Landscape heterogeneity as a determinant of range utilization by African elephants (*Loxodonta africana*) in mesic savannas

by

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ABSTRACT

Landscapes are inherently heterogeneous. However, some portions of a landscape are more heterogeneous than others and are therefore not equally suitable for resource extraction by elephants. Elephants have large energy demands to meet and should spend the majority of their time in areas where they are able to forage optimally. Identifying the determinants of home range location and area may therefore provide insight into aspects of landscape utilization by elephants

Using vegetation structure as a surrogate, I investigated whether landscape heterogeneity explains the variability home range size and location of elephants occurring in the mesic savannas of Zambia and Malawi. I developed a landscape map for each of five study areas. Using these maps, I applied four FRAGSTATS metrics to quantify different aspects of landscape heterogeneity within the study areas, as well as elephant home ranges and randomly located ranges delineated using a 95% Kernel estimation. I placed similar study areas into comparable groups for each of the landscape heterogeneity metrics.

Elephant home range size was not a function of landscape heterogeneity metrics and may therefore be explained by other factors. Landscape complexity and diversity of elephant home ranges varied within groups of similar study areas, suggesting that these metrics were important descriptors of home range location. Within study areas, with the exception of patch density, landscape heterogeneity metrics supported the expectation that wet season ranges would be more heterogeneous than those of the dry season. In addition, female ranges were more heterogeneous than those of males during the wet seasons with respect to both patch density and landscape diversity. In most cases, greater landscape heterogeneity within home ranges was only shown during the wet season and this suggests that water requirements preclude selection for more heterogeneous landscapes during the dry season. However, elephants of the Zambian study areas, besides Kafue, selected for metrics indicative of landscape complexity and diversity during both dry and wet seasons. I therefore concluded that elephants favoured complex landscapes with more vegetation types in irregularly arranged patches and landscape heterogeneity therefore determines the location of elephant home ranges.

At a regional scale, a landscape comprises habitats of varying suitability to elephants. In a metapopulation framework, such areas may form sources or sinks and therefore contribute to driving elephant movements. The ability to identify areas of importance to elephant range utilization is therefore an essential tool to apply within the megaparks for metapopulations conservation framework.

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Finally, my parents deserve special thanks as they have always and continue to provide me with love and unquestionable support in all spheres of my life.

Declaration

I hereby declare all the work to be my own and has not been undertaken at any other university but the University of Pretoria. Furthermore, I have acknowledged all those who helped me and contributed to the production of this thesis.

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GLOSSARY OF TERMINOLOGY, ACRONYMS AND CONTRACTIONS

Bull	Used synonymously for ‘male elephant’ or ‘male’
Cow	Used synonymously for ‘female elephant’ or ‘female’
Diversity Index	Shannon’s Diversity Index used as a FRAGSTATS landscape heterogeneity metric (McGarigal and Marks 1995). Also referred to as ‘landscape diversity’, see Table 6 for a detailed description
Dry Season 1	Period from May to October 2004 for all parks, shortened to ‘Dry 1’ in some tables
Dry Season 2	Period from May to October 2005 for all parks except Kafue, where it represents the period between May and October 2003, shortened to ‘Dry 2’ in some tables
CERU	Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria
Elephant ranges	95% Kernel home ranges based on daily location data of elephants fitted with satellite-tracking devices
Extent	Size of the study area under consideration (Turner et al. 2001)
Fractal Index	Perimeter-Area Fractal Dimension Index (PAFRAC), a FRAGSTATS landscape heterogeneity metric (McGarigal and Marks 1995). This metric is described in Table 6 and is also referred to as ‘patch shape complexity’
Grain	The finest possible level of spatial resolution of a given data set (Turner et al. 2001)
Interspersion Index	Interspersion and Juxtaposition Index (IJI), FRAGSTATS landscape heterogeneity metric (McGarigal and Marks 1995). Also referred to as ‘landscape complexity’, this metric is defined fully in Table 6
Kafue	Kafue National Park (KNP) in Southern Province, Zambia
Kasungu	Kasungu National Park in central Malawi (KsNP)
Landscape Heterogeneity	the complexity and variability of patch mosaics in space (Li and Reynolds 1994), measured in this project using four FRAGSTATS metrics

Lower Zambezi	Lower Zambezi National Park in Lusaka Province, Zambia (LZNP)
Luangwa	North and South Luangwa National Parks (treated as a unit – LNP) in Northern Province, Zambia
North Luangwa	North Luangwa National Park in Northern Province, Zambia
Patch Density	Patch Density (PD), a FRAGSTATS landscape heterogeneity metric (McGarigal and Marks 1995). This metric is defined in Table 6 and is referred to as patch density
Patch mosaic	Formed by the area of a given landscape being divided into contiguous patches with no intervening matrix (Reiners and Driese 2004)
Patch Richness	Patch Richness Density, FRAGSTATS landscape heterogeneity metric (McGarigal and Marks 1995)
Random ranges	95% Kernel estimations of points generated at random locations within each of the study areas
Range size	Used to refer to the area (km^2) of both elephant home ranges and randomly located ranges, to prevent confusion with ‘area’ as a locality e.g. study area
Raster grid	A landscape composed of grid cells of equal size, treated as members of binary units and limited to a number of classes, or with infinitely variable values for the property of interest, e.g. spectral signature given off by different land cover types (Reiners and Driese 2004)
Resolution	Grain size of spatial data (Turner et al. 2001)
Scale	The spatial dimension of an object or process, characterized by both grain and extent (Turner et al. 2001)
South Luangwa	South Luangwa National Park in Northern Province, Zambia
Vwaza	Vwaza Marsh Wildlife Reserve in northern Malawi (VWR)
Wet Season 1	Period from November 2004 to April 2005 for all parks, shortened to ‘Wet 1’ in some tables
Wet Season 2	Period from November 2005 and April 2006 for all parks except Kafue, where it forms the period between November 2003 and April 2004. Shortened to ‘Wet 2’ in some tables

CHAPTER 1

INTRODUCTION

Southern African savannas are heterogeneous across time and space (e.g. Rogers 2003). Since savanna elephants *Loxodonta africana* (Blumenbach 1797) selectively use resources within landscapes (e.g. Kinahan et al. 2007), landscape heterogeneity may underlie their range utilization. My study therefore aimed to examine landscape heterogeneity as a determinant of the variability in elephant home range location and area in the miombo woodlands of the mesic savanna region.

Linking elephant range utilization to landscape heterogeneity

Within populations, range utilization differs between bulls and breeding herds (e.g. Hall-Martin 1987; Stokke and du Toit 2002). Females feed on a wider range of plants and are more selective foragers than males, while they generally occupy smaller ranges (e.g. Stokke 1999; Shannon et al. 2006). Such differences may relate to sexual dimorphism of elephants[1] as well as the energetic implications this may have for foraging (Clutton-Brock and Harvey 1978). Furthermore, group-living (Fritz and De Garine-Wichatitsky 1996) and dependent offspring (Clutton-Brock et al. 1989; Stokke 1999; Stokke and du Toit 2002) constrain the feeding duration and locality of females. These factors effectively render males and females as distinct ecological species (e.g. Bowyer 2004), particularly in terms of range utilization and suggest that females may be more responsive to landscape heterogeneity than males.

Seasonal variation in elephant range utilization may partly be explained by their dependence on water (Osborn and Parker 2003; Ntumi et al. 2005) and therefore ecological factors, particularly rainfall. Elephants range close to water sources, especially during the dry

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[1] According to Shrader et al. (2006), the average shoulder height of adult males is 316.6 ± 12.9 (S.E.) cm, compared to that of females measured at 230.2 ± 1.8 (S.E.) cm.

season (De Villiers and Kok 1984; 1988; Verlinden and Gavor 1998; Osborn and Parker 2003; de Beer et al. 2006) when the distribution of water is limited. Water therefore forms a so-called 'key resource' (see Illius 2006) for elephants and this may explain why dry season elephant home ranges are usually smaller than those of the wet season.

Illius and O'Connor (2000) suggested that since drinking water is a spatial resource, its depletion during the dry season forces herbivores to restrict their ranging to areas accessible from perennial water sources and abandoning outlying areas, regardless of the abundance of food. Therefore range selection by elephants, whether influenced by sex or season should be particularly apparent during the wet season when the distribution of water no longer limits movements. For instance, elephants in Amboseli National Park, Kenya, obtain higher quality food by migrating to bushlands during the rains (Western and Lindsay 1984). Furthermore, Verlinden and Gavor (1998) demonstrated that in northern Botswana some elephants moved away from perennial water sources during the wet season to range in nutrient rich patches[2]. Differences in range size may also be attributed to landscape heterogeneity (e.g. Grainger 2005), should the indices of such heterogeneity reflect on resource availability. However, following the habitat-diversity hypothesis (as first proposed by Gleason 1922; and reviewed by McGuinness 2000), larger home ranges should be more heterogeneous.

Landscapes are inherently heterogeneous (Turner 1989). Such heterogeneity reflects on resource availability to animals (Wiens 1989). However, some portions of a landscape are more heterogeneous than others and could be more suitable for resource extraction by elephants and other species.

For my study, I defined landscape heterogeneity as the complexity and variability of patch mosaics in space (see Li and Reynolds 1994). Landscape heterogeneity is indicative of

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[2] Patches may be defined as spatial units and a particular resource value can be attributed to each of these (e.g. Mitchell and Powell 2004).

different attributes (e.g. soil types, degrees of transformation, vegetation classes, temperature gradients, water availability) arranged in patches across the landscape (Li and Reynolds 1994), which can be studied at various scales (Sparrow 1999). Elephants and other herbivores may benefit from heterogeneous landscapes since these have more habitat edges that increase resource availability and forage opportunities (Tufto et al. 1996; Saïd and Servanty 2005). By implication, landscape heterogeneity suggests variety in patch types, which in turn may result in increased resilience and therefore resource stability for herbivores (e.g. Peterson 2002; van de Koppel and Rietkerk 2004). Therefore, patch shape, which influences edge length, along with the number, arrangement and diversity of patches may explain patterns in foraging efficiency.

At least two previous studies demonstrate the importance of heterogeneity of vegetation classes at the landscape scale to elephant range utilization. In the Sebungwe Region of Zimbabwe, areas in which elephants occur are characterized by a larger number of different patches than those from which elephants were absent (Murwira and Skidmore 2005). Grainger et al. (2005), using a different set of metrics to the four I have chosen, suggest that indices of heterogeneity may explain variability in home range area for elephants in the Kruger National Park, South Africa. Furthermore, Kinahan et al. (2007) established that temperature gradients imposed by landscape differences influence elephant ranging in Kafue National Park and Lower Zambezi National Park, Zambia.

By definition, the home range[3] fulfils the resource requirements of an animal (Mitchell and Powell 2004). According to Powell (2000) home ranges are structured by an animal's need to efficiently locate and utilize resources. Indeed, morphological and physiological constraints limit animals to only a portion of the total landscape available to them, and within that region, social, energetic costs and risk factors further influence movement patterns

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[3] An area to which animals are confined through energetic, morphological and social constraints, in which they enact their daily activities, including resource-gathering (McNab 1963; Ford and Krumme 1979; Powell 2000)

(McNab 1963; Ford and Krumme 1979; Mitchell and Powell 2004). Since landscape heterogeneity determines the spatial arrangement of such resources, I argue that it may affect the movement patterns of animals through its influence on foraging behaviour (e.g. Johnson et al. 1992). Indeed, Morris (1989) proposed that optimal foraging theory (as first proposed by Emlen 1966; MacArthur and Pianka 1966), influences habitat selection as a result of the energetic costs associated with avoiding or moving through unbeneficial patches. An animal may therefore gain resources more efficiently through the optimal selection of patches containing resources (Mitchell and Powell 2004). I would expect these costs to be particularly high for a large-bodied mammal such as the elephant, for which much energy is utilized to locate patches containing resources (McNab 1963). In addition, it is possible that elephants living in landscapes that are more heterogeneous would have smaller home ranges, since more resources are available than in less heterogeneous landscapes. Elephants may only be able to react to heterogeneity and begin to range optimally during the wet season, when selection is not dictated by the distribution of water.

Allometric laws suggest that larger species require larger home ranges (McNab 1963; Ford 1983; Kelt and van Vuren 2001), but differences in landscape heterogeneity may mask such a relationship. For instance, home ranges in a heterogeneous landscape may be smaller than predicted by body size due to increased resource availability (Harestad and Bunnell 1979; Ford 1983; Turner 1989; Wiens et al. 1993; Gough and Rushton 2000; Saïd and Servanty 2005).

The uneven distribution of elephants within the protected areas of my study region (see Caughley and Goddard 1975; Jachmann and Bell 1979; Guldemond et al. 2005) suggests that resources of importance to elephants are unevenly distributed across these landscapes. However, to the best of my knowledge, the relationship between elephants and resource distribution within these study areas has not been examined.

