April	16	0	*141*
May	19	11.6	*12.25*
June	0	16.5	0
July	0	0	0
August	0	0	0
September	0	7.6	7.6
October	24.4	9.8	12.3
November	46	70.8	58.2
December	61.4	109.5	246.8

2.3 Habitat model. I developed a multi-grain (multiple scale parameters) habitat model using ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, California, USA) and ET Geowizards (ET Spatial Techniques) from all geographical data based on elephant location data and important environmental parameters that could influence home range size, shape, and reflect resource use at

varied temporal and spatial scales. These included raster model of indices of vegetation productivity (represented by Normalized Difference Vegetation Index; NDVI), slope, aspect and elevation and vector models of distance to water, and distance to drainage lines, were incorporated in the seasonal models as independent variables. I used these six geographic-information-system (GIS) layers to represent biotic and abiotic components of resources. The consistent coordinate system used was WGS 1984 and projected to UTM 35S (Rahimi and Owen-Smith 2007; B. Erasmus *pers. comm*.).

2.3.1 NDVI. I used MODIS imagery (MODerate Resolution Imaging Spectroradiometer) as a measure of spatial and seasonal vegetation productivity and, hence, available green biomass (Huete *et al*. 2002; Pettorelli *et al*. 2005; Muriwa and Skidmore 2005). The NDVI data from April 2008 to September 2010 obtained is at a spatial resolution of 250 m, with NDVI values calculated from 16 day composites with a range of 0-1, where the larger values represent the greenest vegetation. The mean of the summed maximum NDVI values for the seasons was calculated, furthermore choosing maximum NDVI limits cloud noise (Young *et al*. 2009; B. Erasmus *pers. comm*.). Additionally the NDVI values ranged from 75-207 (without units) over all seasons and was converted to 5 equal classes in ArcGIS 9.3.1.

2.3.2 Elevation, slope and aspect. Raster digital elevation model (DEM) at 90 m resolution was obtained for the locations from the Earth Remote Sensing Data Analysis Centre (ERSDAC) DEM. The Spatial Analyst Extension for Arc Map 9.3.1 was used to determine elevation, slope and aspect from the DEM.

The aspect was categorical data divided into five classes (SE-E, SW-W, NE-E, N-NW and Flat), i.e. where the elephant was either present or absent. Elevation with a range of 395 m to 1692 m was also divided also in five equal classes. Slope range from $0\text{-}49^0$ was also classified into five equal classes - ArcGIS 9.3.1 (ESRI, Redlands, CA, USA).



Figure 2.2: Vegetation and waterhole in the uplands, outside the reserve (June 2009) showing *Combretum* spp. and *C. mopane* broadleaved woodland on sandy soils (luvisols and regosols). Note the vegetation *C. mopane* browsed to a consistent height of estimated 1.4m by elephant (Leonard©).

2.3.3 Distance to closest water and drainage lines. Artificial waterholes supply water year round as well as the perennial Limpopo River for the herd outside the reserve. Pans and earth dams were assumed to continue providing water during summer only. I did not distinguish between water types, just water sources separating winter from summer sources (Figure 2.2). Locations of all water points, including pans and earth dams were identified by local knowledge, management maps of the reserve and ground-truthed with a GPS (Garmin Oregon

300). Google Earth was also used since pans are permanent geological structures. Locations were subsequently transferred to ArcGIS 9.3.1 to create a vector layer of closest water. Hawth's Analysis Tools and ET Geowizards (ET Spatial Techniques) were used to extract values on the specific use/availability location points from all the ArcGIS layers. The drainage lines were all digitized from the ERSDAC DEM, and Google Earth was georeferenced using Elshayal Smart GIS version 4.1 software obtained from the web (SmartWebOnLine.com).

2.4 Rainfall. Daily rainfall data was obtained from the average of the six stations across the study area for the duration of the study period determined. Standard rainfall gauges were used.

2.5 Analysis

2.5.1 Determining elephant home ranges and core areas

The locations of the elephant cows were converted to WGS84 UTM 35S datum (Rahimi and Owen-Smith, 2007; B Erasmus *pers comm*.). The Local Convex Hull (LoCoH) 'fixed-k' method, interfaced with ArcMap 9.3, was used to calculate the seasonal home ranges (95% isopleths) and core areas (50% isopleths) using the elephant location data (Getz and Wilmers 2004; Douglas–Hamilton *et al.* 2005; Getz *et al*. 2007). The year was divided in two based on rainfall: the wet season (October – March) and the dry season (April - September).

Comparisons of home ranges and core areas sizes were made. Firstly, comparing seasonal sizes inside (and also outside the reserve), and secondly,

seasonal sizes inside with those outside the reserve. Lastly, between seasonal home ranges and core areas inside with those outside the reserve after pooling the seasons. Non-parametric Kruskal-Wallis (Median, Van Der Waeden and Savage analysis) will be used to compare home range and core area sizes (SAS v 9.3, SAS Inst, Cary, NC). Pearson correlations between rainfall, home ranges, and core areas were determined.



Figure 2.3: This illustrates the effect on large trees prior to elephant population reduction in the LLGWR from 88 to 36, before November 2008 during the winter of 2008 (Leonard©).

In addition, Pearson correlations between all other variables (NDVI, distance to water, and distance to drainage lines, slope, aspect, and elevation) were also determined to reflect possible associations.

2.5.2 Statistical method and model

Manly (2002) defined resource selection functions (RSF) as statistical models which characterize the probability that a resource unit is used, or alternatively avoided by elephant cows under study. In addition, RSF describes the utilization of resources and space (Meyer and Thuiller 2006), quantifies habitat selection (McLoughlin *et al*. 2010) and can incorporate multiple scale parameters (multi-grain) in the same model. The seasonal RSF models used in this study therefore will aid in answering the questions surrounding spatial scale related, and seasonal preference or utilization of resources (Figure 2.3). Availability and scale of resources are indispensable in RSF applications, since sampling scale can influence strength of habitat associations and recognition that habitat selection occurs along scales of space and time (Wu and Loucks 1995; O'Neill *et al*. 1996; Boyce 2006; Meyer and Thuiller 2006; Beyer *et al*. 2010; De Knegt *et al*. 2010).

In this study to obtain the RSF, the use-availability design was used to determine the probability of use (or avoidance) of selected resources, which were also considered specific home range determinants at the applied scale of study (Alldredge *et al*. 1998; Beyer *et al*. 2010). By definition, when use is greater than what is randomly available, resources are considered to be selected, while when availability is greater than what is used; resources are considered to be avoided (Manly *et al*. 2002).

Because home ranges already includes resources and landscape attributes that an elephant has selected, whereas other avoided features lie outside the home range.

Therefore basing resource availability contained only within the home range is tautological, as some selection for resources has already occurred (Kie *et al*. 2002). Therefore, the spatial scale selected for available resources were larger than the home ranges, otherwise analysis of resource selection within the home range (third-order selection, Johnson 1980) may produce biased results. In addition, the RSF can also now be regarded as home range determinants. Furthermore, the temporal scale was selected based on seasonality, inferred from rainfall.

The data of elephant locations in the landscape occurs sequentially (every 3 hrs) and is correlated in time and space. In this paper, it is accepted that the elephant locations have some dependency and the GLIMMIX (SAS v 9.3, SAS Inst, Cary, NC) extends the GLM by actually incorporating the correlations among the responses. The correlation in time is not eliminated by reduction to the original data location points from 3 to 4 hours in time (Cushman *et al*. 2005; Dormann *et al*. 2007; Koper and Manseau 2010). Therefore, I used a Generalized Estimating Equation (GEE) model with a classical sandwich estimator, in PROC GLIMMIX (SASv 9.3, SAS Inst, Cary, NC) to accommodate the dependence of data problem (Liang and Zeger 1986; Johnston and Stokes 1996; Johnston undated; Kachman, 2000; Schabenberger 2005; Flom *et al.* 2006; Gillies, 2006; Carl and Kuhn 2007; Aarts *et al* 2008; Bolker *et al*. 2008; SAS, 2007; Koper and Manseau 2009; Duchesne *et al*. 2010; Isik 2011).

A final model was selected, screened from sub-models produced by PROC GLMSELECT (SAS v 9.3, SAS Inst, Cary, NC) using general linear modelling by backward selection, with fivefold k validation (the data was randomly subdivided reserving 50% for training, and 25% each for validation and testing); significance levels and ASE (average square error) to give an indication which parameters were indeed significant. The fit statistic of the model; the ratio of generalized Chi square (a quadratic form in marginal residuals that takes correlations into account) to degrees of freedom had to be as close to one as possible to rule out model under- or over dispersion.

The next step was to use this final model, for each season and elephant cow selected, in PROC GLIMMIX to produce the significant odds ratios, which are the resource selection functions of Manley *et al*. (2002). Furthermore, these final seasonal models were used to determine how the degree of use varied with changes in greenness (NDVI), distance to drainage lines, slope, aspect, and elevation. The model produced was based on *use* (GPS location points) and *availability* (randomly generated points) design, using modified logistic regression with logit link function (Alldredge *et al* 1998; Manley *et al*. 2002).

Random locations were generated using ArcGIS 9.3.1 (ESRI, Redlands, CA, USA) in the defined area (polygon) of availability. The distance to water parameter was used in the model to block variance, which is a similar response as a random effect in a GLMM model. By making the distance to water random, the marginal responses will be correlated due to the fact that that the same random effect is shared between parameters and over dispersion is varied. There the

model, models covariance on the scale of the data and distribution (binomial), which is conditional on the distance to water parameter.

GEE models in the broader sense, are considered more robust than the mixed random model of a GLMM given the different (and unknown) correlation structures of the random available points compared to the 'use' GPS elephant location data (Gillies *et al*. 2006; Bolker *et al*. 2008; Koper and Manseau 2009). In addition, the mixed model with a random intercept is equal to GEE with exchangeable correlation (SAS Inst, The GLIMMIX procedure). This method will also reveal possible 'functional responses' when resource use changes due to availability alterations due to fencing and biotic factors (Mysterud and Ims 1998). The resource selection functions are reflected as odds ratios, which is the probability of use, produced by the final marginal model. One final model, that met all requirements, was produced per season per elephant cow. The odds ratios, with the confidence intervals at a 5% significance level, are presented in the results section. Where 1 (one) is indicative of random use, or neither avoidance nor selection, >1 (greater than one) is considered selected for and <1 (smaller than one) would be avoidance of that specific biotic or abiotic resource.

The available area for the inside elephant herd was defined as the whole reserve (Kie *et al* 2002). While the available area outside is 955.23 km^2, defined by larger than the seasonal home ranges and boundaries, with north-eastern and southern border the Thune-, Motloutse-, and Limpopo Rivers respectively. The available area for the outside herd was reduced to 892.31 km^2 after the corridor was fenced off at the Saambou Bridge, end of September 2009. Therefore, availability of resources was defined as larger than home range size (Kie *et al* 2002; Boyce

2006; Bowyer and Kie 2006). The second order of resource use is considered the home range scale, indeed large scale (Johnson 1980; Senft *et al*., 1987). Vegetation zones and core areas would be considered third order of selection scale, and lastly feeding station at smallest scale of selection. This hierarchal concept is used to relate resource use to spatial scale (Kotliar and Wiens 1990).