Conservation Implications

It is widely accepted that elephants may threaten biodiversity when occurring at high densities (Skarpe et al. 2004; Owen-Smith et al. 2006). Van Aarde et al. (2006), amongst others advocate the development of conservation paradigms that will naturalize landscape utilization patterns to ameliorate the apparent impact of elephants on biodiversity. Van Aarde and Jackson (2007) take this a step further and posit that the application of a metapopulation model may lead to regional stability in numbers, as well as reducing local impacts. The application of their ideas depends on identifying appropriate linkages between existing populations, to allow for the restoration of traditional movements and dispersal. For such linkages to be successful, their delineation needs to cater for resource selection by elephants (see Chetkiewicz et al. 2006). Factors that underlie elephant range utilization therefore need to be understood to effectively manage such a system (Nielsen et al. 2006). Selection expressed in terms of landscape heterogeneity metrics may therefore be a step towards informed conservation planning, especially since this method may be applied across the distributional range of free-ranging elephants within southern Africa. My thesis aimed at determining how elephants select for landscape heterogeneity across miombo woodlands. The overall approach is novel but incorporates both spatial and temporal aspects of the landscape with the elephants’ needs as advocated by amongst others, Chetkiewicz et al. (2006), using standard landscape ecology procedures.

Predictions

Given the potential of heterogeneity to influence elephant range utilization explained above, I hypothesize that landscape heterogeneity should be a determinant of the location and size of elephant home ranges. In this thesis, I will investigate a number of predictions that could collectively validate this hypothesis.

I will be using four FRAGSTATS metrics to quantify landscape heterogeneity, two of these (Patch Density and Fractal Index) take into account the area of the landscape being assessed, whilst the other two (Interspersion Index and Diversity Index) do not. All four these metrics reflect on aspects of patchiness of the landscape and conceivably, patchiness in resource distribution. An increase in the value of a metric suggests an increase in aspects of landscape heterogeneity. For instance, an increase in the number of patches (measured by Patch Density) suggests an increase in the number of places within the home range to forage. If these patches are irregular in shape (measured by Fractal Index), the amount of edge and thus resource availability may further increase (as suggested by Tufto et al. 1996). In addition, if these patches are arranged evenly across the landscape (calculated by Interspersion Index), more different patch types are available per unit area which is further improved if patch diversity is high (measured by Diversity Index). Consequently, changes in these metrics reflect on changes in resource characteristics. I therefore expect that elephant home range size will decrease with increases in all of the metrics.

Should elephants be selecting for these aspects of landscape heterogeneity, I expect the randomly located home range sizes to increase with increased Patch Density and Fractal Index, but to vary independently of Interspersion and Diversity Index.

- I expect that elephant home ranges will be located in more heterogeneous areas than randomly located ranges of similar size and shape in the same study area.

Following my earlier arguments, the data allowed me to investigate whether the variability in the size and the location of elephant home ranges can be explained by metrics of landscape heterogeneity that reflects on patchiness in vegetation structure. I expected that:

- The landscape heterogeneity of the elephant home ranges will not vary significantly between comparable study areas.
- Landscape heterogeneity of elephant home ranges during the wet season will be greater than during the dry season.
- Landscape heterogeneity in home ranges of females will be greater than that of males.

Approach

In this thesis, I quantified landscape heterogeneity of elephant home ranges across miombo woodlands within Zambia and Malawi. I assumed that all landscapes within the study areas are equally available to elephants for selection.

I relied on Landsat TM imagery with a pixel of size of 30 × 30 m to generate landscape maps based on verified structural vegetation classes for each of the five study areas. I estimated the 95% Kernel home ranges of remotely tracked satellite-collared elephants within these areas using locations collected at 24-hour intervals, during two dry and two wet seasons. I also used the 95% Kernel method to delineate randomly located ranges of similar size to the elephant ranges.

I used four metrics to quantify different aspects of the landscape heterogeneity of study areas, elephant home ranges and randomly located ranges. These metrics describe both spatial (Fractal and Interspersion Index) and compositional (Patch Density and Diversity Index) aspects of the landscape (see Reiners and Driese 2004). I investigated whether the size of elephant home ranges was a factor of increasing landscape heterogeneity. Furthermore, I compared landscape heterogeneity metrics of elephant home ranges for each study area, season and sex. I also compared the metrics of the elephant ranges with those of similar-sized randomly located ranges using a modelling approach. Selection for landscape heterogeneity was inferred when the heterogeneity metrics for elephant ranges exceeded those of similarly sized randomly located ranges. To the best of my knowledge, this analytical approach is novel.

CHAPTER 2

STUDY REGION

My study took place in six conservation areas situated across southern Africa's miombo woodlands in Zambia and Malawi (Table 1). These include Kafue National Park, Lower Zambezi National Park, North and South Luangwa National Parks (later treated as a single entity), Kasungu National Park and Vwaza Marsh Wildlife Reserve (Figure 1). The spatial extent of my study is that of a reserve as defined by its boundaries and its adjoining Game Management Areas.

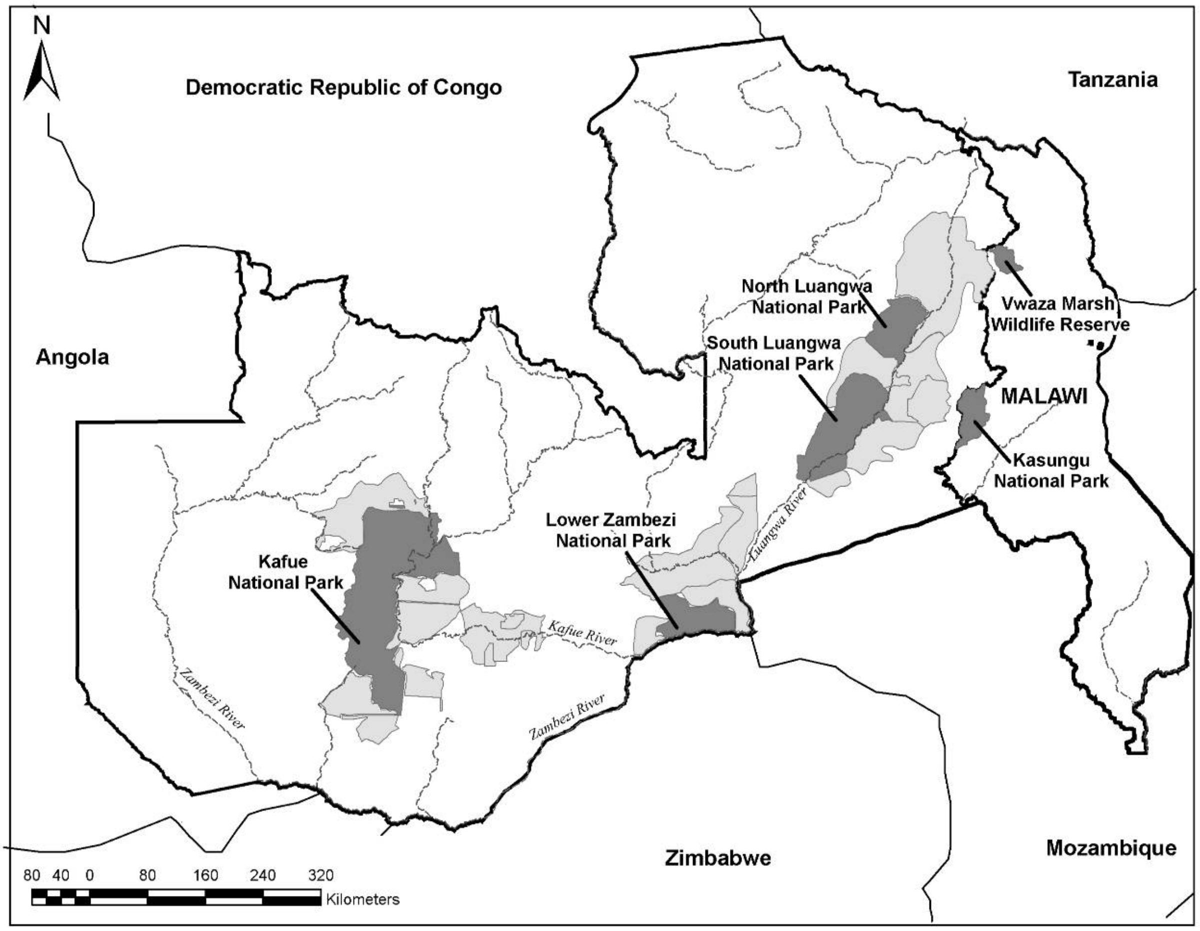

Figure 1. A map that illustrates the locations of the conservation areas (dark grey) included in this study. The Game Management Areas and Forest Reserves that surround these are depicted in light grey. Dashed lines indicate major rivers within Zambia and Malawi.

The miombo woodlands cover about 2.7 million km^2 of the continent, dominating the southern African savannas, and constituting a substantial proportion of the current range of elephants (White 1983; Campbell et al. 1996). These woodlands occur on dystrophic non-calcareous soils (Huntley 1982; Frost 1996) and usually receive more than 700 mm of rain per year, most thereof from November to March (Cole 1986). All the conservation areas in my study region are situated in the mesic or unstable savannas as defined by Sankaran et al. (2005). Such savannas receive more than 650 ± 134 mm mean annual precipitation and disturbances, such as fire, apparently enable trees and grass to coexist (Sankaran et al. 2005). Indeed, fires occur often in the miombo woodlands during the dry season (Frost 1996). Tree species dominating the miombo woodlands are deciduous, but leaves are only shed in the late dry season and the trees thus remain leafless for less than three months. Triggered by increased temperatures and humidity, the new flush appears before the onset of the rains, possibly because most of the species are able to tap water from underground sources and have water storage organs (Cole 1986; Frost 1996).

Table 1. The locations and sizes of the study areas included in this study. The number and sex of elephants satellite tracked in each of these is also presented. The areas are of the parks alone and exclude surrounding Game Management Areas (GMA).

Study Area	Location		Size (km^2)	Number and sex of satellite tracked elephants
	Latitude (d° mm')	Longitude (d° mm')		
Kafue National Park	14°05' - 16°41'S	25°12' - 26°45'E	22 270	10 (5 ♀♀, 5 ♂♂)
Lower Zambezi National Park	15°09'- 15°39'S	30°57'- 32°07'E	4 150	6 ♀♀
North Luangwa National Park	11° 27' - 12° 19'S	31° 48’ - 32° 34’E	4 530	3 ♀♀
South Luangwa National Park	12° 24' - 13° 46'S	30° 57’ - 32° 07’E	8 970	5 ♀♀
Kasungu National Park	12° 33' - 13° 22'S	32° 56’ - 33° 21’E	2 350	2 ♀♀
Vwaza Marsh Wildlife Reserve	10° 49' - 11° 11'S	33° 20’ - 33° 45’E	950	3 ♀♀

The parks in the study region are not fenced and wildlife is able to roam onto surrounding lands. The surrounding lands of the Zambian parks are mostly Game

Management Areas[4] (GMA's) where few people lead subsistence livelihoods. These areas form buffer zone around each of the parks and many large mammal species occur here. However, the parks of Malawi (Kasungu and Vwaza) are surrounded by densely populated, transformed land. Here, the stark contrast between human-dominated landscapes and conservation areas is clearly visible on both raw Landsat TM images and classified landscape maps (see Plate 4).

Description of study areas included in the study region

I discuss the major vegetation associations found within each study area in this section. These are different to the structural vegetation classes that I used to classify the maps of each study area.

Kafue National Park, Zambia

The Kafue National Park[5] in south-western Zambia is the largest of Zambia's parks. The park is surrounded by 15 GMA's. My study concentrated on elephants moving across the southern part of the park and the surrounding GMA's. Regional altitudes vary between 1000 and 1500 m above sea level (NPWS/JICA 1999). The Kafue valley is relatively flat and the Kafue River descends by only 15 m over 410 km, forming many floodplains (Rees 1978; Ellenbroek 1987) that are inundated during the wet season (NPWS/JICA 1999; Munyati 2000). The park forms 21% of the catchment area of the main drainage system for the region, the Kafue River, which also delineates the eastern boundary of the southern part of the park (Rees 1978). A number of seasonal tributaries run throughout the park, but usually only the Kafue and Lunga Rivers flow during the dry season (May to October). During the wet season, water is widely available along tributaries in pans, oxbow lakes and lagoons. Pans in dambo grasslands that occur

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[4] Game Management Area (GMA): legally designated area of land, adjacent to a National Park, where hunting wildlife managed as a resource by the local people (Astle 1999)

[5] Kafue National Park will be referred to as 'Kafue' from this point forward

throughout this study area are additional sources of water through most of the year. The Itezhi-tezhi dam, which covers ~ 370 km^2, 90 % of which is inside the park, is another source of water for wildlife. Given the wide distribution and varying sources of water, its availability may not be limiting animal movements.

Mean annual rainfall for the north and south of Kafue is 1200 and 600 mm respectively (NPWS/JICA 1999)[6]. Most of the rain falls between November and April, a period that I will refer to as the wet season for all study areas. A relatively cool dry season follows the wet season until August, whilst September and October form the hot, dry season (Ellenbroek 1987). However, for all my study areas, I have defined a single dry season as the period between May and October. During the hottest month (usually October), mean minimum and maximum temperatures are 18 and 35°C, respectively. During the coolest month (usually July), these values are 15 and 28°C respectively (NPWS/JICA 1999).

The NPWS/JICA Project (1999) distinguished nine vegetation types in Kafue (on which we later based our classification). These included *Baikeaia* forest, Secondary *Baikeaia* woodland, Riparian woodland, Miombo woodland, Kalahari woodland, Mopane woodland, Munga shrubland, Termitaria vegetation and Grasslands.

***Baikeaia* Forests** have a tall canopy layer (15 – 20 m height), which mainly comprises *Baikeaia plurijuga* and *Pterocarpus antunesii*. These forests are restricted to well-drained Kalahari sands (Cole 1986; NPWS/JICA 1999). A 2 – 5 m tall shrubland in these forests includes species such as *Friesodielsia obovata* and *P. antunesii*. In some places, dense clusters of *Baphia massaiensis* occur adjacent to the forests.

Secondary *Baikeaia* woodlands are usually dominated by the same species as the forests, but is not as tall (12 – 16 m height) and the canopies of individual trees do not overlap. In addition, in the canopy layer *Combretum collinum* and *Xeroderis stulmannii* are

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[6] These authors reported on neither the variability, nor the source of these mean values.

more common than in the canopy of the forests. The shrub layer is dominated by *Markhamia obtusifolia*.

Riparian woodlands on the riverbanks and islands of the Lufupa and Kafue Rivers are evergreen and the canopy reaches a height of between 2 – 8 m, although some trees could be 15 m tall. Common tree species include *Diospyros mespiliformis*, *Sapium ellipticum* and *Syzygium guineense* (NPWS/JICA 1999). The shrub layer is dominated by various low-growing species.

The canopy layer (8 – 15 m height) of the Kafue **miombo woodlands** are dominated by *Brachystegia spiciformis* and *Julbernardia paniculata* (Rees 1978; Ellenbroek 1987; NPWS/JICA 1999). Lower layers vary in height and coverage depends on soils, climatic conditions and the incidence of fire. Few shrubs and small trees such as *Bauhinia petersiana* and *Uapaca* sp. grow here.

Some of the species in **Kalahari woodlands** are the same as those of the miombo woodlands, but canopy cover is discontinuous and at a height of 12 – 16 m, with a 2 – 4 m high shrub layer. In addition to the characteristic miombo species, the Kalahari woodlands also support *Burkea africana*, *Parinari curatelifolia* and *Julbernardia globiflora*.

Mopane woodlands are characterized by homogeneous stands of *Colophospermum mopane* and are restricted to alluvial soils (Rees 1978; Ellenbroek 1987; NPWS/JICA 1999). Singular *Adansonia digitata* and *Acacia nigrescens* are occasionally associated with these woodlands, and the shrub layer is dominated by *Boscia matabelensis*, *Markamia acuminata*, *Sclerocarya birrea* and *Balanites aegyptiaca*.

Munga shrublands comprise sparse clumps of low-growing (2 – 6 m height) trees and shrubs on black clay soils (vertisols). Dominant species include *Bauhinia thonningii, Acacia nilotica*, *A. polyacantha* and *Combretum fragrans*.

Termitaria vegetation consists of plant associations (usually Mopane, Riparian or Munga) on termite mounds. Other species in the canopy layer include *Diospyros mespiliformis, Euphoribia ingens* and *Capparis tomentosa* (14 – 16 m height).

Grasslands are predominantly treeless, but some trees do occur occasionally. Dominant grass species include members of the genera *Loudetia*, *Monocymbium*, *Eragrostis*, *Setaria*, *Digitaria* and *Themeda* (NPWS/JICA 1999). Dambo grasslands are discussed in further detail on page 19.

Giraffe *Giraffa camelopardalis* (Linnaeus 1758), tsessebe *Damaliscus lunatus lunatus* (Burchell 1823) and black rhino *Diceros bicornis* (Linnaeus, 1758) may be locally extinct but large mammal species considered typical for the region continue to occur in Kafue (NPWS/JICA 1999). Much like in other conservation areas in Zambia, Kafue's elephant population historically suffered from unsustainable hunting and later, poaching for ivory (NPWS/JICA 1999; Guldemond et al. 2005). Regular aerial censuses of large mammals only began in 1994 and in 2005 an estimated 1 738 ± 181 (S.E.) elephants occurred in the park. This is a density of 0.07 elephants per km^2 and this paper also suggested that the population may be declining (Guldemond et al. 2005). Elephant density is higher in the southern portion of the park than in the north (NPWS/JICA 1999). Nine GMA's and Forest Reserves adjoin Kafue. The GMA's serve as traditional subsistence areas but some commercial sugarcane agriculture and mining takes place in some areas (NPWS/JICA 1999; Munyati 2000).

Lower Zambezi National Park

Situated on the northern bank of the Zambezi River, Lower Zambezi National Park[7] is flanked by five GMA's in Zambia. The Zambezi Valley was formed by trough-faulting during the mid-Cretaceous period which caused the Karoo strata to sink several hundred metres. As a result, the northern escarpment is very steep in places and generally inaccessible, but the

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[7] To be referred to as 'Lower Zambezi' from this point forward

northern valley floor between the escarpment and the Zambezi is flat (Jarman 1972; Kerr and Fraser 1975; Dunham 1986; 1988). The escarpment bisects the north-western half of the park as it angles away from the Zambezi to the north-east to connect with the western wall of the trough (Cole 1986). The park is not fenced.

The Zambezi River lies in the trough for almost its entire length and is accessible to large mammals along most of its northern bank. Water is also available in streams and ponds throughout the wet season, whilst in the height of the dry season the only available water is that of the Zambezi River and its major tributaries (Jarman 1972). The Zambezi's annual floods are caused by rain over the upper river catchment in Barotse Province. However since the establishment of the Kariba Dam (known as Lake Kariba), such flooding no longer occurs annually (Jarman 1972).

The climate of the Zambezi Valley is very hot and humid, with mean daily temperatures of 30ºC in July and 39ºC in October – the hottest month (Jarman 1972; Dunham 1986). Mean annual rainfall is 800 mm and falls between November and April (Jarman 1972; Kerr and Fraser 1975; Dunham 1986; 1988)[8].

Mopane woodlands dominate the Zambezi Valley, occurring on alkaline black clay soils weathered from Karoo basalts. These woodlands are leafless for five months of the year (White 1983). North-east from the floodplain the vegetation is dominated by tall, closed mopane woodland on sandy or clay soils, whilst open mopane woodlands form the majority cover over most of the valley floor (Kerr and Fraser 1975; Cole 1986; Dunham 1988). At the foot of the escarpment sandy soils support thick deciduous associations characterized by a band of dry **deciduous woodlands** that comprise *Commiphora* and *Combretum* species. Scattered amongst these are *Kirkia* spp., *Sterculia* spp., *Adansonia digitata, Pterocarpus angolensis* , *P. brenanii* trees and a dense shrub layer (Cole 1986).

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[8] These authors reported on neither the variability, nor the source of these mean values.

Miombo woodlands (dominated by *Brachystegia* spp. and *Julbernardia globiflora*) cover the escarpment (Cole 1986) as is the case along the Luangwa Valley (discussed in greater detail on page 17).

Riparian forests along the banks of the major rivers are dominated by *Faidherbia albida* trees growing in dense groves and forming a continuous canopy with a very open grass understorey. Other associated tree species include *Kigelia africana*, *Combretum imberbe* and various *Acacia* spp (White 1983).

In watershed areas **dambo grasslands** also occur in mosaic with shrublands and grasslands. Species associations of these are similar to those of the Luangwa Valley dambos and are discussed on page 19.

Elephant, buffalo *Syncerus caffer* (Sparrman 1779) and hippopotamus *Hippopotamus amphibious* (Linnaeus 1758) apparently make up the bulk of biomass of the Zambezi Valley. The area's black rhino population is small due to poaching pressure. The elephant population is no longer exposed to culling as was the case between 1960 and 1980's (White 1983; Dunham 1988). Elephant regularly cross the Zambezi River between Lower Zambezi National Park and Mana Pools National Park (Dunham 1988). In 2003 there were about 1 500 elephant in the park (a density of 0.36 elephant per km^2) and the surrounding GMA's within Zambia (Dunham 2004).

The Luangwa Valley

The Luangwa Valley forms part of the broad forested trough that covers approximately 144 000 km^2 and runs from the Nyika Highlands in the north to the Zambezi Valley in the south (Caughley 1976; Jachmann 1995; Dunham 2004). The valley contains four National Parks. North and South Luangwa National Parks[9] are the largest of these and are located in the north-eastern section of Zambia. South Luangwa covers the mid-Luangwa valley between the

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[9] North and South Luangwa National Parks will be referred to as the North and South Luangwa respectively, or Luangwa as a whole, from this point forward

Muchinga Escarpment in the west and the Luangwa River flowing southwards. North Luangwa extends from the Munyamadzi GMA to the Lufila River in the north (Smith 1997). The Munyamadzi Corridor GMA links these two parks, spanning about 40 km between them. On the Luangwa River's eastern bank, additional GMA's and two National Parks (Lukusuzi National Park and Luambe National Park) form a continuous buffer zone along the parks' eastern boundary (see Figure 1). Within these, people practice subsistence fishing, hunting and agriculture (Astle et al. 1969). South Luangwa boasts several lodges and has a good road network, whilst North Luangwa is relatively inaccessible.

The down-faulting which formed the trough of the Luangwa Valley (during the same period in which the Zambezi Valley was formed), preserved the Karoo strata on the valley floor. The dual effect of volcanic action during down-faulting and ancient sedimentary rock formed a nutrient-rich parent rock. It is through these strata that the Luangwa River has carved its path, depositing alluvium (Smith 1997). The flat-floored trough and soft rock resulted in a meandering river with flood plains and oxbow lakes along its periphery (Caughley and Goddard 1975; Smith 1997).

The western boundary of the valley is distinctive as the Muchinga Escarpment rises at places to 700 m above the valley floor, with an even crest at 1 400 m (Astle et al. 1969). The eastern boundary is less well defined. The middle reaches of the valley are 100 km wide. In other places, the river flows through a meander belt that can be up to 5 km wide (Astle 1999).

Other than the Luangwa River and its major tributaries that arise from the plateau, there are few permanent sources of water in the Luangwa Valley. Smaller rivers that drain the valley floor only flow during the wet season. All rivers are subject to flash flooding during the wet season (Astle 1969). Approximately 700 – 800 mm of rain, usually in the form of heavy storms, falls during a single wet season from November to April (Astle et al. 1969; Hanks 1972; Jachmann 1995). The coolest month in both North and South Luangwa is usually June, when a maximum temperature of 29 and 27ºC have been recorded, respectively. October is usually the hottest month, when a maximum of 36ºC was recorded in both parks (Astle et al. 1969; Smith 1997)[10].

The various sedimentary rocks of the Karoo system each form distinctive landscapes with characteristic soils and vegetation (Astle 1999). The dominant vegetation of the plateau areas and south-facing slopes is miombo woodlands, dominated by *Brachystegia* spp., *Julbernardia* spp. and *Isoberlinia* spp. (Astle et al. 1969; Cole 1986; Smith 1997). The woodland canopy varies between 5 and 25 m in height and the mature woodlands have a short to medium height herb layer beneath them (Caughley and Goddard 1975). There are also vast areas of coppiced and shrubby *Brachystegia* with short grass indicative of past elephant utilization and human settlement (Astle et al. 1969). Smith (1997) identified two types of miombo woodlands; upper escarpment and plateau miombo and lower escarpment and hill miombo.

Upper escarpment and plateau miombo woodlands are further separated into three sub-types: upper escarpment miombo, plateau miombo and rupicolous miombo. Upper escarpment miombo is multi-layered with a canopy of 15 – 20 m in height occurring at elevations of more than 1 000 m. In addition to the dominant species, the canopy includes *Marquesia macroura, Parinari curatellifolia* and *Pericopsis angolensis* (White 1983; Smith 1997). Plateau miombo is characterized by nutrient poor, leached soils. The growth of *Brachystegia* and *Julbernardia* spp., interspersed by *Uapaca, Protea, Faurea* and *Monotes* species is stunted, but the grass layer is well-developed. Rupicolous miombo woodland occurs in rocky areas of the escarpment and in addition to the dominant species mentioned above, may also include *Pterocarpus rotundifolius* and *Kirkia acuminata*.