I generated random locations within areas defined to be available to the elephant cow to represent resource units the animal could have chosen. The use/availability ratio was 1:10, covering the whole area of availability (sampling intensity of 1/34 m^2). Furthermore, ensuring use remains small in proportion to availability and to limit contamination of points. However, the model is robust and can handle greater than a 10% contamination rate (Keating and Cherry 2004). Availability was assumed to be constant except for the corridor that was closed to the Limpopo River end of September 2009. Thus the area available was reduced for the period summer 2008/9 and winter 2010 by 62.9 km^2.

3. RESULTS

I analysed rainfall data and GPS location data for two elephant mature cows over two and a half years from April 2008 (beginning of winter) – end September 2010 (end of winter). This produced a total of 8909 locations within the 95% isopleths. The mean number of locations during winter was respectively 931, outside and 926 inside and for the herd prior to escape, 926 locations. During summer, the mean number of locations was 848 outside, and 853 inside the reserve (Table 3.1).

3.1 Home range and core areas

Both elephant cows during winter (2008) frequent the southern central part of the reserve with considerable overlap of home ranges. The initial elephant population density was 1 per 3.35 km^2 prior to removal of fifty two elephant, including the collared cow (313) (Appendix A and Figure 2.3). Furthermore, building activities commenced in 2009 in the south-western part of the reserve.

The core area for the herd remaining inside (312) was the smallest (6.96 km^{-2}) compared to all the other core areas during the entire study period. Therefore, it was also the most contracted around waterholes and drainage lines at low elevation during the period of lowest rainfall of the study period (Table 2.1, Table 3.1 and Figure 3.1). During the following wet season 2008/9, the reserve herd explores the north-eastern *Colophospermum-Combretum* woodlands at higher elevations (Appendix B and Figure 2.2).

The escaped herd (313) spent the early winter initially along the reserve eastern border and the uplands, broad-leaved deciduous woodland *Colophospermum-Combretum* veld. The mid-latter dry period of 2009 was spent at the lowest elevation, riparian habitat of the Limpopo (Appendix C).

Comparison during the dry season of 2010 (Appendix E) reveals that the elephant herd inside the reserve have excluded the central and south west corner, preferring remoter areas. The herd outside the reserve during this period, due to the fencing off access to the riparian area south of the reserve (Saambou fence), have subsequently increased their range by ± 31km^2 to the east (172.08 km^2).

Table 3.1 Seasonal number of location points, size of core area and home range size of elephant inside and outside the reserve

	Year	Season	No. of location points for core area (50%isopleth)	Core zone surface area (m^2) (with Z point)[1]	Size of Core area(km^2)	No. of location points for home range (95% isopleth)	Home range surface area (m^2)(with Z point)	Size of home range(km^2)
Outside (313)	*2008(inside)*[2]	*winter*	*471*	*33972313.82*	*33.97*	*926*	*118797425.32*	118.79
	2008/9	summer	431	34965930.21	34.96	833	242520099.20	242.52
	2009	winter	521	20977336.14	20.97	997	138739969.61	138.73
	2009/10	summer	451	52004237.46	52.00	863	176001988.61	176.00
	2010	winter	451	68193151.24	68.19	865	172085209.48	172.08
Inside (312)	2008	winter	451	6960669.44	6.96	868	80063650.67	80.06
	2008/9	summer	426	33918071.72	33.91	811	123100560.54	123.10
	2009	winter	480	32620064.74	32.62	917	140677327.52	140.66
	2009/10	summer	471	25809884.26	25.80	894	78592662.72	78.59
	2010	winter	490	24947815.11	24.94	935	128572759.04	128.57

[1] Z point determines surface area along the surface contours
[2] The herd (313) prior to escape from inside the reserve

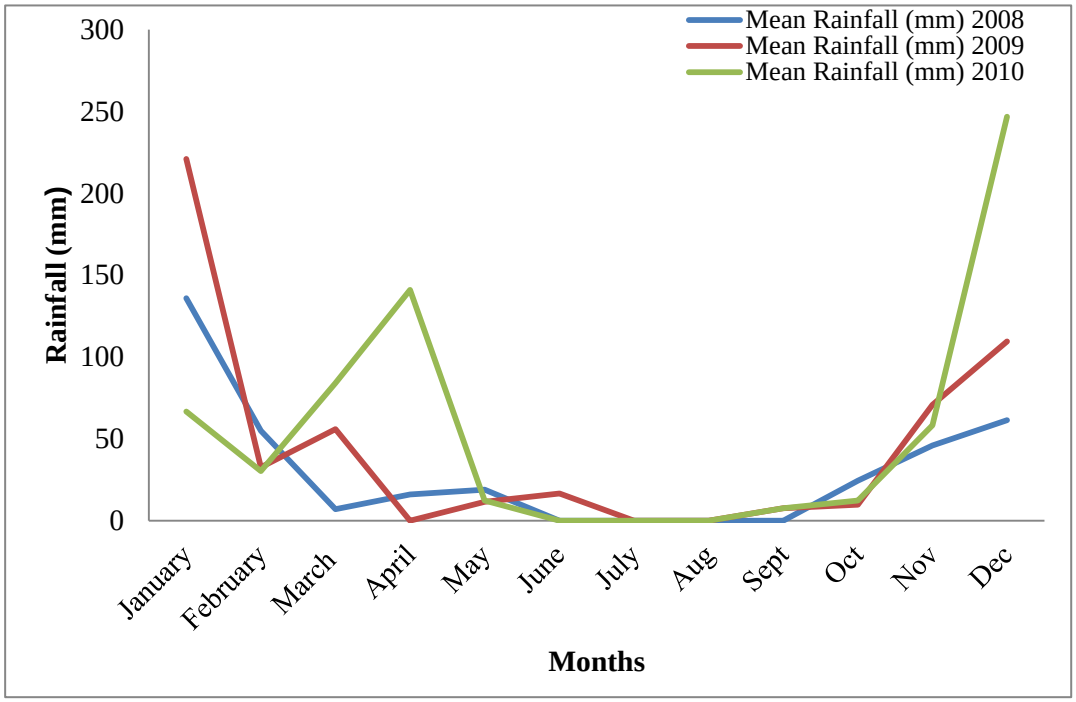


Figure 3.1 Mean monthly rainfall from 2008-2010

The increased late precipitation during April and May (Table 2.1 and Figure 3.1) enabled the herd to expand into the more remote north-east, with the closest water on average 5.32 km away, the farthest in any season from permanent water.

During the summer, 2009/10 (Appendix D) the herd inside shares the core area in the north-west of the reserve with the dry season. Here a combination of needs such as water, forage, and remoteness are met. The higher elevation is preferred for the core area. The mean winter home range size inside the reserve was 27% larger than summer over five seasons (Table 3.1). Comparison of winter home ranges with the dry season of 2010 reveals that the elephant herd inside the reserve have excluded the central and south west corner, preferring remoter areas (Appendix E). During this period the herd outside the reserve, due to the fencing off access to the riparian area south of the reserve (Saambou fence) have

subsequently increased their range by ± 31km^2 to the east (172.08 km^2). The increased late precipitation during April and May (Table 2.1 and Figure 3.1) enabled the herd to expand their range to the remoter north-east. Here the closest water on average 5.32 km away, the farthest in any season from permanent water.

For home ranges grouped seasonally inside compared to outside the reserve there is a significant size difference (Kruskal Wallis exact p =0.0175, Median Analysis, p=0.02, Van der Waeden analysis and the Savage analysis, p=0.02). However, the Dunn's test (1964) (non-parametric analogue of Holm-Sidak multiple t-test) was not significant for home ranges between the inside and outside herd.

Comparing similar seasons between the herd inside and outside the reserve three salient points emerge. Firstly, the summer home range for the herd outside is more than double the size of that of the herd inside the reserve, i.e. 108.41%. Secondly, during winter, the outside elephant cow home range is 33.62% larger than that of the elephant cow inside the reserve. In addition, the winter home range size variation for the herd inside the reserve is greater than the herd outside the reserve. Thirdly, the winter home range outside the reserve is still 64.8% larger than the summer home ranges inside the reserve (Table 3.1).

Inside the reserve, the core areas do show seasonal differences with the summer core area, 27.87% larger than the winter core areas. The outside core areas are 43.58% larger than the core areas of the elephant herd inside the reserve. The core areas during the summer and winter for the herd outside are similar in size.

However, the variation in size is greatest during the winter. Furthermore, the core areas are generally larger in summer by 19.19%. The core areas, represent 23.8% of the home range space on average, i.e. the breeding herd spend 50% of their time in 23.8% of their home range. The non-parametric exact tests did not prove significant respectively for core zones grouped seasonally inside and outside the reserve for Kruskal Wallis (exact p= 0.144) or for the Van der Waeden analysis (p= 0.1698).

The total home ranges, i.e. when the seasonal home ranges are pooled, the home ranges outside the reserve generally are much larger (72.14%) than inside, while the core areas outside the reserve are larger by 56.41% than inside the reserve. The summer home ranges outside the reserve are 25.74% larger than winter home ranges, i.e. showing seasonal influence related to rainfall and NDVI, with some minor contraction around winter permanent water. The herd inside the reserve, however, shows only some contraction at relatively smaller scale, i.e. core area, during winter. In contrast in the more natural open system outside the reserve, the home range size is well correlated (r^2=0.899) with annual rainfall.

3.2 Resource selection

3.2.1 Inside the reserve

Winter NDVI (Figure 3.3) as a landscape variable is a consistent indicator of use, with the strongest selection in 2008 when one unit increase in NVDI represents an increase of 1.19 (1.159-1.224, p<0.05) in selection for use. During the years, 2009

and 2010, NDVI was also strongly selected for [1.038 (1.023-1.0520, $p<0.05$) and 1.08 (1.059-1.093, $p<0.05$)]. Furthermore, the driest year showed the strongest selection for use, as the availability of green productivity decreased (Figure 3.3). Low elevations (Figure 3.2 and Figure 3.4) were preferred during the winters of 2008 and 2009 [(0.962; 0.96-0.965, $p<0.05$); (0.98; 0.977—0.982, $p<0.05$)]. This was also reflected in their core areas and home range, south in the reserve at low elevations (Appendix A and C).



Figure 3.2: Typical dry season mixed bushveld, where luvisol soils give way to cambisol soil type, in the southern-eastern, and lower elevation, part of the reserve facing north east, to the outside of the reserve, towards Baines Drift. The *Mooimeisie* (perrenial) spring in the forefront forming a drainage line (Leonard©).

During winter 2010, elevation has a positive influence on resource use (1.016, 1.013-1.1018; $p<0.05$). Furthermore as evidenced by their core areas, most time was spent at higher elevations, in the north-western part of the reserve (Figure 3.4).