The dominant species of **Lower escarpment and hill miombo woodlands**, like plateau miombo, is *Julbernardia* spp. and *Brachystegia* spp. and this woodland type covers

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[10] These authors reported on neither the variability, nor the source of these mean values.

the lower reaches and foothills of the escarpment. Lower escarpment and hill miombo is separated into two sub-types: *Brachystegia stipulata – Julbernardia globiflora* miombo scrub woodlands and *Julbernardia – Brachystegia* open miombo woodlands. The scrub miombo occurs at elevations between 700 – 1000 m, usually in mosaic with open miombo woodland. With few small trees, it forms tall scrub woodland at 3 – 5 m in height. In addition to the dominant miombo species, *Diplorhynchus condylocarpon*, *Combretum zeyheri* and *Monotes africanus* also occur. The grass layer is sparse but has a similar composition to that of escarpment miombo. The open miombo woodlands are found on deep, slightly acid sandy soils of the hill tops and ridges of the lower escarpment. It comprises scattered small trees, ranging in height from 15 – 20 m, and a well-developed grass layer with occasional shrub patches. Co-occurring species to the miombo dominants include *Burkea africana*, *Pterocarpus angolensis* and *Terminalia sericea*.

The vegetation of the alluvial complex is composed of a mosaic of Dambo grasslands, floodplains and floodplain grasslands, riparian woodlands, *Combretum – Terminalia* woodlands, mopane woodlands and *Kigelia – Combretum* woodlands (Caughley and Goddard 1975). Mopane woodlands occur in shallow alkaline clay soils, whilst *Combretum – Terminalia* associations are found in well-drained sandy soils (Caughley and Goddard 1975; Lewis 1991; Jachmann 1995). These vegetation types are discussed in more detail below. This information was extracted mainly from the checklist of the vegetation of North Luangwa prepared by Smith (1997).

Valley riverine grasslands are associated with the oxbow lakes, drainage lines, floodplains and dambos of the large rivers in the valley. These features are composed of deep, recently deposited alluvial soils of varying textures. The various substrate textures support different communities and three grassland associations have been recognized. ***Cynodon-Eragrostis* grasslands** form on the sandy soils of the sand bar deposits and inside curves of the rivers and streams. A wide range of height classes and species of grass occur, including

Andropogon gayanus, Digitaria milanjiana, Eragrostis spp. and *Heteropogon contortus. Cynodon dactylon* carpets the compacted sand bars and dry river channels. ***Setaria-Hyparrhenia* grasslands** and wooded grasslands occur on clay soils associated with the floodplains of larger rivers, to form distinctive tall grasslands. Dominant species include *Hyparrhenia rufa* in brown clay-loam soils, and pure stands of *Setaria incrassata* on black clays. These clay soils also support herbaceous vegetation in some areas, dominated by species of the Acanthaceae family. This riverine grassland association often grades into wooded grassland consisting of scattered trees, like *Kigelia africana, Acacia* spp. and *Combretum* spp. Associations of **aquatic grasslands** are found in the seasonally waterlogged clays of the Luangwa River's oxbow lakes and dambos. They remain under water for most of the wet season and are dominated by grasses such as *Oryza barthii*, *Sporobolus pyramidalis* and *Setaria* spp. Sedges, including various *Cyperus* species, and herbs also inhabit these areas.

Dambo grasslands are localized, seasonally inundated grasslands and are found in all the study areas. These occur in low-lying watershed areas and can be up to one km wide and several kilometres long (Astle et al. 1969; Caughley and Goddard 1975; Smith 1997). They may have pans in their centre that hold water well into the dry season due to a seasonally high water table (Astle et al. 1969). Dambos have characteristic herb and grass components. The soils of dambos are compacted and poorly drained, leached alluvial soils with a low pH. Early in the wet season the dambos are typified by a few species such as *Loudetia simplex* and *Setaria* spp.. Towards the end of the wet season, *Hyparrhenia* species dominate. Some of the herbs usually associated with dambos of the upper escarpment include *Euphorbia cyparissioides*, *Gladiolus* and *Thunbergia* spp. Dambos of the lower lying areas have a similar species composition but various water-associated grasses and herbs may also occur. Grasses include species such as *Themeda triandra, Digitaria. milanjiana* and *Setaria* spp..

Secondary grasslands occur in recently deposited alluvium on degraded mopane woodland. The characteristic grasses are *Chloris virgata, Dactyloctenium aegyptium* and *Echinochloa colona*, punctuated by clumps of *Combretum obovatum* thicket.

***Combretum – Terminalia* woodlands** are apparently maintained by dry season fires and form close associations with *Combretum* and mixed alluvial thickets parallel to the Luangwa River. This association is a likely consequence of fire-induced succession. *Combretum – Terminalia* woodlands cover large areas of the valley floor in mosaic with lower escarpment miombo at altitudes of 650 – 700 m above sea level. They are open, one to two-storey woodlands, with canopy species of up to 20 m tall. Other large tree species include *Pseudolachnostylis maprouneifolia, Pterocarpus angolensis,* and *Burkea africana*. In deeper soils, there is a well-developed grass layer with both grass species of various height classes (Smith 1997).

The ***Combretum – Terminalia – Diospyros* associations** form wooded grasslands covering the shallow, stony soils occurring on the slopes and flatter regions of the upper valley floor. The dominant species are *Combretum apiculatum*, *Terminalia stenostachya* and *Diospyros kirkii*. This association is often juxtaposed with lower escarpment miombo and mopane woodlands in thin rocky and sodic or calcareous soils, respectively. These wooded grasslands are characterized by a well-developed herb and grass layers with small trees and shrubs covering 10 to 40% surface area. Some other tree species include *Terminalia stuhlmanii, Combretum fragrans* and *C. zeyheri*. Shrublands are dominated by *Bauhinia petersiana*, *Acacia hockii* and *A. gerrardii* (Smith 1997).

Mopane woodlands are widespread in all the study areas, and only the associative species change due to differences in soils. In the Luangwa Valley, mopane woodlands occur on poorly drained on sandy loam soils that are waterlogged during the wet season. Since *C. mopane* occurs as an almost homogenous stand, associated tree and shrub species are few but include *Albizia quanzensis, Balanites aegyptica and Ximenia americana*. Scrub mopane woodlands occur on compacted silt loams covering impermeable calcareous or sodic clay-loam soils. Such soils are alkaline and preclude herbaceous growth, which may in turn result in the erosion of these islands of mopane woodland (Smith 1997).

Elephant, buffalo, hippopotamus, bushpigs *Potamochoerus larvatus* (Cuvier 1822) and baboons *Papio cynocephalus* (Desmarest 1820) are known to damage crops in this region. In the early 1900's, experienced hunters were appointed by the British South Africa Company to facilitate village crop protection. More than 100 elephants were shot every year and according to the Pitman report of 1935, villagers were also entitled to shoot any animal damaging crops, but were required to report the incident (see Astle 1999). The remains of these animals and their ivory belonged to the government and would be redistributed by the Chief or Council and not sold. Unsustainable hunting continued until South Luangwa was proclaimed a National Park in 1971 (Astle 1999). Poaching remains a problem, but recent anti-poaching efforts may see the increase of elephant populations. To date elephants occur throughout the valley, concentrating within reserves and GMA's, mostly away from settlements. North Luangwa had 3 750 ± 1 076 (95% confidence limit) elephants in 2001 and South Luangwa 4 459 ± 1 519 (95% confidence limit) in 2002 (Astle 1999). Densities for these two parks are 0.69 (Blanc et al. 2007) and 0.52 (Dunham and Simwanza 2002) elephants per km^2, respectively. These numbers exclude the unknown number of elephants in the GMA's. However, estimates of Cumming and Jones (2005) suggest that the density of all of the Luangwa Valley is 0.30 elephants per km^2.

Kasungu National Park

Kasungu National Park[11] is located in central Malawi and is separated from Zambia's Lukusuzi National Park by between 12 and 25 km of land dominated by human activity. A buffer zone of 113 km^2 separates Kasungu from a densely populated settlement on its eastern

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[11] Kasungu National Park will be referred to as Kasungu from this point forward

boundary, but is utilized as a resource area by these communities (Bell 1981). The park encompasses a large portion of the Kasungu Plateau at 1000 to 1500 m above sea level (Bhima et al. 2003). Together with their tributaries, the perennial Dwangwa, Lingadzi and Liziwazi Rivers form an extensive river network through the park. There is also an artificial dam near the Lifupa camping area in the south of the park. Kasungu's mean annual rainfall is 780 mm (Bhima et al. 2003).

The majority of the park's soils are low in nutrients and slopes and troughs are characterized by different soil types (Jachmann 1986). Miombo woodlands dominate this park, with Dambo grasslands in more nutrient-rich soils along drainage lines and alongside rivers (Bhima et al. 2003). Bell (1981), differentiated two types of vegetation associations, plateau areas, making up 80 % of the park and valley areas contributing to the balance.

Plateau areas are flat and are made up of deep sandy soils with a low nutrient status and high infiltration rates. Closed canopy miombo woodlands dominated by *Brachystegia* and *Julbernardia* spp. inhabit these areas (Bell 1981; Jachmann and Bell 1985) and the species associated probably mirror that of the Upper escarpment miombo woodlands of Luangwa (page 17). These woodlands have a short to medium height herb layer, and the wide, sandy dambos between the woodlands sustain poor quality grasses of medium height.

Valley areas are defined by the river valleys and slopes of the Dwangwa and Lingadzi Rivers which form the two major dambo systems of the park. The erosion of the valleys by the rivers has resulted in higher clay contents than plateau soils, and therefore a higher nutrient content and less leaching. This forms a distinctive ecotone where vegetation changes to open woodland characterized by *Pericopsis spp., Combretum spp.* and *Terminalia spp.*, with tall *Hyparrhenia* grasslands. Dambos in these soils support tall grasses of a high quality and *Acacia* species dominate troughs (Jachmann 1980; Bell 1981). The structure and species association of these woodlands is similar to that of the *Combretum – Terminalia* woodlands of the Luangwa Valley (page 20).

Malawi was a popular destination for sport hunters, and by the early 1970's elephants occurred mainly in small isolated sub-populations. This is still the case and elephants are principally confined to protected areas - populations are generally small and isolated from each other. In addition, the poor food quality caused by the lack of nutrient-rich soils may explain relative low wildlife densities. Elephants in Kasungu used to concentrate in south-eastern portion of the park, probably in response to poaching and habitat preference (Bell 1981; Jachmann 1986). These localized high densities may have given rise to the short, coppiced miombo woodlands typical of the area (Bell 1981). Although Jachmann and Bell (1985) suggested that at that time, elephants moved between Kasungu and the Luangwa Valley ecosystems, it is unclear whether such movement still takes place. Jachman (1986) reported that recruitment from source populations in the Luangwa Valley are negligible. Since Jachmann and Bell's (1979) studies, when an 2 250 ± 250 (95% CL) elephants were estimated to occur in the park, this population has declined to a mere 58 ± 111 (95% CL) elephants (Ferreira et al. 2005) – a density of 0.02 elephants per km^2.

Vwaza Marsh Wildlife Reserve

Information on the vegetation and other aspects of this reserve is limited and most of this summary is based on an unpublished report (Hall-Martin and Modise 2002). Originally proclaimed a protected area in 1941, the Vwaza Marsh Wildlife Reserve[12] was enlarged in 1956 at the request of the local authority under King Katumbi. The reserve is separated from the Nyika National Park in the north by a narrow band of settled country known as the Katumbi area. Vwaza shares its western and part of its northern borders with the Lundazi Forest Reserve in Zambia, where trophy hunting and subsistence farming occur.

Low hills to the east with a large region of alluvial deposits and wetlands to the west characterize Vwaza's landscape. The reserve lies at an altitude of about 1 125 m. Most of the

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[12] To be referred to as 'Vwaza' from this point forward

exposed rock outcrops are biotite gneiss, and soils vary from alluvial to sandy clays, and sand around marsh and wetlands to leached sandy loams in higher-lying areas.

Vwaza Marsh is an extensive wetland in the north of the reserve characterized by reed beds (*Phragmites australis, Cyperus papyrus, Typha latifolia*) and seasonally inundated grasslands fed by the Hewe Stream (Dowsett-Lemaire et al. 2001). The wetland drains into the Luwewe Stream that in turn flows into the south Rukuru River that feeds Lake Malawi (Dowsett-Lemaire et al. 2001). Part of the south-east wetlands form Lake Kazuni which may at times cover up to 80 ha, depending on rainfall.

Once again, miombo woodlands (described above) form the dominant plant cover. The reserve also houses the northernmost distribution of mopane woodlands. In places a mosaic of mopane and miombo woodland has formed. Extensive thickets characterized by shrubs and climbers exist in the south-eastern corner of Vwaza and these are dominated by *Landolphia kirkii*. There are extensive tracts of Dambo grasslands.

Only 35 elephants lived in Vwaza in 1997 (Dowsett-Lemaire et al. 2001) and this is another small, isolated population, typical of Malawi. More recently Ferreira et al. (2005) observed 41 elephants during a fixed-wing survey of the reserve, resulting in an unreliable estimate (270 ± 352 Jolly S.E.) using Jolly's Method II (Jolly 1969), this yields a density of 0.28 elephants per km^2. Potential conflicts between crop-raiding elephants and people at park boundaries are an ongoing problem, although Vwaza does not have as stark a border of transformed land as Kasungu. The park is partially fenced to mitigate human-elephant conflict.

CHAPTER 3

MATERIALS AND METHODS

Data Compilation

Landscape classification

I conducted the study on elephants living in five study areas situated in southern Africa's miombo woodlands across Zambia and Malawi (Figure 1). Chapter 2 provides a description of each study area. This project was largely based on landscape maps that had to be generated using field data.

To generate such maps ground (4X4 vehicle) and air (helicopter) surveys were conducted to collect landscape data to aid in landscape classification of each of the study areas. Survey routes were set using Landsat Thematic Mapper (TM) 7 images and unsupervised classification routines (see Jensen 1996). North Luangwa has a limited road network and as a result, surveys of this park were done using the helicopter only. During ground surveys we distinguished between different structural classes based on the dominant vegetation types at locations defined using Global Positioning System (GPS) points and as defined in Table 2. Digital images were made at each survey point (determined using a Garmin® eTrex handheld GPS unit with an accuracy of <15 m (http://www.garmin.com/manuals/eTrex)) in the four cardinal directions with a Canon D10 single reflex digital camera. These were archived for confirmation of classes in cases of uncertainties while preparing structural maps. The structural class assigned to each of the survey points depended on it appearing homogeneous for at least a 30m radius[13]. We also recorded the locations of ecotones as reflected by abrupt changes in structural classes.

The structural classes that we defined (Table 2) did not require species-specific information, although certain species (e.g. *Colophospermum mopane*) and plant associations (e.g. miombo woodlands) could be identified easily, also from the helicopter. The landscape data for Kafue and a set thereof for Lower Zambezi were extracted from the CERU archives. These were collected during four ground surveys between July of 2003 and October 2004. For Lower Zambezi, a second data set was collected during the September 2005 ground surveys described above. Due to difficulties in classifying the Luangwa study areas from dry season data alone, we conducted a supplementary helicopter survey at the end of the wet season in April 2006.

The assessment of landscape heterogeneity relied on classified landscape maps that depict patches of structural vegetation classes. At a coarse grain, a landscape map based on a raster grid, as used in the present study, forms a patch mosaic (Reiners and Driese 2004). Pearson (2002) claims that patch mosaic models that separate landscapes into homogeneous classes are insufficient for landscapes formed by gradients rather than discrete patches, such as savannas. Murwira and Skidmore (2005) further state that the application of a patch mosaic classification may lead to a loss of information and subjectivity. However, changes in landscape structure are scale-dependent (Turner 1990). Therefore, although Pearson (2002) and Murwira and Skidmore (2005) may be correct, information loss depends on the scale and grain (resolution) at which one works (Gustafson 1998). I therefore used the Landsat TM pixels (30 × 30 m) as a minimum mapping unit, resulting in a relatively fine-grained raster grid landscape map for each of the study areas. As a result, each of the generated landscape

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[13] The minimum mapping unit was a Landsat TM 7 pixel (~30 × 30 m)

maps were at the grain size and extent that retain landscape heterogeneity and the variance of habitat characteristics, respectively (see Boyce 2006).

I used the software package ERDAS Imagine 8.7 (Leica GIS Geosystems and Mapping, LLC 2003) to classify Landsat TM image tiles and develop structural maps for each study area. I followed the routines as described by Jensen (1996). The Landsat TM tiles used were all for the dry seasons of 2004 or 2005 and bands 4, 5 and 3 were used in that order for classification. Only dry season images were used because wet season images were often partially covered by cloud, making classification impossible. Using the ERDAS 'Signature Editor' tool, I generated at least three signatures per class using "grow at enquire" at points identified during the fieldwork. Signature assignment was based on a given structural class (Table 2) allocated to a location as confirmed by images that were recorded at these survey points and confirmed by digital vegetation maps for North and South Luangwa (Smith 1997 and Astle 1999, respectively). Confirmation using vegetation maps could not be done for the other areas which were not available in digitised format. The platform from which data were collected for the signature and accuracy processes of landscape classification differed for the study areas (see Table 3).

Identified signatures were examined and edited through an iterative process. For this, I visually evaluated the extent to which each of the landscape classes on the classified images matched the survey points, original Landsat TM images, and existing digitised vegetation maps. I used these signatures to conduct a supervised classification by applying maximum likelihood procedures using ERDAS. In the case of the two Malawi study areas, the tile used was clipped to optimize classification, since the transformed vegetation surrounding these areas complicates classification. I smoothed each of the landscape maps by running a fuzzy convolution (McGarigal and McComb 1995) to remove pixel scatter. I did this by applying a 3 × 3 majority filter with a neighbourhood weight by distance window (weight factor of 85).

The elephants of North and South Luangwa range between these two parks and I therefore formed a mosaic of these two tiles to allow for simultaneous analysis as the Luangwa Valley.

Table 2. A description of the structural classes distinguished to produce landscape maps for each of the study areas included in my study. Respective classes are indicated as present in each study area by a ✕ in the 'Study area' column.

Class	Description	Study area					
		Kafue	Lower Zambezi	South Luangwa	North Luangwa	Kasungu	Vwaza
Baikiaea Forest	Homogenous stand of tall (>20m) *Baikiaea plurijuga* (Zambezi Teak) trees with a nearly closed canopy and an understorey of predominantly grasses	✕					
Faidherbia Forest	Homogenous stand of mature (>20m) *Faidherbia albida* (Winterthorn) trees with a nearly closed canopy and an understorey formed by grasses.		✕				
Miombo Woodland	Mature woodland composed of *Brachystegia* spp., *Isoberlinia* spp. and *Julbernardia* spp. varying in height from ~6 to15m. Sometimes separated as 'Open' for smaller more widely spaced trees and 'Closed' for mature stands of overlapping canopies.	✕	✕	✕	✕	✕	✕
Woodland	Structural class separated into Mopane, *Acacia* or mixed woodland where trees are from ~6 to 10m high. Separated into 'Open' and 'Closed' as in Miombo woodlands		✕	✕	✕		
Woodland Thicket	Woodland (mopane or mixed association, varying in height between ~6 and 10m) with thicket or shrubland understorey <5m high.	✕	✕				
Seasonal Woodland Mosaic	A sparse open woodland comprised of few deciduous trees and a grassland understorey during the wet season. Clay soils result in these stands being inundated during the rainy season. Bare ground dominates the understorey during the dry season.			✕	✕		
Shrubland	Most of the woody vegetation is shrub (<5m high), usually occurring in clumps. Few trees may be present. Includes the Munga shrubland of Kafue.	✕	✕	✕	✕		✕
Grassland	More than 80% of basal cover is formed by grass with no woody components		✕				
Dambo Grassland	Grasslands occurring in watershed or run-off areas with a high water table. They are thus inundated for much of the year.	✕		✕	✕	✕	
Watershed Grassland	Grasslands with standing water in the wet season, transformed to bare ground in the dry season.			✕	✕		
Transformed Land	Landscapes transformed through agriculture, usually adjoining study area boundaries					✕	✕
Marsh	Shallow, permanently inundated and vegetated water body						✕

On these maps, patches of different structural classes were formed by adjacent pixels of the same signature based on the nearest-neighbour parameters specified during classification (see page 27). However, the raster grid itself is not eliminated and each discrete patch is comprised of many pixels. Such maps represent large-scale landscape patterns that result from the characteristics of patches of the structural classes that were defined when preparing them. The maps therefore illustrate an aspect of resource distribution.

Table 3. A synopsis of the data used for the various procedures of landscape classification in each of the study areas. The 'Signature' column refers to the data set used for identifying and editing signatures. 'Accuracy' refers to the data set used for verification and to calculate the accuracy statistics. Both the 'Signature' and 'Accuracy' columns are split into 'Survey Data' and 'Date' columns. For Kafue, I used archived data from previous surveys (as discussed in text).

Study area	Signature		Accuracy	
	Survey Data	Date	Survey Data	Date
Kafue	Ground	Jul 2003 – Sept 2004	Ground	Jul 2003 - Sept 2004
Lower Zambezi	Ground	Oct 2004	Ground	Sept 2005
North Luangwa	Ground & helicopter	Sept 2005	Helicopter	Apr 2006
South Luangwa	Ground & helicopter	Sept 2005	Ground Helicopter	Sept 2005 Apr 2006
Kasungu	Helicopter	Sept 2005	Ground	Sept 2005
Vwaza	Helicopter	Sept 2005	Ground	Sept 2005

Verification data consisted of locations that were recorded in the same way as the survey points. However, in this case, the classification had taken place and the class types to which the verification points had to be assigned, were set. The verification process assessed agreement between the structural class assigned to a survey point on the classified map (see Jensen 1996). Accuracy was assessed for each of the landscape maps through Kappa statistics and error matrices (as reviewed by Jensen 1996; Pouncey et al. 1999; Corsi et al. 2000) using the verification data (Table 3).

Location success, accuracy and precision of the satellite tracking collars

My project used spatial data collected from elephants in the various study areas. Africa Wildlife Tracking (Pretoria, South Africa) designed and assembled the collars that we used. The GPS units themselves employ a Garmin® GPS receiver and Vistar satellite unit to communicate with a geostationary[14] satellite (Inmarsat's I-4 satellite, see www.inmarsat.com). Locations calculated by these GPS receivers were downloaded automatically via the Inmarsat satellite to StarTrack (Australia). From here, data were transferred to Skygistics (South Africa) and downloaded to CERU via an FTP[15] connection. According to Garmin's technical data (http://www.garmin.com/manuals/eTrex), the accuracy of locations from similar GPS units is expected to be within the range of 10 – 15 m. However, the accuracy and precision of the GPS units used in Africa Wildlife Tracking's satellite collars (model AWT SM 2000E, Africa Wildlife Tracking, Pretoria, South Africa) has not been assessed prior to my study.

GPS receivers operate by line-of-sight. Consequently, many factors can influence their ability to record accurate or precise positions. These factors include vegetation cover, terrain and interference from the animal's body (see Moen et al. 1996). Furthermore, satellite geometry (the position of satellites in the sky relative to the unit) also influences the precision with which locations are calculated by the GPS unit. A minimum of three satellites are required for a GPS to calculate a location, whilst four or more satellites allow a more accurate and precise calculation as the GPS may then use the most optimal satellite geometry (D'Eon et al. 2002). Inadequate GPS line-of-sight and satellite geometry result in a failure of the GPS receiver to calculate its location (Moen et al. 1996). For this reason, the biased recording of information on location can compromise GPS-telemetry studies. The most important factors considered to influence GPS collar accuracy are vegetation canopy type and cover (e.g. Moen et al. 1996; Moen et al. 1997) and terrain (e.g. Dussault et al. 1999; D'Eon et al. 2002). Rugged terrain and dense cover also influence precision, since only some of the available satellites are 'visible' to the GPS unit, interfering with the satellite geometry. The GPS units

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[14] A geostationary satellite follows a circular orbit in plane of the Equator at a height of 35 600 km, therefore appearing stationary relative to a point on the Earth's surface

[15] File Transfer Protocol: allows two computers to connect over the internet, so that the user of one may transfer files from the other

of the collars in this study require a communication corridor equivalent to a 60° angle to the vertical axis, suggested that dense vegetation cover and rugged terrain would negatively affect the location success of these collars (M.A. Haupt[16] pers. comm.). Many procedures exist to correct location biases (e.g. Frair et al. 2004). However, I did not apply such procedures to my data, since rather than using the location data directly, I delineated 95% Kernel home ranges. Despite this, I opted to investigate the effect of vegetation canopy cover and gradient on the GPS tracking collars that were deployed on the elephants tracked for this project.

To determine the accuracy and precision of satellite collar locations I conducted two trials at the University of Pretoria's Experimental Farm. I used five GPS satellite collars that had been retrieved from elephants in my study. I used plastic conduit piping and steel stakes to secure these collars 2 m above the ground to mimic their deployment on the neck of an elephant. The satellite network was set to collect data on the calculated position of the GPS units at hourly intervals.

GPS unit performance was assessed for different categories of canopy cover (forest, open woodland, bare ground), based on the criteria used by D'Eon et al. (2002). I also examined the effect of landscape gradient (gentle, hill, steep, sheer), as defined in Table 4, on the performance of the collars. The locations chosen for the gradient trial were all between the east- and west-facing aspects of a hill and all in open woodland areas. The 'open woodland' locations from the canopy cover trial were all on gentle terrain (see Table 4). I rotated the five collars between categories approximately every 24 hours for three days each.