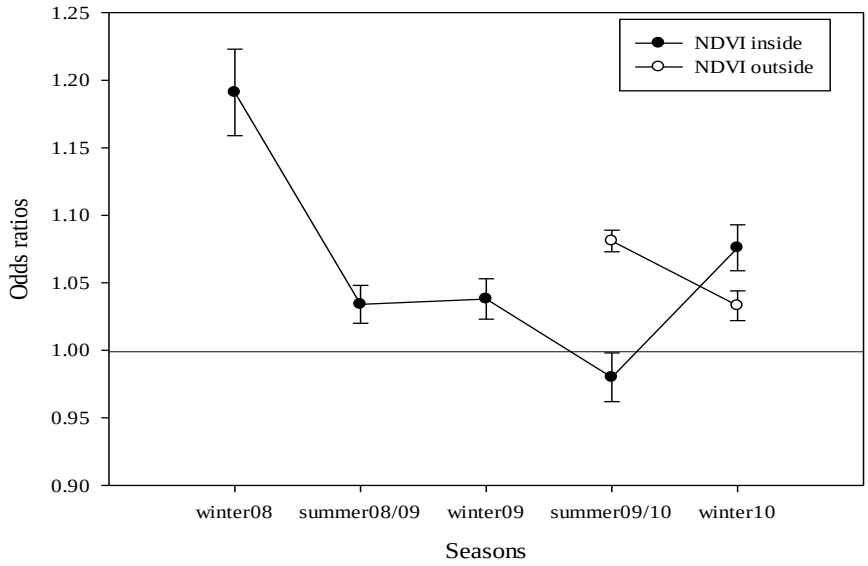


Figure 3.3: Comparison of odds ratios of NDVI inside and outside the reserve with corresponding seasons, with confidence interval (CI) .Where 1 is indicative of random use, >1 is selected for and <1 avoided. Where absent the parameter did not enter the model (All graphs were generated by Sigma Plot, Sysat Software Inc, San Jose, CA).

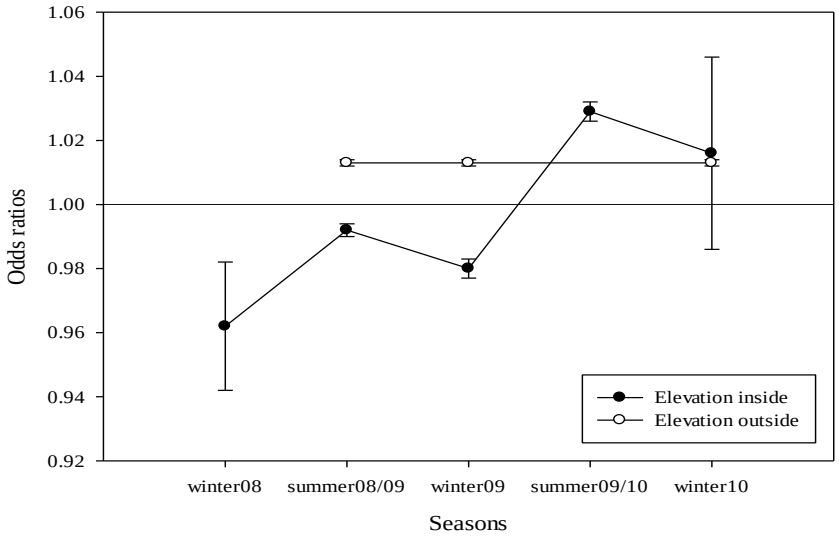


Figure 3.4: Comparison of odds ratios of elevation inside and outside the reserve, with corresponding seasons, with CI. Where 1 is indicative of random use, >1 is selected for and <1 avoided. Where absent the parameter did not enter the model.

Slope, during the dry season (Figure 3.7), also reflected an increased likelihood of selection during 2008 (1.298; 1.261-1.335, $p<0.05$) such that that use increased 1.298 times for each degree in slope increase for the elephant population average. While in 2010 slope indicated avoidance (0.908; 0.891—0.964, $p<0.05$) or reduced likelihood of use.

The elephant herd strongly selected the flat aspects (Figure 3.5) during the winter 2008 (1.969, 1.157-3.348; $p<0.05$) and also avoided NE-E slope four times as often (0.52, 0.418-0.647; $p<0.05$). However, during the following dry season elephant only strongly selected NE-E slopes (1.216, 1.046-1.413; $p< 0.05$). During winter 2010 the NW-N aspect (1.371, 1.174-1.600, $p<0.05$) was strongly selected for and influenced utilization instead of other aspects (Figure 3.5).

The wet season shows different probability of utilization. In 2009/10, NDVI variable (Figure 3.3) had limited influence 0.98 (0.971-0.989; $p<0.05$) on the outcome of probability of utilization of plant biomass, while in 2008/9 there was some indication for use at 1.034 (1.020-1.048, $p<0.05$). Slope also had a positive influence on use (1.037, 1.011-1.064; $p<0.05$) and in 2009/10 a negative or reduced likelihood on probability of utilization (Figure 3.7) for each degree of increase in elevation, during increased rainfall periods.

Elevation, during summer 2008/09 (Figure 3.4) had a slight negative influence on utilization (0.992; 0.99-0.995, $p<0.05$) while the following year had a very positive influence on use (1.029; 1.026-1.032, $p<0.05$) for each meter increase in

elevation for the population average. The aspect parameters indicated that summer slopes SE-E were avoided (0.63, 0.528-0.744 and 0.75, 0.0636-0.887; $p<0.05$) during both years (Figure 3.5).

In summary, for the herd inside the reserve, NDVI and lower elevations are shown to be more strongly selected during the dry season than the wet season. However, winter 2010 being an exception for elevation, when higher elevation are preferred during a better rainfall period (Figure 3.4 and Table 3.2).

Lower slopes are selected during better rainfall times, and steeper slopes during very dry seasons. Aspects the elephant herd prefer during winter are; FLAT and NW-N, except during 2008 when NE-E aspects were avoided and summer 2008/9 and 2009/10 SE-S slopes was avoided (Figure. 3.5 and Table 3.2).

3.2.2 Outside the reserve

During the dry season the distance to drainage lines had no influence on the dependant variable of probability of use at the selected scale (0.99; 0.998-0.999, $p<0.05$). However, for each meter increase in elevation during winter 2009 there was a 1.013 (1.012-1.014, $p<0.05$) likelihood of an increase of use for the population average. The elephant herd avoided the SE-S aspect during winter 2009 (Figure 3.6). During 2010, elevation, NDVI, and NW-N aspect respectively showed increased likelihood of resource use of, 1.013, 1.04, and 1.2. NDVI became important in 2010 due to the April rain with an associated increased home

range of 172 km^{-2}, nearly equivalent to a summer home range in 2008/9 of 176 km^{-2} (Figure 3.3 and Table 3.1).

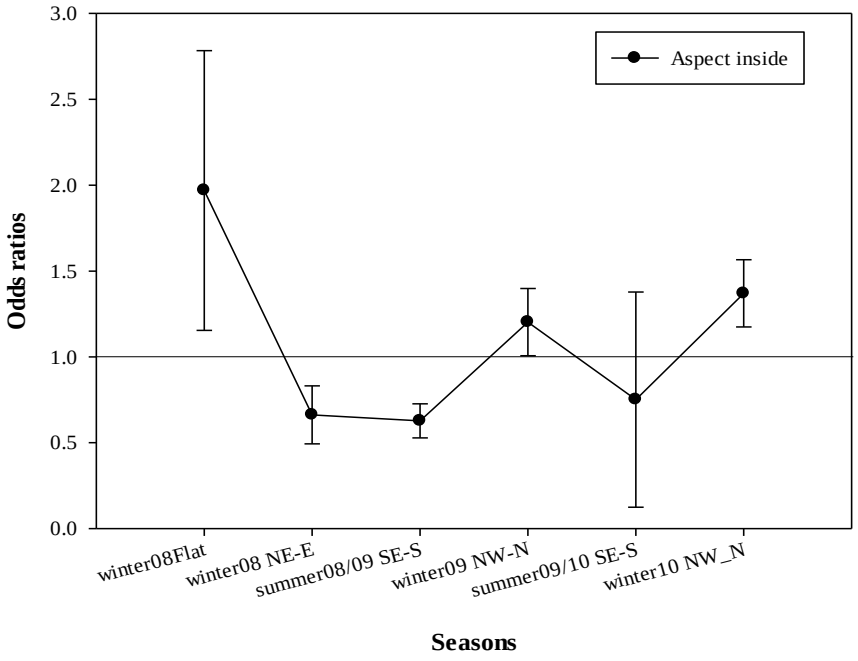


Figure 3.5: Comparison of odds ratios of aspect inside the reserve, with corresponding seasons, with CI. Where 1 is indicative of random use, >1 is selected for and <1 avoided.

During the wet season of 2008/9, the elephant cow (1.013, 1.012-1.015; $p<0.05$) associated with increased elevation more than random locations, while the distance to drainage lines had no real influence on probability of use (1.0; 1.01; $p<0.05$) (Figure 3.4). However, the SW-W slopes were strongly selected for during both summers 1.312 (1.108-1.553, $p<0.05$) and 1.599 (1.326-1.877, $p<0.05$) respectively. During 2009 winter, SE-S aspects were avoided by the cow (Figure 3.7). In 2009/10 the NDVI of 1.081 (1.073-1.088) and slope 1.035 (1.011-1.060) positively influenced the probability of use (Figure 3.3 and Table 3.3).

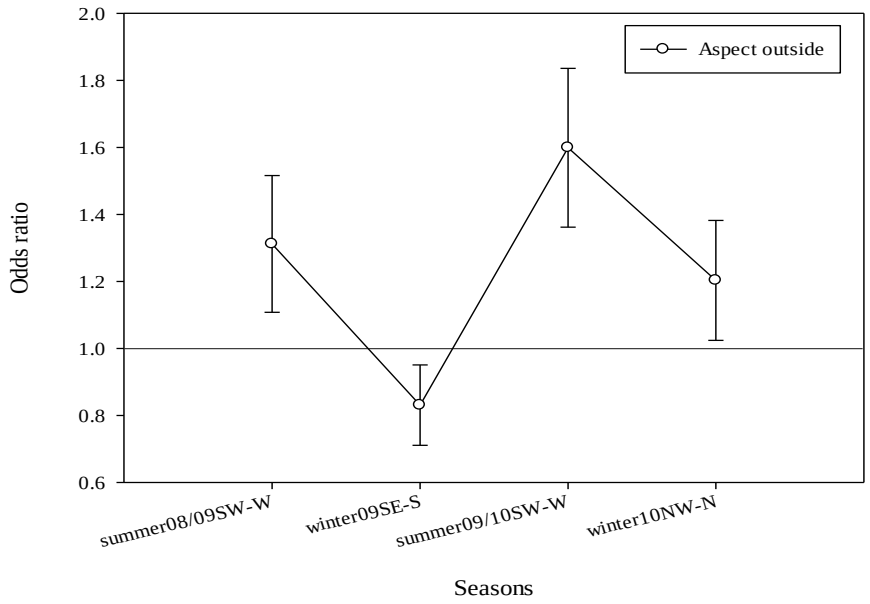


Figure 3.6: Comparison of odds ratios of aspect outside the reserve, with corresponding seasons, with CI. Where 1 is indicative of random use, >1 is selected for and <1 avoided

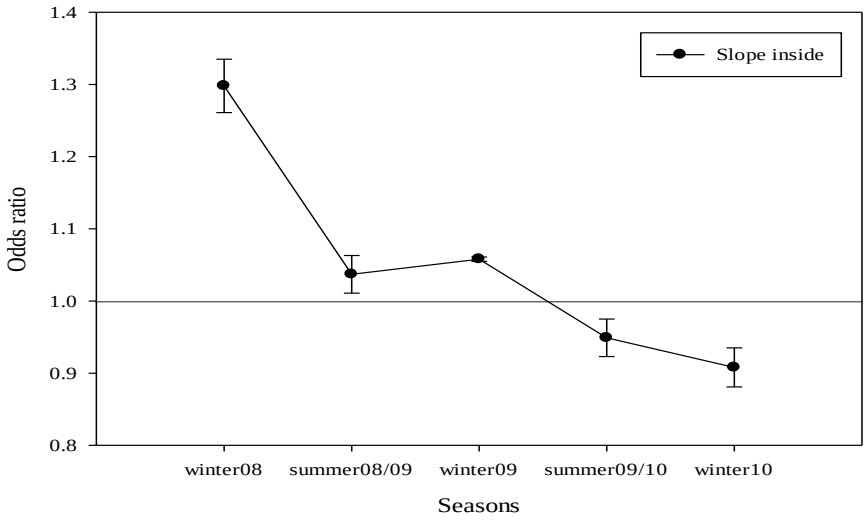


Figure 3.7: Comparison of seasonal odds ratios of slope inside the reserve, with corresponding seasons, with CI. Were 1 is indicative of random use, >1= selected for and <1= avoided.