I marked each of the locations and later used a differential GPS with a maximum horizontal and vertical accuracy of 1 and 2 cm, respectively (Trimble Navigation Ltd, California, April 1991, Model 4000ST GPS Surveyor, Part number 13940) to record the 'true' locations and altitudes (see also Moen et al. 1996). I chose the locations for the collars in the

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gradient trial to include a wide range of gradients. I used the change in altitude over distance to calculate the gradient between locations. Since the gradients varied widely, I grouped them into categories to increase the number of locations per gradient. One of the stakes used to mark a bare ground location was removed by someone and this prevented me from testing the positions recorded by the collar placed there (100% location success for bare ground was therefore 76 positions, rather than 90).

Accuracy is defined as the closeness of a measured value to its true value, whilst precision is the closeness of repeated measurements of the same quantity to each other (Sokal and Rohlf 1995). I used the distances between the 'true' location as recorded by the differential GPS and the positions recorded by the GPS units as measures of accuracy (D'Eon et al. 2002), whilst the S.D. of these distances reflected on precision.

Table 4. Categories of canopy cover and landscape gradient used as a basis to compare accuracy and precision of collars. Canopy percentage cover was determined visually and categories were based on those used by D'Eon et al. (2002). Gradient percentages were calculated between groups or pairs of locations to generate the categories listed here.

Canopy Cover		Landscape gradient	
Category	Canopy Cover (%)	Category	Gradient (%)
Forest	80 – 100	Gentle	0-5
Open Woodland	30 – 60	Hill	6-15
Bare Ground	0	Steep	16-30
		Sheer	>30

I used ArcMAP 9.1 (ESRI Inc. 2005) to generate a map including the 'true' locations as well as the positions recorded by the GPS units for the categories within each trial. For visual purposes only, I generated buffer rings (concentric circles) at 5 m intervals to 30 m around the 'true' location. I used ArcMAP's 'distance tool' to calculate the distance from each 'true' location to the corresponding positions recorded by the collar GPS unit. I also used ArcMAP's spatial statistics tools to calculate the mean centres of the positions recorded for each location (see Figure 2, page 54).

I used a Kruskal-Wallis ANOVA (sample variances were heterogeneous) to determine whether the distances from the 'true' locations to those recorded by the collar GPS unit were significant for each of the categories for both trials (canopy cover and gradient). This allowed me to determine whether various canopy covers and gradients affected accuracy significantly. I also calculated the ability of the Inmarsat satellite to establish a connection with the GPS units as the proportion of successful location events under different slopes and canopy covers, presented as a percentage. I termed this 'location success' (Dussault et al. 1999). I also calculated location success per season for all of the collars whilst they were in the field and presented these as percentages. Further, I compared whether any study area hindered or improved location success compared to that of the other study areas per season. An arc-sine transformation commonly used for proportions or percentages (Sokal & Rohlf 1995), did not result and homoscedasticity and I therefore used the Kruskal-Wallis non-parametric ANOVA to compare location success between parks, within each season.

For the purpose of my study, it was important that in any landscape category, positions recorded by the collars' GPS units fell within at least 15m of the 'true' location. This stemmed from the grain of the maps I used for this project, being that of a Landsat TM pixel (30 × 30 m) and if a location is recorded in the centre of a pixel there is a 15 m radius to the edge. Of course, not all locations would fall in the centre of a pixel, but this formed a guideline.

Elephant home ranges

Twenty-nine elephants (5 bulls and 24 cows) from study areas across Zambia and Malawi were fitted with GPS satellite collars (model AWT SM 2000E, Africa Wildlife Tracking, Pretoria, South Africa) (see Chapter 2, Table 1). We used standard procedures sanctioned by the ethics committee of the University of Pretoria (permit number AUCC-040611-013). Each cow selected for collaring, was from a different breeding herd and each female home range therefore represents the home range of an entire breeding herd. The collars were fitted with a

Garmin GPS receiver and Vistar satellite unit, which communicate with a geostationary satellite (see page 29). These provided locations for each elephant at 12 to 24 hour intervals over two dry and wet seasons between 2003 and 2005 (Kafue) and two dry and wet seasons between 2004 and 2006 (other study areas). I defined seasons as discussed in Chapter 2 (page 11) and since data for each elephant were recorded over two years, the seasons will be referred to as dry season 1 and 2, and wet season 1 and 2 from this point forward.

The data of elephants for dry season 1 in the various study areas (except Kafue) are incomplete since these collars were only deployed after the season had already begun. This may influence metrics sensitive to area (see page 55) if home range sizes estimated from this data were affected. Girard et al. (2002) suggested 30 to 100 locations were required to reach a sampling asymptote for fixed Kernel home range size[17]. All data sets of my study areas met this requirement except those of the Kafue males and the South Luangwa females (see Table 5). To ensure that the incomplete nature of the dry season 1 data set would not influence later analyses, I compared the sizes of the 95% Kernel home ranges calculated from this data, to those of dry season 2 using a paired t-test. This test showed that there was no difference between either of the study areas' dry season home range sizes and I could thus use them for further analyses.

I excluded some seasons due to collar malfunction and failure (see Table 5), resulting in a few or no data points. Two collars placed on elephants in Kafue malfunctioned and provided only one dry season's data for one bull elephant and a single dry and wet season's data for one of the cows. One collar from Lower Zambezi failed towards the end of the second dry season. A collar placed on a cow in Kafue and one in South Luangwa began to malfunction mid-way through the second wet season, after transmitting locations infrequently. One of the collars placed on a cow in Vwaza malfunctioned repeatedly, and eventually failed

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[17] A study by Börger et al. (2006), published since my analysis was completed, suggests that the variation between individuals and study areas contribute most to the total variation in home range size of animals. They confirmed that Kernel home range estimates were efficient, robust and unbiased and that 10 fixes per month, recorded over a regular time interval, was sufficient for the accurate calculation of home range size.

near the end of the second dry season. I therefore excluded data from this cow too, resulting in the home ranges of only two elephants being analysed in Vwaza.

Home range analyses require the recorded locations to be independent of one another in order to form a statistically unbiased home range estimate (Schoener 1981; Swihart and Slade 1985; Rooney et al. 1998; De Solla et al. 1999). However, eliminating spatial autocorrelation may not make ecological sense since animals usually move over the landscape in a non-random manner and spatial autocorrelation therefore forms a tool in understanding the underlying causes of spatial or temporal structure (De Solla et al. 1999). Spatial autocorrelation does however increase the likelihood of committing a Type I error in statistical analysis as it inflates the degrees of freedom (Legendre 1993). To reduce spatial autocorrelation I sub-sampled each data set as suggested by Swihart and Slade (1985) and included only a single observation for each 24-hour period per elephant for Kernel home range estimations[18]. I calculated the 95% fixed Kernel Home Range (Worton 1989) for each of the elephant's data sets using the Animal Movement extension package (Hooge and Eichenlaub 1997) for ArcView 3.3 (ESRI, Inc. 2002). I applied Least squares cross-validation smoothing (LSCV), using *ad hoc* values of h[19] (see Worton 1989) as calculated by the Animal Movement extension. I then converted these into raster format and classified them to reflect the structural classes on the corresponding landscape maps in ArcMAP 9.1. This process meant that the resolution[20] of the ranges matched that of the maps (see Boyce 2006) and reflected on the contribution of each structural class to each of the home ranges. The sizes (area) of home ranges were calculated in km^2 using ArcView 3.3 (see Table 5).

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[18] Kernel density estimators are often referred to as the best home range estimators and are a non-parametric statistical method that produce an unbiased density estimate from location data (see review by Powell 2000). However, a study published since my analysis suggested that it is best to avoid the 95% Kernel Home Range estimator and rather use Kernel estimations of between 50 and 90% (Börger *et al.* 2006). Furthermore, Hemson *et al.* (2005) suggested that the Least Squares Cross-Validation used in Kernel estimation is problematic and limits the application to fewer studies than suggested by the literature.

[19] h_{LSCV} = smoothing parameter applied in the estimation of the Kernel home range and may be varied by the user.

[20] See Glossary of terminology, acronyms and contractions, page xvi

Most of my investigation focused on cows. I assumed that cows respond directly to environmental pressures to ensure the survival of calves, while range use by bulls seems to be driven by sexual and other behavioural responses (e.g. Stokke and du Toit 2002). In an effort to validate this, data from the five, collared bulls in Kafue were only used for comparisons with the five cows of that study area.

Table 5. Home range size (km^2) of elephants in all study areas, for each season. The 'ID' column identifies the elephant carrying the collar and 'f' or 'm' denotes its sex as female or male, respectively. The 'Code' column provides the collar code as stored in the CERU archive. 'No data' implies incomplete data due to technical failures and cases where all or most of the season's data was missing. The values in brackets denote number of locations on which the estimate was based. The mean, standard deviation (S.D.) and range of the home range sizes are given. The range was used to determine the minimum and maximum size of the randomly located home ranges (see text). Seasons are defined on page xvi.

Study area	Code	ID	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2
Kafue	00036543VTI33F8	K2m	1 186 (160)	370 (162)	1 707 (35)	12 480 (152)
	00036573VTIAC8E	K4m	145 (162)	181 (163)	783 (25)	1 820 (175)
	00036523VTIE394	K7m	124 (157)	304 (162)	1 872 (93)	2 799 (168)
	00036506VTI1F3F	K9m	No data	2 582 (162)	No data	2 364 (132)
	00036722VTI8377	K10m	204 (159)	169 (161)	4 723 (59)	5 096 (174)
		Mean	415	721	2271	4912
		S.D.	515.5	1043.3	1703.0	4410.0
		Range	124 – 1186	169 – 2581	783 – 4723	1820 – 12480
	00036480VTIB6BD	K1f	116 (167)	217 (162)	377 (113)	412 (176)
	00036491VTI62F4	K3f	145 (146)	181 (160)	845 (73)	491 (176)
	00036489VTI5AEA	K5f	193 (81)	993 (162)	1 072 (39)	1 466 (174)
	00036481VTI3AC2	K6f	No data	276 (160)	No data	No data
	00036473VTI1A9A	K8f	162 (155)	403 (161)	307 (133)	272 (177)
		Mean	154	414	650	631
		S.D.	32.4	334.4	368.7	476.3
		Range	116 – 193	181 – 993	307 – 1072	272 – 1466
Lower Zambezi	39973VTI0EF6	LZ 1f	74 (57)	173 (142)	579 (126)	1 212 (161)
	55789VTI63DE	LZ 2f	170 (72)	134 (147)	410 (131)	693 (165)
	55833VTI14BA	LZ 3f	105 (74)	111 (160)	1 497 (146)	2 098 (173)
	38081VTI5A02	LZ 4f	230 (76)	159 (136)	508.5 (141)	619.0 (158)
	39984VTIBB2D	LZ 5f	769 (68)	335 (41)	562.4 (141)	No data
	55805VTIA42E	LZ 6f	232 (74)	233 (157)	1208 (134)	972 (159)
		Mean	264	191	794	1119
		S.D.	255.3	446.1	81.9	596.1
		Range	74 – 769	111 – 335	410 – 1497	619 – 2098
Luangwa	55799VTI8C10	NL 1f	205 (55)	180 (97)	499 (67)	990 (30)
	56218VTIA03F	NL 2f	191 (73)	70 (153)	268 (147)	438 (162)
	38168VTI37B5	NL 3f	136 (74)	210 (134)	587 (156)	458 (159)
	00039748VTI0691	SL 1f	66 (19)	102 (165)	333 (140)	596 (170)
	00039759VTIB2C8	SL 2f	144 (20)	237 (122)	1 385 (117)	1 062 (146)
	00039784VTI9745	SL 3f	199 (12)	212 (149)	143 (149)	153 (163)
	00039991VTI5750	SL 4f	120 (18)	27 (158)	608 (144)	No data
	00055103VTI9E78	SL 5f	96 (18)	354 (158)	272 (142)	1 298 (171)
		Mean	145	174	819	628
		S.D.	50.8	858.5	104.5	450.6
		Range	66 – 206	27 – 354	142 – 2727	26 – 1298
Kasungu	56211VTI041C	KS 2f	138 (73)	214 (164)	351 (124)	355 (168)
	55131VTI0F04	KS 3f	136 (74)	278 (151)	526 (139)	445 (144)
		Mean*	137	246	438	400
		S.D.*	1.3	124.0	44.8	63.7
		Range	136 – 138	214– 278	351 – 527	355 – 445
Vwaza	39983VTI3728	V 2f	509 (66)	87 (151)	563 (129)	678 (162)
	55097VTI865A	V 4f	1190 (69)	100 (150)	790 (130)	920 (162)
		Mean*	341	297	402	799
		S.D.*	236.8	227.8	296.2	171.0
		Range	509 –1190	87– 100	563– 790	678 – 920

* Presented here for comparative reasons only, since these calculations are constrained by sample size.

Randomly located home ranges

I generated home ranges from randomly located data points to sample the landscapes of each of the study areas. I termed these 'randomly located ranges', referred to as 'random ranges' from here on. This sampling allowed me to define the heterogeneity of the study areas, as well as to investigate selection by elephants for landscape heterogeneity through the comparison of heterogeneity metrics calculated for random and elephant home ranges (see Data analysis section, page 41).