3.3 The effect of distance to water

The distance to the closest water inside the reserve for the elephant herd was on average during winter 1.87km (SD±0.756km) and 1.62km (SD ±0.095km) during summer with smaller variation. Outside the reserve, the distance to the closest water during winter is 3.58km (SD±2.458km) and for summer is 1.08km (SD±1.083km). The herd outside the reserve show a high negative correlation (r^2= -0.75) with the closest distance to water and home range size, while the herd inside the reserve show no correlation (r^2=0.08) between home range size and the closest distance to water.

3.4 Effect of rainfall

There is a strong correlation between the seasonal home range sizes of the outside herd and rainfall (r^2=0.898), compared to the inside herd (r^2= -0.28). The seasonal core areas inside the reserve are slightly correlated (r^2 = 0.49), while outside is not correlated with mean seasonal rainfall (r^2 = 0.26).

Table 3.2 Tables of coefficients *inside* the reserve seasonal models, all coefficients of final GEE model significant at p<0.05, with confidence intervals (ddrainl=distance to drainage line, SE = Standard error). Absent values, reflect no incorporation into the final model.

Season	**Winter**						**Summer**			
Parameter	**β coefficients**			**SE**			**βcoefficients**		**SE**	
Year	2008	2009	2010	2008	2009	2010	2008/09	2009/10	2008/09	2009/10
Intercept	6.97	8.24	-23.110	1.478	1.042	1.26	-0.63	-21.49	1.0404	1.352
ddrainline		0.0001			0.0001					
slope	0.261		-0.085	0.0146		0.015	0.036	-0.052	0.0131	0.0142
elevation	-0.039	-0.0199	0.015	0.0013	0.0013	0.0014	-0.0075	0.029	0.0014	0.0016
ndvi	0.172	0.0369	0.073	0.0137	0.0070	0.008	0.033	-0.010	0.0070	0.005
NW_N			0.315			0.079				
NE_E	-0.653	0.195		0.111	0.076					
SE_S							-0.46	-0.28	0.088	0.083
FLAT	0.677			0.271						

Table 3.3 Tables of coefficients *outside* the reserve of final GEE seasonal models, all coefficients significant at p<0.05, with confidence intervals (ddrainl=distance to drainage line, SE = Standard error). Absent values reflect no incorporation into the final model.

Season	**Winter**				**Summer**			
Parameter	**β coefficients**		**SE**		**β coefficients**		**SE**	
Year	2009	2010	2009	2010	2008/09	2009/10	2008/09	2009/10
Intercept	-10.83	-15.47	0.32	0.566	-11.72	-12.38	0.0608	0.44
ddrainline	-0.0014		0.00012		0.0004		0.00009	
slope						0.034		0.012
elevation	0.0133	0.013	0.0005	0.0006	0.013		0.00069	
ndvi		0.032		0.005		0.077		0.034
NW_N		0.185		0.082				
SE_S					0.27	0.469	0.083	0.081
FLAT	-0.185		0.079					

4. DISCUSSION

In this study, the most striking result is the seasonal spatial use as reflected in home range size at the landscape scale which differed significantly between the enclosed herd and the herd roaming in an open system (Senft *et al*. 1987). The herd outside the reserve displayed distinct smaller winter and larger summer home ranges, while the reserve herd, exhibited non- significant differences in seasonal home range sizes.

Seasonal home ranges inside the reserve

Contrary to my expectation the mean winter home ranges were larger than summer home ranges, however, most studies reflects larger summer home ranges but this is study site specific (Ntumi *et al*. 2005; Shannon *et al*. 2006). In this study, the larger winter home ranges are firstly due to the high density of perennial artificial waterholes, with which sufficient forage productivity, makes movement of family groups with calves throughout the reserve possible (Pettorelli *et al*. 2005; Harris *et al*. 2008). Secondly, the water available during the winter is more spatially variable than in summer. Thirdly, winter severely limits utilization of the herbaceous layer, and elephant cows being more forage selective, have to roam slightly further, yet are constrained by the closest artificial water source. Furthermore, interspecific competition, density dependence, and social factors (dominance and family unit size) could have possibly played a role during winter 2008 with both herds inside the LLGW reserve. Water, either artificial or natural, is a vital resource at different scales in arid and semi-arid savannas. Therefore, water is a key determinant of elephant seasonal distribution patterns (Gaylard *et*

al. 2003; Harris *et al*. 2008; Young *et al.* 2009; Smit *et al*. 2009; Loarie *et al*. 2009).

Seasonal home ranges outside the reserve

The first summer home range outside for this herd that was initially inside the reserve is the largest (242 km^2). This is due to initial exploratory behaviour and compensation of the inhibitory fence effect with respect to movement, space, and resources (Druce *et al*. 2008). This expansion initially was not evident inside the reserve (by either herd) due to the limiting effect of fencing on movement during resource abundant times. Additionally, being a sub-population separated from the inside herd possibly also stimulates some cautious exploratory behaviour with no core area set up directly neighbouring the reserve eastern border during two seasons (Thouless 1995; Thouless 1996; Leggett 2006; Druce *et al*. 2008). Herds initially stayed in areas with known resources and took about two seasons to adapt to the new area (Druce *et al*. 2008).

During late winter and early summer the herd outside the reserve utilizes Limpopo-riverine habitat due to improved quality browse, shelter, shade and water supply (Harris *et al.* 2008; Smit and Ferreira 2010; De Knegt *et al.* 2010). The outside herd revealed a landscape scale feeding pattern, that shift up and down the catena or elevation gradient through the seasons (*sensu* Johnson 1980; Senft *et al*. 1987). This occurs at the largest spatial and temporal scale, i.e. larger than home range scale. Movement in the mid-wet season was towards the uplands and higher elevation when foraging conditions have improved. This cross-catenary movement pattern is driven by phenological differences, water supply,

forage quality and also the existence of a possible productivity gradient (Ben Shahar 1990; Stokke and Du Toit 2002; Douglas-Hamilton *et al.* 2005; Leggett 2006; Smit *et al*. 2007). This larger scale distribution pattern of resource use is impossible in the smaller fenced neighbouring reserve.

However, electrical fencing erected at the end of September 2009 at the Saambou Bridge blocked this riparian corridor south of the reserve and affected this trans-seasonal cross-catenary movement of the outside herd between the uplands and lowlands, limiting the possible recovery of the local vegetation in both the uplands and lowlands (Van Aarde and Jackson 2007). This movement restriction could result in increased homogenization of the vegetation structure (Figure 2.2) The piosphere phenomenon is the development of a utilization gradient around water sources, with increased foraging (grazing and browsing) with decreasing distance to a water point by mostly water-dependant species (Farmer 2010). Therefore, the increased foraging pressure and associated trampling around permanent waterholes- piosphere formation, in the uplands can be expected (Chamaillé-Jammes *et al*. 2007; O' Connor et *al*. 2007; Boundja and Midgley 2009; Farmer 2010). This can eventually expose certain woody species close to water, to overuse if a grazing gradient is assumed (Chamaillé-Jammes *et al*. 2007; O'Connor *et al*. 2007; Farmer 2010; O'Connor 2010).

The home ranges of the outside herd during the dry season show contraction, as expected, indicating that water and forage quality interaction and the scale thereof has an important influence on elephant seasonal distribution and resource utilization. This contraction during winter occurs due to the concentration of their

foraging activities closer to water (Owen-Smith 1988; Stokke and Du Toit 2002; Gaylard *et al.* 2003; de Beer *et al*. 2006; Chamaillé-Jammes *et al*. 2007). However, this is dependent on rainfall variation and elevation. Furthermore, rainfall variability affects dispersion pattern variability of the outside elephant herd.

For other studies with similar rainfall, the seasonal home ranges are larger; with size negatively related to reduced vegetation productivity (Thouless 1995 and 1996; Ntumi *et al*. 2005; Douglas-Hamilton *et al*. 2005; Osborn 2004; Shannon *et al*. 2006; Roux and Bernard 2009). However, most home ranges were estimated by the minimum convex polygon (MCP) method, which overestimates home range size due to the sensitivity of distant points. In addition, these points are usually only exploratory locations and not necessarily for survival (Getz *et al*. 2007).

Core areas

The core areas represent more productive forage areas where more time is spent in relation to available space in the home range. Regrowth of vegetation is possibly stimulated by defoliation with access to water (McNaughton *et al*. 1988; Fornara and Du Toit 2007). When core areas overlap between years and seasons it indicates more stability of the vegetation with productive richer patches (Bailey *et al*. 1996; Young *et al*. 2009). Well-defined and multiple core areas suggest that habitat utilization does not occur in a random fashion, and these are areas most likely to be affected by over utilization (Douglas-Hamilton *et al*. 2005; Young *et al*. 2009). Furthermore, the emergence of many core areas suggests that localized

resources, including water, are available throughout the reserve. It might also indicate that trans-seasonal movement throughout the reserve is necessary to meet their resource requirements. Thirdly, that the newly fenced reserve (eighteen months) has been subject to removal of a sub-population of fifty-two animals during early November 2008, limiting competition and increasing relative space. This, no doubt with building commencing created some social disturbance. Other factors for core area selection or establishment are; higher forage quality (Bailey *et al*. 1996; Loarie *et al*. 2009), water, canopy density (De Boer *et al*. 2000), specific nutrients (Holdo 2003 and 2004), remoteness **(**Vanak 2010; Jackowski *et al*. 2012), sub-population (Thouless 1996; Leggett 2006), heterogeneity (Cromsigt *et al*. 2005) and possible 'edge effects' related to the electric fence (Vanak *et al*. 2010).

The herd outside the reserve however utilized seasonal core areas as 'stepping stones' of larger resource patches while traversing the catenal and fragmented landscape between the uplands and lowlands (Forman 1995; Wu and Loucks 1995). This pattern of core area utilization occurred prior to fencing off the riparian corridor. Because of energy constraints, Baines drift- and the Maropong River pools were used as a 'halfway stop', for two seasons, which is understandable for a family unit with calves. In addition, forage production via coppicing also depends on catena position, with some species improved re-growth in the bottomlands compared to the uplands (Kaschula *et al*. 2005). Because the catena also provided a nutrient gradient where sodium, calcium, nitrogen, and phosphate increase down slope, the elephant herds move to utilize this productivity (Schimel *et al*. 1985; Ben Shahar, 1990; Seagle and McNaughton

1992; Bailey *et al*. 1996; Venter *et al.* 2003; Holdo 2003 and 2004; Shannon *et al.* 2006). The abandonment of the core area between Baines drift and the river post-fencing suggests that the Limpopo riverine vegetation is an important source of forage.