The number of spatial points that defined each of the random ranges was set as the mean number recorded during each season for the satellite-tracked elephants, in each of the study areas. Using the Random Normal Points tool in the Animal Movement extension package, I placed these points randomly over the landscape. The Random Normal Points tool places the set number of spatial points randomly within a circle of a designated radius. I calculated the radii of these circles such that the resultant 95% Kernel estimations would fall within the range of elephant 95% Kernel home range sizes of each study area (see Table 5). From these points, I derived the 95% Kernel 'home range' estimation as was done for the elephant locations. Using ArcView 3.3, I calculated the size, in km^2, of each of the random ranges. Since the study areas differed in size, the number of random ranges in the 10 series that I created for each study area differed to prevent overlap of more than 80% of the areas of ranges in the smaller study areas. I placed 56 to 358 95% fixed Kernel random ranges at randomly selected locations across each of the study areas. I classified each of these, using the same procedure as for the elephant home ranges.

Measuring landscape heterogeneity

I quantified landscape heterogeneity using metrics calculated by the raster edition of FRAGSTATS v 3.3 (McGarigal and Marks 1995). Resolution of the input image (landscape map) does not limit FRAGSTATS calculations (McGarigal and Marks 1995).

FRAGSTATS is capable of calculating more than 40 absolute and relative measures of landscape heterogeneity, however, many of these are autocorrelated and I did not use them in my study. The criterion for selection that I applied to reduce the number of metrics were based on recent studies that used similar applications, or that described the strengths and weaknesses of these metrics (Li and Reynolds 1994; McGarigal and Marks 1995; Riiters et al. 1995; Li and Reynolds 1995; Li et al. 2001). I excluded metrics considered by others as problematic and redundant, as well as those not used at all by these authors. This left me with 15 metrics. I also excluded metrics that required user-defined value input, such as buffer width for edge detection, to prevent observer biases. Finally, I carried out a preliminary analysis of data from the collared elephants of Kafue (first set of data I had available for assessment) using the remaining 11 metrics. Only five of these represented the two types of variance in landscape heterogeneity as reviewed by Reiners and Driese (2004) on which I wanted to focus: spatial (Fractal Index and Interspersion Index) and compositional variance (Patch Density, Patch Richness Density and Diversity Index) and these were selected for further analysis. Spatial variance is a statistical measure of two-dimensional aggregation between patches, whilst compositional variance is the representation of patches that differ qualitatively from one another in a landscape (Reiners and Driese 2004). I used STATISTICA (Statsoft 2004) to assess whether the metrics for random and elephant ranges, in each study area and during each season were distributed normally (Appendix XI). Both the random and elephant ranges for Lower Zambezi and random ranges for Vwaza displayed a normal distribution (non-significant Kolmogorov-Smirnov p-value) for all metrics. Those for the remaining study areas were normally distributed for all but Patch Density and Patch Richness

Density. The values for both these metrics were close to zero and their variances could not be calculated. For both, $\log_{10}$ transformation normalized the distribution. Those ranges that displayed a normal distribution for these two metrics without transformation remained normal after $\log_{10}$ transformation. I therefore transformed all Patch Density and Patch Richness Density data in order to apply parametric statistics in further analyses.

For all study areas, for both random and elephant ranges, a Pearson correlation (Appendix II) confirmed that Patch Density explained more than 50% of the variance in Patch Richness Density. I therefore abandoned Patch Richness as a metric for all further analyses. This left me with four FRAGSTATS metrics representing different aspects of landscape heterogeneity, to apply in all future analyses (Table 6).

Table 6. Description, contractions and acronyms for the FRAGSTATS landscape metrics used to describe landscape heterogeneity in each of the study sites. The descriptions have been adapted from McGarigal and Marks (1995). A descriptive phrase (Contraction column) and the range (Range column) for each is also presented. Arrows, '↑' and '↓', indicate an increase and decrease in values, respectively.

Metric	Contraction	Description	Range
Patch Density	Patch Density (PD)	Number of patches of a specific class per unit area, facilitating comparisons among landscapes of varying size	$PD > 0$ ↑ PD = ↑ landscape heterogeneity
Perimeter-area Fractal Dimension	Fractal Index (PAFRAC)	Measures patch-shape complexity across a wide range of spatial scales; specifically to what extent perimeter increases per unit area	$1 \leq PAFRAC \leq 2$ ↑ PAFRAC = ↑ landscape heterogeneity
Interspersion & Juxtaposition Index	Interspersion Index (IJI)	This metric is based on adjacent patches, not adjacent cells like contagion, it isolates interspersion or intermixing of patch types	$0 \leq IJI \leq 100$ ↑ IJI = ↑ landscape heterogeneity
Shannon's Diversity Index	Diversity Index (SHDI)	A diversity measure from community ecology. Sensitive to rare patch types, it measures the number of different patch types, including the proportional area each covers	$SHDI \geq 0$ ↑ SHDI = ↑ landscape heterogeneity

Increases in each of these metrics suggest an increase in landscape heterogeneity (see Introduction, page 5) and each of the four metrics quantifies a different aspect of landscape heterogeneity in terms of the number, shape, arrangement and diversity of patches within the landscape under investigation. These four aspects of landscape heterogeneity are measures of landscape pattern that may affect the movement of animals in the environment, a landscape process (Turner 1989; Turner et al. 2001). I investigated the effect of an increase in range (elephant or random) size on the four metrics, using linear regression analyses to determine whether they were independent of area. I expected such an effect for both Patch Density and Fractal Index, due to the inclusion of a variable involving area in their calculation. However, Interspersion and Diversity Index did not include such a variable and I therefore did not expect an area-effect for these two metrics.

The methods I used to quantify landscape heterogeneity are used routinely in landscape ecology (Li and Reynolds 1995; Turner et al. 2001; Li et al. 2001). However, few studies use such metrics to explain variability in range utilization by animals (e.g. Kie et al. 2002; Grainger 2005).

Data Analysis

Landscape heterogeneity of study areas

Spatial heterogeneity of a landscape must be properly characterized before attempting to understand the response of wildlife to it (Turner 1989; Murwira and Skidmore 2005). In this section I compare the landscape heterogeneity of the study areas using random ranges. This allowed me to group similar study areas for future analyses, as well as to compare elephant home ranges within these groups, whilst controlling for inherent differences in heterogeneity of the landscape.

Using the entire study area for these comparisons would result in n = 1 for each study area, which complicates statistical analysis. To overcome this, as well as problems associated with pseudo-replication (Hurlbert 1984; Schwarz 2002), I calculated heterogeneity metrics for random ranges located in each study area. For this procedure I standardized the size range and number of random ranges to be used by analysing 29 random ranges (maximum number available for Kasungu) varying between 100 and 500 km^2 for each of the study areas.

In addition to the normality tests applied earlier (page 39), I evaluated the homogeneity of the data variances using the Hartley *F*-max test[21] (Sokal and Rohlf 1995). In cases of heterogeneous variances, I transformed data in an attempt to achieve homogeneity. I used one-way Analysis of Variance (ANOVA) to compare the landscape heterogeneity metrics of the study areas for normal and homogenous data. For such data, I applied Tukey HSD *post-hoc* tests to determine where differences lay. Where transformations failed, the Kruskal-Wallis non-parametric ANOVA and multiple comparison *post-hoc* tests (where necessary) were applied to data with heterogeneous variances (Sokal and Rohlf 1995). I used STATISTICA to perform all statistical analyses. These comparisons allowed me to place the similar study areas into groups for comparisons between elephant ranges.

Landscape heterogeneity of elephant home ranges

I calculated the landscape heterogeneity metrics of individual elephant home ranges for each of the seasons as described above for the random ranges. In this section, comparisons of elephant ranges within and between study areas were based on the same statistical procedures as those described for study area comparisons, i.e. one-way ANOVA or Kruskal-Wallis non-parametric ANOVA (see page 42).

Should elephants select for landscape heterogeneity, I expect heterogeneity as measured by the four FRAGSTATS metrics, to be a determinant of the size of their home ranges. To validate this expectation, I plotted the elephant home range sizes within groups a-c (see previous section), as a function of each landscape heterogeneity metric. I also plotted the metric values of the same number of randomly located home ranges as elephant ranges, for each of the study areas within each group, forming separate graphs. I generated graphs to

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[21] I carried out this test on the data sets to determine whether parametric or non-parametric ANOVA's were to be applied. Transformations were only successful in the form of the $\log_{10}$ transformation applied to all Patch Density results. In all other cases of heterogeneous variances, the Kruskal-Wallis ANOVA with its associated multiple comparison *post-hoc* test was applied (Sokal and Rohlf 1995).

illustrate my expectations and compared slopes resulting from least square regression analyses using a paired t-test.

I compared the landscape heterogeneity of the elephant ranges between study areas within each group. If a study area did not form a group with another for a particular landscape heterogeneity metric (previous section), I did not use its elephant ranges for inter-area comparisons of that metric. Therefore, if inter-area comparisons of elephant ranges yielded differences in landscape heterogeneity, it would be indicative of differences in elephant ranging and not differences between the landscapes themselves. Further, I compared the landscape heterogeneity of seasonal and sex-specific elephant ranges within each study area.

I compared the metrics for the elephant ranges and the random ranges using randomization procedures that enabled me to determine whether landscape heterogeneity of areas used by elephants (selected areas) differed from those available (see Lacher et al. 1982). This would imply selection. To the best of my knowledge, this analytical approach has not been used before.

The two study areas in Malawi are relatively small. Consequently, the randomly located home ranges overlapped extensively. For this reason, I did not include these study areas in this analysis. For the remaining study areas (Kafue, Lower Zambezi and Luangwa), I used Monte Carlo simulations (Manly 1997) to compare the four metrics of observed elephant home ranges with those of randomly located home ranges. I selected at least 80 random ranges from those that were generated for each study area and season. The criterion for this selection was that the sizes of random ranges were within the range of the observed elephant home range sizes. For instance, the Lower Zambezi elephant ranges for dry season 1 varied from 74 to 768 km^2 - consequently random ranges varied from 70 to 770 km^2.

As part of this procedure, I used a macro in Microsoft® Office Excel 2003 (Copyright © 1985-2003 Microsoft Corporation) to randomly select the same number of randomly located ranges as the number of collared elephants for each season within a study area. For instance, with five collared elephants in Lower Zambezi, this procedure returned the metric values for five random ranges. The macro repeated this procedure 10 000 times with replacement (Legendre and Legendre 1998), and each time recorded the mean values and variances for each of the metrics.

For each metric, I used the minimum and maximum of the 10 000 values to calculate the class width required to generate 20 classes or 'bins' of equal value range (i.e. 0.10 - 0.20, 0.21 - 0.30, etc.). By placing values of the random ranges for each metric in the relevant 'bins', I constructed a frequency distribution of their mean values and variances. Using Microsoft Excel's 'NORMSDIST' and 'GAMMADIST' functions, I fitted a Normal and Gamma distribution to the frequency distributions of the mean values and variances for each metric. The Gamma distribution was truncated at zero since variances cannot be smaller than zero. To facilitate fitting the distributions, I used arbitrary parameters for each of the distributions as initial input values for the Excel functions. This allowed me to predict the expected frequency for each bin. I then calculated the squared difference between observed and expected frequencies and summed these across bins to find the residual sum of squares. I used Microsoft Excel's 'Solver' tool to adjust the parameter values of each fitted distribution function until the residual sum of squares were minimized.

For illustrative purposes I divided the fitted frequencies by 10 000 and added different constants to the frequencies of the different seasons. The bins containing mean values of the elephant ranges as well as individual observed ranges for each of the metrics within each season and study area were marked. I repeated this process for the variances of the metrics for each season and study area. Observed mean values of a metric that fell outside the 95% confidence limit of a specific distribution, suggested selection for a given heterogeneity metric. I expected observed variances to fall outside the 95% confidence limit of the random variances when the corresponding mean values for the elephant ranges also fall outside the

95% confidence limit of the random range curve. This would suggest that the positions of the elephant home ranges are determined by selection for landscape heterogeneity.

CHAPTER 4

RESULTS

Landscape Classification

The interpretation and classification of Landsat TM images of the five study areas resulted in maps based on structural vegetation classes (Plates 1 – 5). Kappa statistics suggested that accuracies of the classifications were high and values ranged from 50 to 82 % (Table 7).

Table 7. The classification accuracy for the landscape maps of each of the study areas. The 'Verification points' column indicates the number of points used in total for each of the maps and values in brackets denote the number of verification points for each class. The zero and negative values correspond to classes for which there were few verification points. 'N/A' indicates where classes were not verified, since the signature was obvious, e.g. sand.