Furthermore, the post-winter 2009 loss of 62.9 km^2 of prime riparian vegetation with relatively reduced resource availability for the outside herd was compensated for by range expansion during the following year. In addition, this compensation is reflected by the lack of functional responses for key-resources. However, the opposite would be expected with reduced resource availability. Therefore, the fence enforced reduced resource availability is compensated for by increased home range sizes at higher elevations, made possible by higher rainfall (Mysterud and Ims 1998; Roever *et al*. 2012). Both the landscape scale foraging behaviour and compensatory behaviour is probably determined by matriarchal, familial learning, cognitive mapping and possibly inter-generational knowledge and foraging spatial memory (Bailey *et al*. 1996; Lewison and Carter 2004; Powell 2010).

The riparian habitat represents maximization of foraging and resource use including proximity to water (Mitchell and Powell 2004). In comparison, other landscape types during the late winter, early summer represent resource shortages and reduced forage quality which occurs in the deciduous broad-leaved *Colophospermum-Combretum* woodlands, in the uplands (Seagle and McNaughton 1992; Ngene *et al*. 2009a and 2009b). The core areas for the outside herd, covered an area twice as large as the inside core areas, and are areas where a

combination of resource requirements for elephant are met (De Boer *et al*. 2000; Leggett, 2006; Ngene *et al*. 2009a 2009b).

Rainfall

The high positive correlation between the seasonal home range sizes of the outside herd and rainfall indicates the close association between the two. Therefore, the outside herd is more dependent on rainfall in the dry savanna to extend their range, than the herd inside the reserve (Osborn, 2004). Indeed, the inside elephant herd is constrained by fencing but the access to a high density of artificial water points reduces rainfall dependence. Furthermore, pans and natural waterholes allow range expansion for the outside herd by a few kilometres from permanent waterholes during the wet season (Gibson *et al.* 1998; Legget *et al*. 2006; Shannon 2006; Ntumi *et al*. 2006; Thouless 1996). In addition, the strong linear relationship between rainfall and vegetation productivity (NDVI) in these savannas should reflect the amount of available forage related to the distribution of key resources (Nicholson and Farrar 1994; Sankaran *et al*. 2005). Herbivore-resource interactions with seasonal and spatial resource distribution are important determinants of home range size and shape (Osborn 2004).

The seasonal core area inside the reserve is slightly correlated, while outside it is not correlated with seasonal rainfall. Rainfall clearly effects vegetation heterogeneity at various spatial- and temporal scales. However, elephant core areas are highly dependent on permanent water availability. Rainfall additionally is a stronger determinant of movement for the outside elephant than the inside elephant at the landscape scale (Senft *et al*. 1987). Therefore, rainfall influences elephant distribution at the largest scale by affecting vegetation production and

decouples the influence of permanent artificial water at the smaller scale in the open system by reducing the distance to closest water in the landscape (Nicholson and Farrar 1994).

Artificial waterholes

In Chobe, (Northern Botswana) breeding herds did not move further than 3.5 km in winter and 5 km from rivers in summer (Stokke and Du Toit 2002; Gaylard *et al*. 2003 Smit *et al*. 2007b; Smit and Ferreira 2010). The elephant herds in this study preferred artificial waterholes, especially after the corridor was fenced off. This preference can be associated with the low average precipitation, ephemeral rivers and easier access, possible improved potability, availability and abundance of artificial waterholes with concomitant foraging cost saving (Harris *et al*. 2008). However, inside the reserve there is no association between distance to closest water and the seasonal home range sizes. In contrast, an exponential reduction in the home range size with increasing density of waterholes, during both dry- and wet seasons, was demonstrated in Northern Botswana with higher rainfall (Verlinden and Gavor 1998). Similarly, the trend for the outside herd is toward a positive association between home range size and rainfall. Therefore, the distribution of either natural or artificial water, in dry savannas, is a strong determinant of elephant spatial use (Harris 2008; De Beer and Van Aarde 2008; Young *et al*. 2009).

The surface water for the outside herd, typically supplied by artificial waterholes, likely restricted the foraging range during normal rainfall seasons (Chamaille-Jammes *et al*. 2007 and 2008). Indeed, because resources are more dispersed than

for the inside herd, female elephants moved longer distances. In contrast, inside the reserve heterogeneous vegetation patches and water are in closer proximity. The resultant effect is reduced home ranges, constrained by limited and reduced spatial scale due to fencing (Wiens 1989; Wu and Loucks 1995; Forman 1995; Cromsigt *et al*. 2005; Grainger *et al*. 2005).

The stronger association inside the reserve, between the vegetation productivity (NDVI) and the distance to the closest water, can result in possible local overuse of vegetation, especially during the dry season. The waterhole density and size of the reserve exclude possible vegetation refugia. This strong coupling exists inside the reserve for the following reasons. Firstly, more frequent correlation between these parameters. Secondly, available space is reduced due to fencing. Thirdly, rainfall influence is reduced due to increased density of waterholes and fencing. Fourthly, near similar distances to travel for winter and summer water points while the variation of closest distance to water outside is much larger between seasons. In addition, the increased rainfall (2009/10 summer and winter 2010) uncouples this relationship between vegetation biomass and the distance to the closest water outside the reserve. Furthermore, the resource selection study confirms this.

Vegetation greenness (NDVI)

For the herd inside, NDVI reliably predicted use and home range characteristics. Furthermore, it also showed the strongest selection of all resources during both years, especially during the dry season. Seasonal selection strength differences are likely due to differences in the spatial scale of resource distribution, during the

wet and dry seasons. During the winter, the availability of the herbaceous (grass) layer is reduced, leaving mostly browse remaining (Owen-Smith 1988). This would result in the possible increased relative distance between forage sites, which are more intensely utilized, yet constrained by the distance to the nearest water. Hence, the stronger selection during winter, resulting in the increased home range size based on selection without water constraints. The strongest selection for NDVI and increasing slope occurred during winter 2008. This was the lowest rainfall season during the study period; in addition, the other elephant herd was still inside the reserve. This could indicate to the possibility of sub-population competition for resources affecting the RSF (Van Aarde *et al*. 2008).

For the herd outside the reserve, NDVI was only a good indicator of resource utilization during higher rainfall periods in the seasonal models, especially when NDVI was correlated with elevation. The weaker selection for vegetation greenness during winter possibly means there were primarily more available forage and a possible trade-off with drainage lines vegetation (which represents heterogeneity at small scale) and elevation. The utilization of vegetation biomass outside the reserve at landscape scale is dependent on higher rainfall.

The mean NDVI selected for both herds is similar with Kruskal Wallis not being significant, which means that they select from similar range of vegetation greenness. Therefore, the scale of utilization and strength of selection differs between them either due to fencing, distribution, and availability of resources and possibly size of the family units. Furthermore, there was no significant difference between the mean NDVI selected and available, except during winter 2009, which

indicates that possibly only lower quality forage was available and utilized due to the low seasonal rainfall.

Forage characteristics such as tree cover and heterogeneity of vegetation can drive the home range at larger spatial scales, more than surface water availability (Johnson 1980; De Knegt *et al*. 2010; Marshall *et al.* 2010). Therefore, NDVI is an indicator of use at large scale outside the reserve, especially during periods of improved rainfall. Furthermore, Marshal *et al*. (2010) found that selection for NDVI occurs at a broader scale during summer and finer scale during winter for cows in higher rainfall areas. My finding was that vegetation greenness selection is occurring at larger scale during winter for the herd inside and during summer for the herd outside the reserve. The seasonal home ranges and core areas confirm this. The reduced vegetation production during winter is due to the gradual herbaceous layer senescence and results in increased patch distance and increased NDVI selection by the elephant. However, on the other hand, during summer the grass layer adds to the greenness component, reducing the grain, with coalescence occurring between foraging patches. So during summer 2009/10, and winter 2010, the late rain allowed higher NDVI than normal to persist. This allowed foraging at smaller grain to occur due to reduced spatial heterogeneity, but wider extent as NDVI relates to distance to water in the model. This implies that elephant herds utilize vegetation more homogenously during summer (higher rainfall), as indicted by the outside herd and more heterogeneously during winter, as indicted by the inside herd during winter. Therefore, space use varies between seasons and between enclosed areas *versus* open systems in vegetation biomass utilization.

Drainage lines

Drainage lines are sources of vegetation heterogeneity due to the water runoff and run-on and higher local levels of soil moisture. They also contribute to the spatial heterogeneity in the landscape (Senft *et al*. 1987, Wiens 1989; Forman 1995; Scoones 1995; Wu and Loucks 1995; Nellemans *et al*. 2002; Källe 2003; Venter *et al*. 2003; Wu and Archer 2005). Furthermore, soil moisture feedback with the woody layer has important implications for dry land ecosystems in that it leads to pattern formation in drainage lines (D'Odorico *et al*. 2007). Rainfall, climate, and geomorphology affect vegetation changes over the larger scale (Sankaran *et al*. 2005). At the landscape scale, the catena is responsible for diversity. At home range and smaller scale the range in slope variation, aspect, soil type and vegetation disturbance affect vegetation changes. These differences (heterogeneity) affect the attractiveness of drainage lines and influence the herbivore utilisation and movement in the surrounding landscape. Due to the spatial scale of NDVI (250m), the higher NDVI of drainage lines, during the dry season was not captured, and only reflected during higher rainfall seasons when the scale (grain) increases. Therefore, this finer scale parameter of NDVI is not captured consistently in seasonal models at the selected scale (O'Neill *et al*. 1998).

Rainfall was correlated with distance to drainage lines during the summer and winter with higher than average rainfall. However, there is a reasonable correlation with core area size and distance to drainage lines. It seems plausible that vegetation greenness and heterogeneity contribute to home range size as it relates to distance to water at landscape scale; and smaller scale as it relates to distance to drainage lines. Spatial heterogeneity and not just fencing and

waterhole density contributes to home range size which is evident during winter inside the reserve and summer outside the reserve (Ritchie and Olff 1999; Murwira and Skidmore 2005; Cromsigt *et al*. 2005).

On a temporal scale, strong seasonality and available space created improved conditions for movement between patches. This was furthermore dictated by phenological conditions, especially when the corridor was open until end of September 2009. Whereas weaker seasonality enables the herd inside the reserve to remain, more locally distributed (Hopcraft *et al*. 2009).

Elevation

There is a south to north elevation gradient in the study area, being part of the Greater Limpopo basin. Elevation, during average seasonal rainfall periods (Table 2.1) is a good indicator of use at large (landscape) scale and therefore home range determinant throughout wet and dry seasons. Lower elevations were utilized during winter, and during higher rainfall periods higher elevation was preferred with more leached luvisols with broadleaved woodland savanna (*C. mopane, Combretum apiculatum, Grewia monticola* and mixed *Dichrostachys cinerea*). The higher rainfall allowed possibly over-browsed, less nutritious or productive areas, on at higher elevation, to be utilized (Nicholson and Farrar 1990; Erasmus 2009; Ben Shahar, 1994). Rainfall, low slope and improved soil moisture also stimulates re-growth and this savanna exhibits pulsed nutrient cycles exploited by the more selective elephant cows (McNaughton *et al.* 1988; Farmer 2010). Furthermore, the quality and quantity of forage (NDVI) is highly correlated with rainfall and elephant select from a narrower range of habitats during the wet

season (Nicholson and Farrar 1994; Sankaran *et al*. 2005; Young *et al*. 2009; Birkett *et al*. 2012).

Rainfall, however, did not affect the home range size inside the reserve at landscape scale, but did at core area level and hence seasonal movement along the elevation gradient at smaller scale. The lower elevation vegetation is 'mixed bushveld' with greater variety or heterogeneous areas of *C. mopane, C. apiculatum, D. cinerea, G. monticola, Grewia bicolour, Acacia nigresence, A. tortillis,* i.e. fine leaved woodland on fluvisols and disturbed areas of *G. bicolour, C. mopane* and *D. cinerea*. A spatially heterogeneous landscape does provide opportunities to forage across range of scale, which is more evident during the winter.

During late winter or when resources are scarce, low elevations with more productive clay arenosol soil types and riparian cambisols soils were preferred by the elephant outside the reserve. Furthermore, the elevation gradient was utilized by migration from summer 2008/09 to winter 2009 from the uplands to lowlands (Nicholson and Farrar 1994; Erasmus 2009). Higher rainfall stimulated the use of higher elevations and proximity to drainage lines for forage maximization of *C. mopane* and *Combretum spp.* This reveals a somewhat hierarchy in resource selection with landscape scale selection of elevation, linked with NDVI down to smaller scale, utilization of drainage line vegetation. During higher rainfall periods, higher elevations were preferred once this cross-corridor fence was erected in September 2009. The positive correlation of elevation and NDVI existed respectively during both summers but not during winter.

Elevation inside and outside the reserve drives the distribution of elephant at moderate to large scale, therefore also affecting the home range size due to its possible influence on heterogeneity (Bailey *et al*. 1996; Sanders and Rahbek, 2011). Furthermore, the broader scale abiotic edaphic (geological) template, aspect, slope, and elevation underpin fine scale patterns such as vegetation structure. Higher elevations (e.g. uplands) supporting nutrient-poor vegetation on sandier soils and the lowland (riparian) higher production of more nutrient-rich vegetation on clayey soils (Scholes and Walker 1993; Erasmus, 2009).

Aspect and slope

Aspect and slope contribute to the amount and variation of incoming solar radiation. With a higher level of radiation and associated temperature results in a higher growth rate of vegetation and increasing concomitant water losses from vegetation cover and also elephant skin and their respiratory tract (Holland and Steyn 1975; Schulze 1997; Kinahan *et al*. 2007). On gentle slopes, north facing areas have lower radiation in the winter months (Schulze 1997). Furthermore, in landscape functional analysis, areas with gentler slopes were found to have greater functional integrity caused by the slower movement of nutrients leading to increased uptake by the vegetation (Ludwig *et al.* 2004; Farmer 2010). In addition, female elephants generally also avoid steeper sloped areas due to limited mobility of calves, energy constraints, and the possibility of injury (Wall *et al.* 2006; Knegt *et al.* 2010).

Inside the reserve, warming slopes and flat terrain were selected during winter, (Schulze 1997). However, during summer months the SE-S aspects were avoided

significantly. The outside elephant herd consistently preferred SW-W aspects during winter, which means that elephants were exposed to more radiation during the cooler months. In addition, SW-W was also the preferred aspect during the summer, meaning that up to 38% less radiation (on clear days) was preferred (Schulze 1997). Presumably, this large scale behaviour is linked to thermoregulation, energy saving, and resource use and a significant home range determinant (Kinahan *et al*. 2007). Could fencing affect the larger scale behaviour of aspect selection because of the proximity of waterholes inside the reserve during summer? The aspect inside the reserve may be less important at the landscape scale with close proximity to water for family units.

By comparison, relatively steeper slopes are selected during different seasons, respectively in a very topographically even environment, where slopes of 2.8^0 are preferred under normal conditions. The inside herd selected steeper slopes during the driest winter (2008), while the outside herd selected the steeper slopes during the wet season 2009/10. The most likely reason is to exploit dwindling resources in the case of the elephant inside the reserve; while the outside herd select, the steeper slopes to exploit more available resources. Rugged terrain, of which distance to drainage lines would be included, is occasionally selected to exploit nutrient hotspots especially during the winter inside the reserve and during the summer for the herd outside the reserve (Nellemans *et al*. 2002). During the wetter seasons inside the reserve, the slope at the larger scale is avoided due to a trade-off between elevation and NDVI, due to increased availability in resources and increased disturbance. The seasonal model also intimates that the baobab trees, *Adansonia digitata* are relatively safe from selection where they occur on hilly outcrops and steeper slopes inside the reserve during normal or average

rainfall years. However, during very dry winters (2008), there is some risk of being utilized inside the reserve (Edkins *et al*. 2007).

Fencing

Heterogeneous resources are distributed in the landscape, patchily. Furthermore, the resource variation increases to the power of the square root of the area accessible to the elephant, according to Ritchie and Olff (1999). This means that, fencing limits access to patches higher in quality and biomass. Fencing, by limiting space, affects the degree and strengths of selection of these resources, and thereby possibly influences the selection hierarchy of specific resources due to choice limitations, such as aspect (Boyce 2006). Furthermore, range expansion and seasonal cross-catenary movement similar to the outside herd is not possible, limiting resource availability to a threshold. Fencing, additionally limits access to favourable resources and corridors, and subsequently reshapes elephant spatial dispersion in the landscape and affects resource utilization as modelled at the larger scales. The Saambou bridge fence which prevented the elephant from moving westward along the riparian corridor did affect resource availability. However, due to the open system the herd could compensate by altering their distribution relative to resources. This is seen by increased home range sizes, winter, 2010 and summer 2009/10 of the outside herd. Therefore, elephants in unfenced areas have increased options to exploit resources that are distributed heterogeneously in time and space compared to movement restriction induced by fencing (Boone and Hobbs 2004).

Enclosure can influence trade-off between resources, such as slope, elevation, and NDVI for the inside herd especially when moving from resource restricted period (winter) to a more resource abundant period (summer). Fencing, especially smaller-medium sized reserves fragment the landscape and have the potential to cause trans-seasonal, and within seasonal resource re-utilization due to unavoidable overlapping between home range and also between core areas. Furthermore, in overlapped areas, impact on vegetation is increased and also the animal biomass resources can support is therefore reduced (Boone and Hobbs 2004; Shannon *et al*. 2006; du Toit *et al.,* 2008; Boundja and Midgley 2009; Cromsigt *et al*. 2009; Smit and Ferreira, 2010). In this study, enclosure was effective in separating two sub-populations of elephant and demonstrates the differences in seasonal distribution and utilization of space as it relates to resources.

The herd size and social factors can be a possible contributing factor affecting the spatial scale at which elephants use resources (Mitchell and Powell 2004; McLoughlin *et al*. 2010). Furthermore, movement shown by the outside elephant is a landscape scale foraging tactic (Senft *et al.* 1987). The resource selection functions in this study, without the number of social groupings and behaviour defined (e.g. dominance) between them, remains a statistical snapshot. Furthermore, fragmentation of the habitat might affect RSF accuracy (Meyer and Thuiller 2006; McLoughlin *et al*. 2010). RSF as indicated do fluctuate due to differing life history requirements and resource availability variation due to rainfall variation. Therefore, for elephants to maximize use of the available resources, it is crucial that these mega-herbivores exhibit plasticity in forging behaviour to cope with sudden and gradual variation in their resources (Mitchell

and Powell 2004; Hansen *et al*. 2009). These trade-offs occur during different seasons, based on availability of water and vegetation greenness with slope, aspect and elevation. This helps fulfil different requirements such as thermoregulation and water requirements, forage quality, forage quantity, and the energy cost incurred (Mitchell and Powell 2004).

The study agrees with the notion that when abiotic factors such as distance to water, slope, are equal, then sites with improved forage (e.g. lower tannin content, higher nutrient quality) will be selected (Bailey *et al*. 1996; Nellemann *et al*. 2002; Holdo 2003). Therefore, elephant cows select areas in relation to vegetation greenness and geographical characteristics at large spatial scales (although constrained by distance to the nearest artificial waterhole).

Resource utilization, as expected, occurs at various scales, especially with alteration of availability. However, without fencing limiting space, space therefore becomes more important with concomitant increase in resource availability with increasing scale (Wiens 1989; Ritchie and Olff 1999; Meyer and Thuiller 2006). It is important that the scale and seasonal factors be interpreted knowing that elephants do not use space randomly (Harris *et al*. 2008; Loarie *et al*. 2009; Young *et al*. 2009) and that these generalist, mega- herbivores react to spatial patterns in topography and distribution of forage and water (Senft *et al*. 1987; Seagle and McNaughton 1992; O' Neill *et al* 1998; Otis 1998; Murwira and Skidmore 2005; Boyce 2006; Meyer and Thuillier 2006). In this context, multigrain (multi-scaled) models are more accurate and that variables that are highly correlated are either eliminated or known and modelled (e.g. GLMM or

GEE). The GEE approach, allowed for explicit incorporation of various interdependencies of parameters through the 'working' correlation matrix. Moreover, the coefficients estimates are robust to misspecification of the correlations, since the correlations can be unknown. Additionally, this approach has given substantive insight of determinants of correlation and reduces autocorrelation to nearly zero (Ziegler *et al*. 1998; Zorn 2001; Carl and Kuhn 2007).

Future smaller scale studies of resource selection, especially in small reserves will aid understanding of possible future vegetation impacts. In this specific study site, RSF at a range of smaller scales, to determine the influence of drainage line vegetation (smaller scale) and spatial heterogeneity will have on seasonal resource use. Nevertheless, Meyer and Thuiller (2006) found that RSF with grains smaller than the geographical range with large species and home ranges also had the highest predictability, if predictability is required. It is suggested that 16 day home ranges, 1-3 monthly home ranges and core areas, or 8 km buffers (mean daily distance) around use locations will give a different perspective and context on elephant resource use than the larger scale study. Furthermore, Boyce's (2006) method of three-term local quadrant variation (3TLQV) to determine dominant scales of heterogeneity would also be useful to indicate hierarchal scales of use.

Human disturbance, an important predictor variable can be added to the models as distance to roads and permanent buildings would have indicated the effect of disturbance on the family unit distribution. In addition, it would test the idea of

temporary refugia in the landscape (Ntumi *et al*. 2005; Ngene *et al*. 2009a; Ngene *et al*. 2009b).

Further study to include the density of populations, or group size in the RSF to reflect possible density-dependant effects on the RSF (McLoughlin *et al*. 2010). Alternatively, discrete choice models (Manley *et al*. 2002) might be a possibility for the purpose of comparison of resource selection of the herd inside compared to outside the reserve.

The study area is furthermore part of the general Southern African aridity gradient with a latitudinal eastward shift and is located in a high risk area with respect to global warming. Moreover, climate change may affect range expansion of large mammals with the space limitation imposed by fencing (Thuiller *et al*. 2006). The seasonal and the landscape scale utilized for this study answers only general questions for resource selection and space use at this scale. For example, which parameters influence the home range formation and size inside and outside the reserve? Future studies should consider and include the effects of climate change on their range distribution. Furthermore, model selection must be underpinned by strong ecological parameters and life-history characteristics of elephant to be meaningful (Bowyer and Kie 2006).

5. CONCLUSION

The relationship of elephant seasonal resource use and distribution in the landscape is highlighted between an enclosed herd and a herd free to roam. The fenced reserve does not allow increased summer range and limits the response by

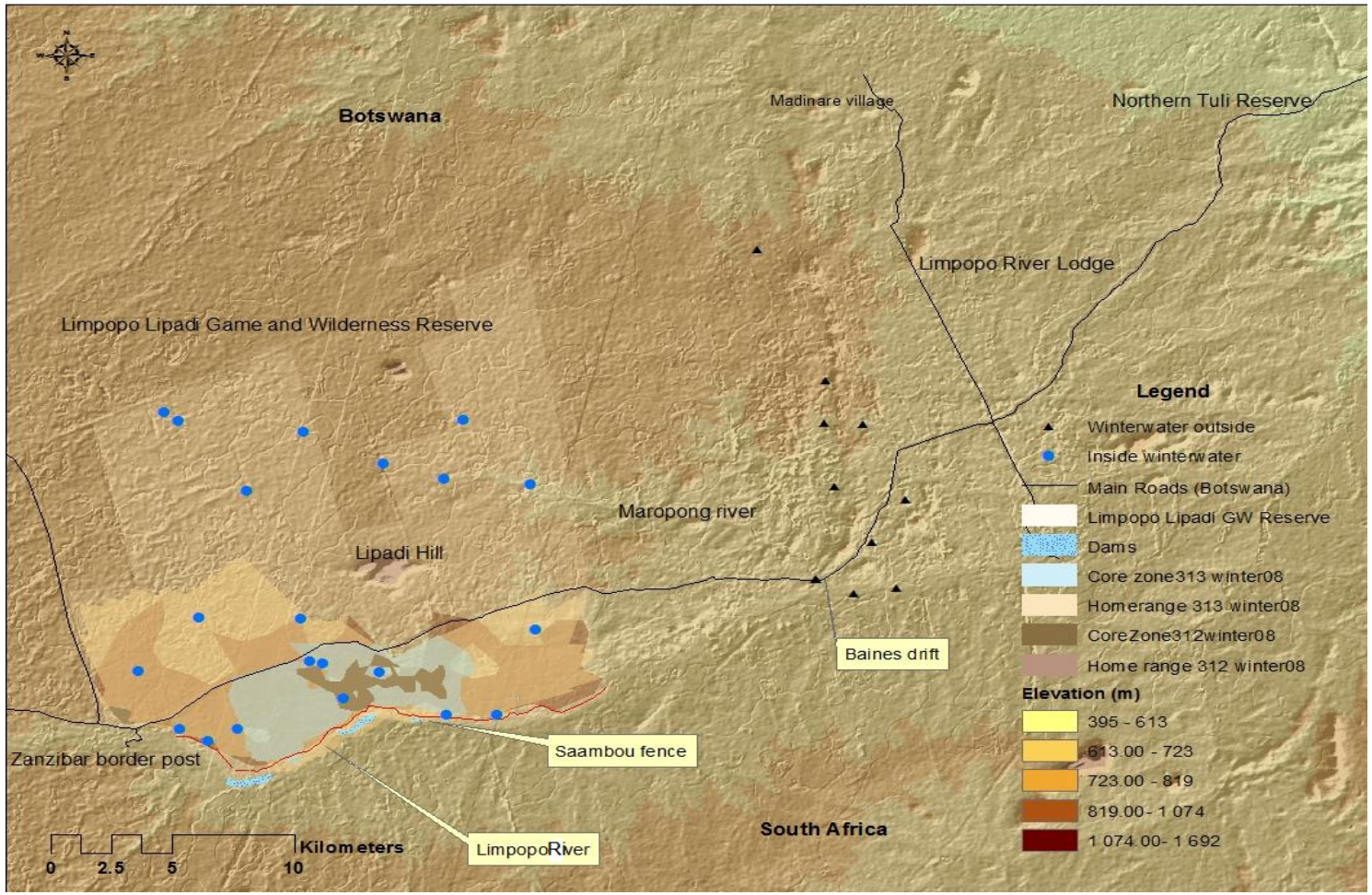
elephant to seasonal variations. Furthermore, fencing enhances limitation of resource availability during resource restrictive periods such as during the dry season. It also limits increased exploitation during improved availability of resources during the rainy season. Whereas in a large open, unfenced system with access to riverine habitat and reduced artificial waterhole density allows for seasonal shifts in ranging and thereby possibly limiting localized vegetation impacts compared to fenced core areas. There must be a trade-off for elephant herds between energy expenditure and maximizing forage utilization. Utilizing spatial memory is evident in the elephant home ranges outside the reserve, by cross catenary movement and recognition of a resource destination.

In an open system, the associations between resources that influence elephant distribution are reduced due to increased availability related to space with increased options to select resources. In a closed system, the resource selection associations during winter affecting home range size are stronger. Vegetation biomass, available space, abiotic factors, and rainfall drive elephant distribution at the largest scale in this study. Drainage lines (as a proxy for heterogeneity) affect resource use at smaller spatial scale. The way that the abiotic variable distance to water is used in the random statement, in the seasonal models, reflect that it is important at a range of spatial scales. Therefore, elephant cows show a scale dependent response to resources use. However, NDVI, elevation, aspect, and slope all have a significant influence on resource use and therefore are determinants of seasonal home range.

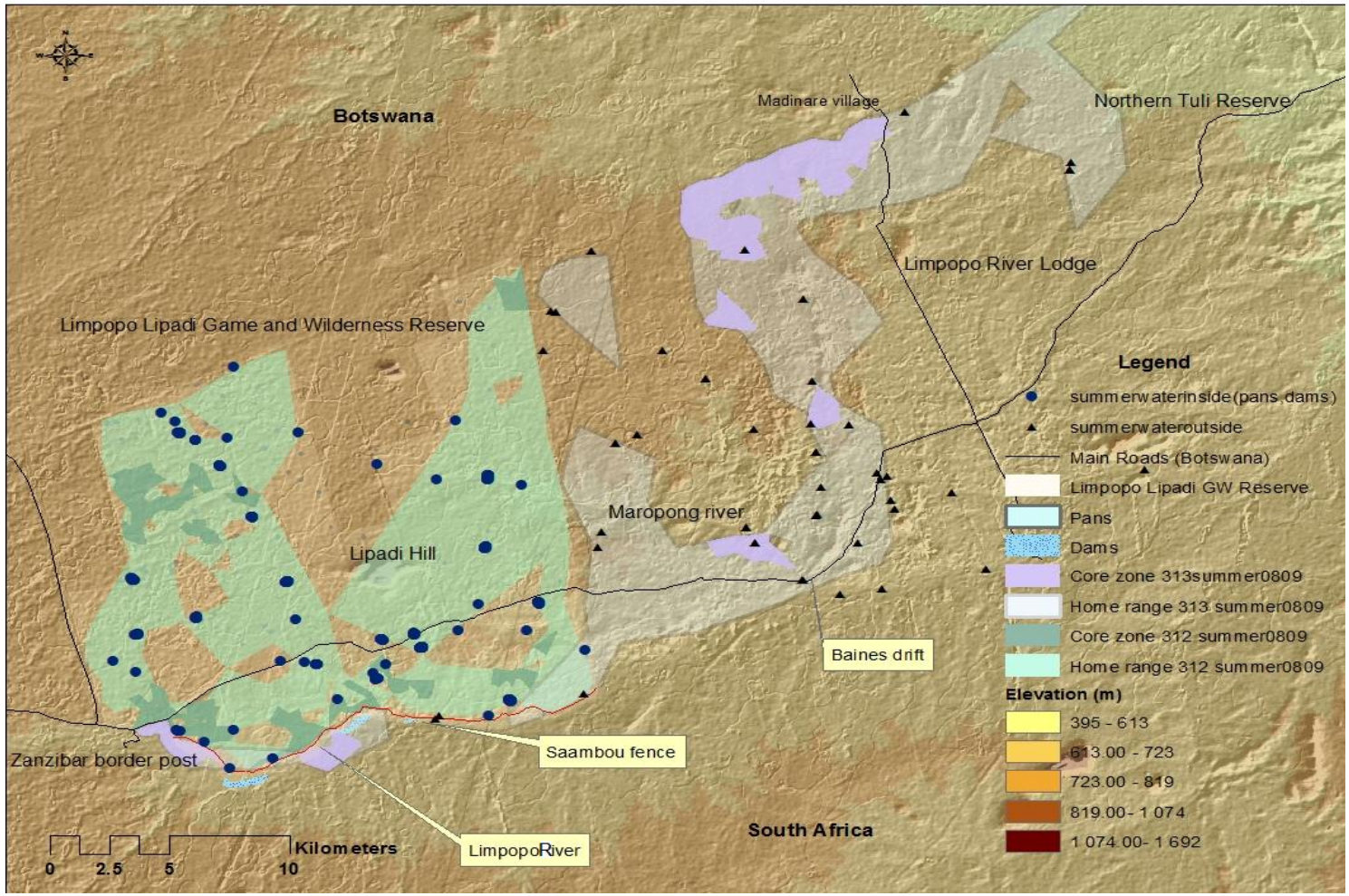
Elevation, slope and vegetation biomass relation to distance to water are being more selected during winter by the inside elephant cow in comparison. On the other hand, vegetation biomass and slope are strongly selected for during higher rainfall periods, when the vegetation can recover, outside the reserve.

The inside elephant herd response to increased rainfall is observed in elevation, and core areas; while during reduced rainfall it is more reflected in increased vegetation biomass selection, slope utilization and home range size expansion. The outside herd response to increased rainfall is observed in increased NDVI utilization, elevation, slope, and home range size. The importance of spatial heterogeneity is reflected during winter by the inside herd, while more homogenous use is reflected by both herds during summer. This highlights the differences in space use and resource selection between the herd in an open system and an enclosed herd, with rainfall emphasizing its influence on resource availability.

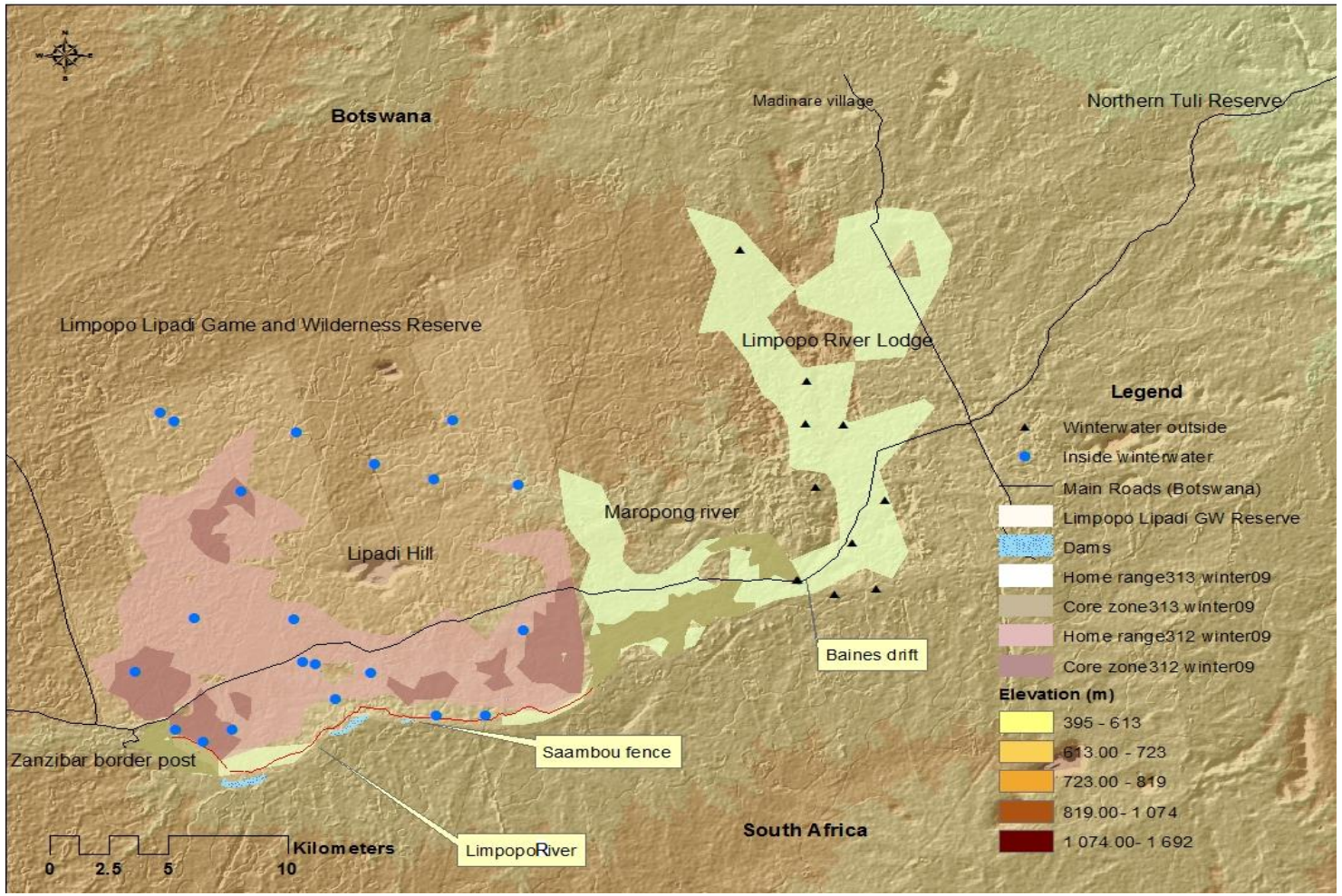
The studied elephant prefer above mean NDVI, in proximity to available water, lower elevation during the dry season and drainage lines, minimal human disturbance, and lower sloped areas. The distribution of family units in the landscape is a 'complex' interaction within and between various biotic factors at different seasonal and spatial scales with possible functional responses to limit energy expenditure and maximizing foraging in this highly mobile, opportunistic, mega-herbivore (Cilliers 2001; Ngene *et al*. 2009a and 2009b; Owen-Smith 1988). Therefore, fencing and density of artificial waterholes are serious future considerations in managing reserves' resources with consequences for heterogeneity (Thuiller *et al*. 2006; Rogers 2003a and 2003b).



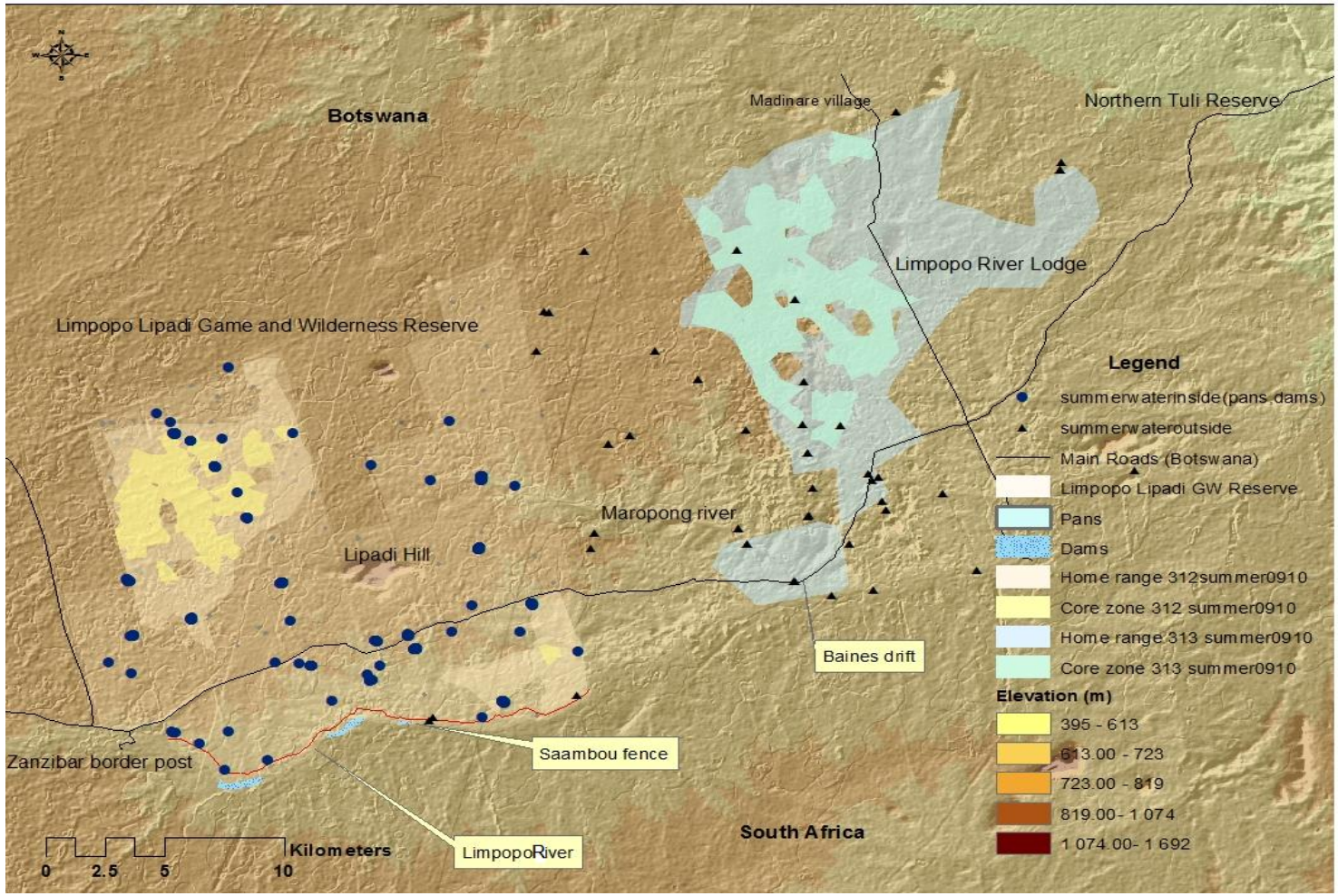
Appendix A: Home ranges and core area with both herds inside the reserve, winter 2008 (herd 312 remained inside) **APPENDIX A**



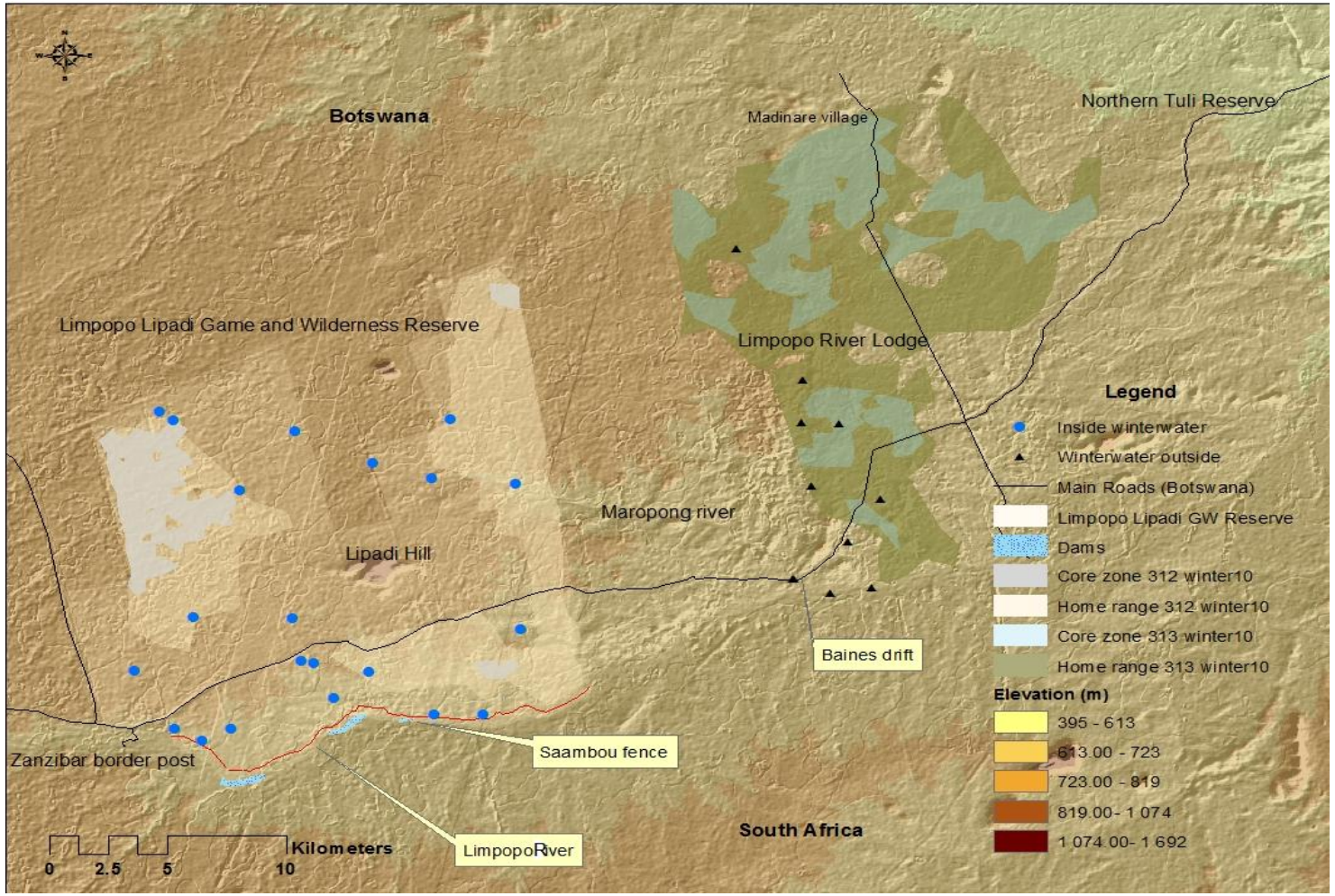
Appendix B: Home ranges and core area during summer 2008/9 (herd 313 – the herd outside the reserve) **APPENDIX B**



Appendix C: Home ranges and core area during winter 2009 (herd 313 – the herd outside the reserve) **APPENDIX C**



Appendix D: Home ranges and core area during summer 2009/10 (herd 313- the outside herd) **APPENDIX D**



Appendix E: Home ranges and core areas during winter 2010 (herd 313- the herd outside the reserve) **APPENDIX E**

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