Park	Verification points	Overall accuracy (%)	Kappa statistic (%)	Conditional Kappa statistic for each vegetation class (%)	
Kafue	996	85	77	*Baikiaea* Forest (195)	88
				Miombo Woodland (486)	79
				Woodland Thicket (42)	80
				Munga Shrubland (98)	59
				Dambo Grassland /Grassland (175)	73
Lower Zambezi	296	85	82	*Faidherbia* Forest (41)	97
				Closed Woodland (21)	90
				Open Woodland (16)	66
				Miombo Woodland (3)	0
				Woodland Thicket (83)	95
				Shrubland (13)	6
				Grassland (36)	66
				Bare Ground (83)	90
Luangwa	246	66	51	Miombo Woodland (80)	60
				Open Woodland (87)	62
				Seasonal Woodland Mosaic (19)	45
				Grassland (3)	59
				Watershed Grassland (14)	43
				Shrubland (42)	36
				Sand	N/A
Kasungu	69	83	72	Closed Miombo Woodland (30)	63
				Open Miombo Woodland (30)	80
				Dambo Grassland (4)	73
				Transformed Land (3)	100
				Granite outcrops	N/A
Vwaza	59	76	63	Closed Miombo Woodland (1)	-2
				Open Woodland (32)	57
				Shrubland (8)	32
				Dambo Grassland (8)	85
				Grassland (1)	100
				Transformed Land (8)	86
				Vwaza marsh	N/A

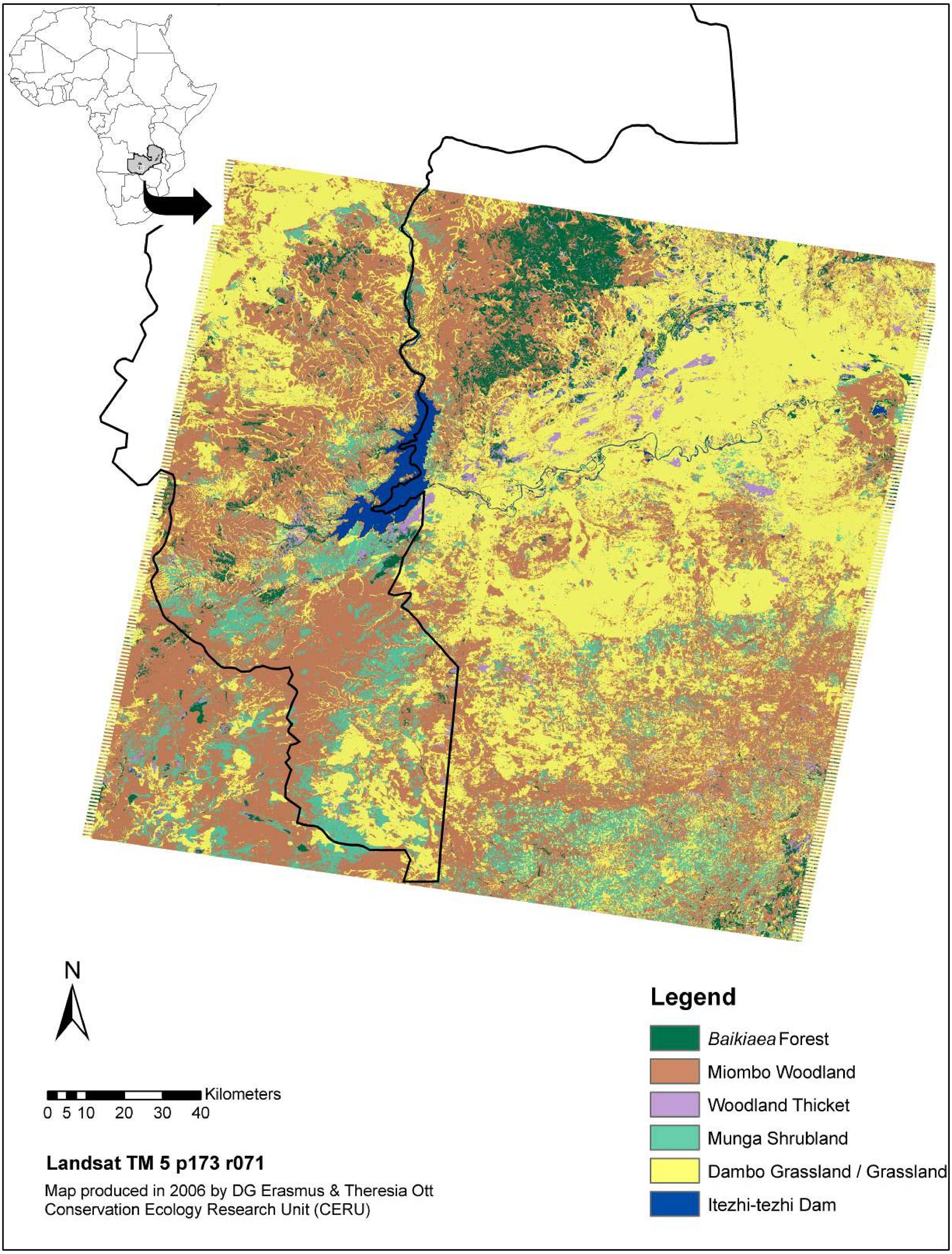


Plate 1. A landscape map of the study area within Kafue National Park, south-western Zambia. The Landsat TM tile number on which the landscape map is based, is provided below the scale bar. The park boundaries as illustrated here, were sourced from the Peace Parks Foundation (PPF) database, and represent the boundaries as recorded by the World Conservation Union (IUCN).

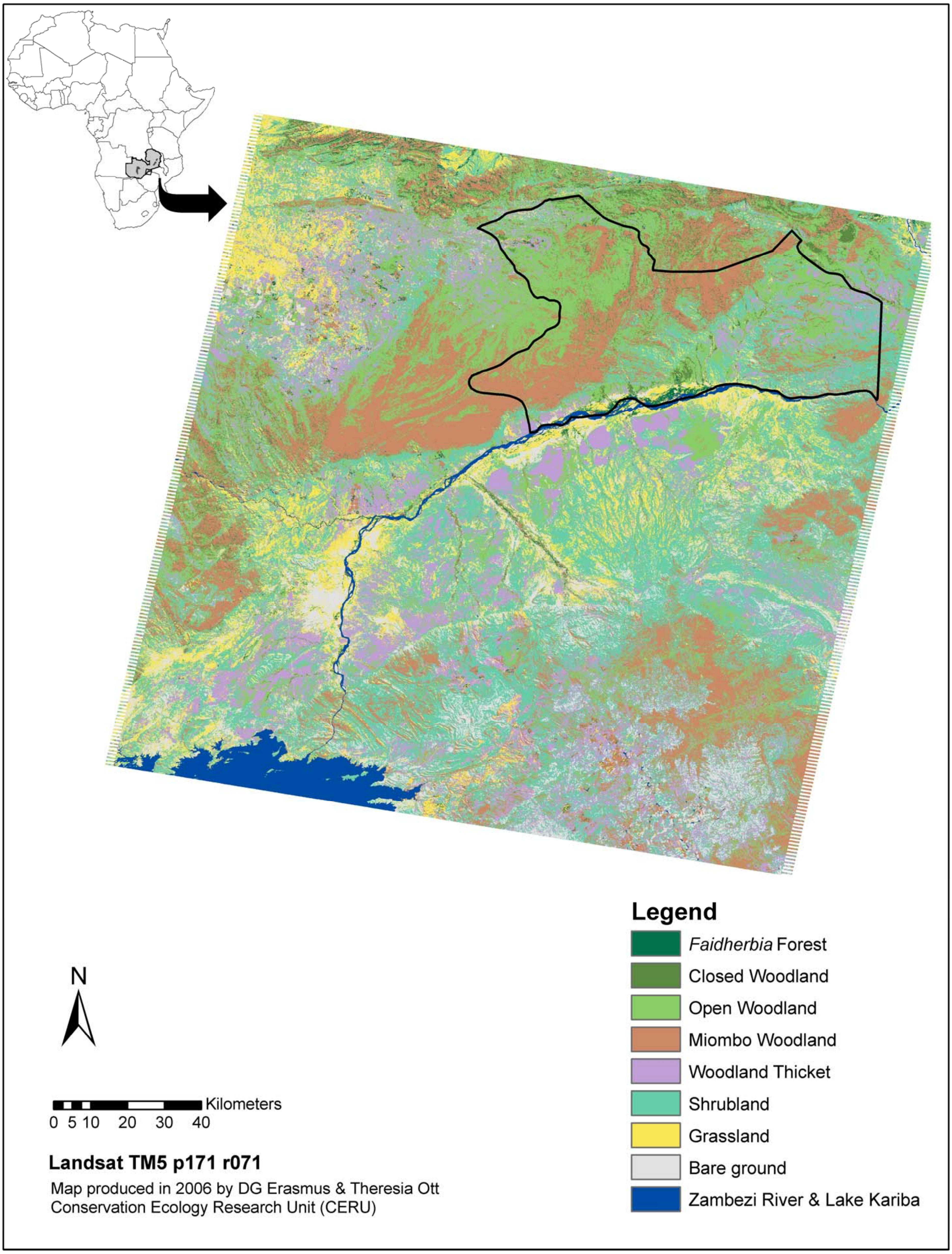


Plate 2. Landscape map of the study area in and around Lower Zambezi National Park, southern Zambia. Further explanation is as given for Plate 1.

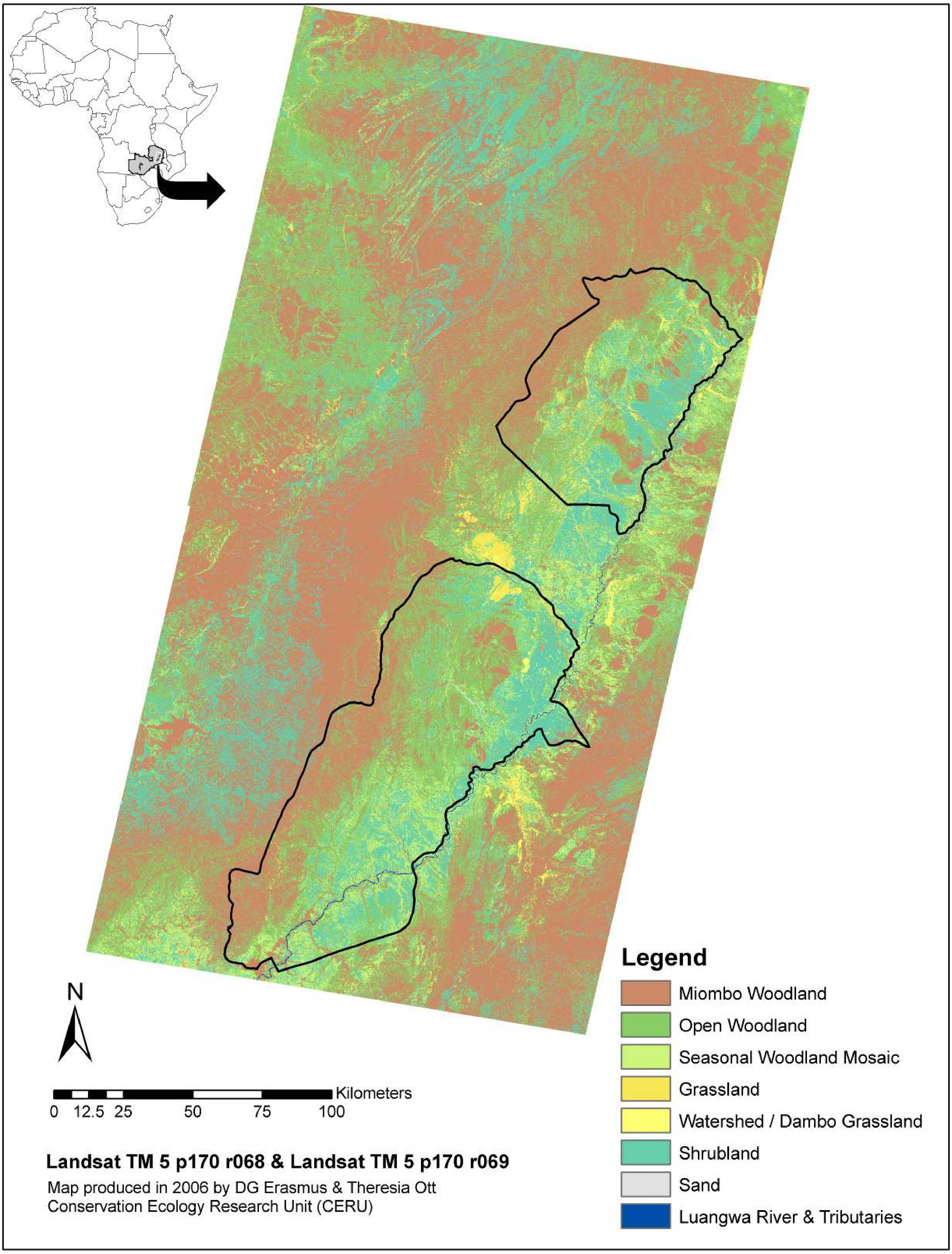
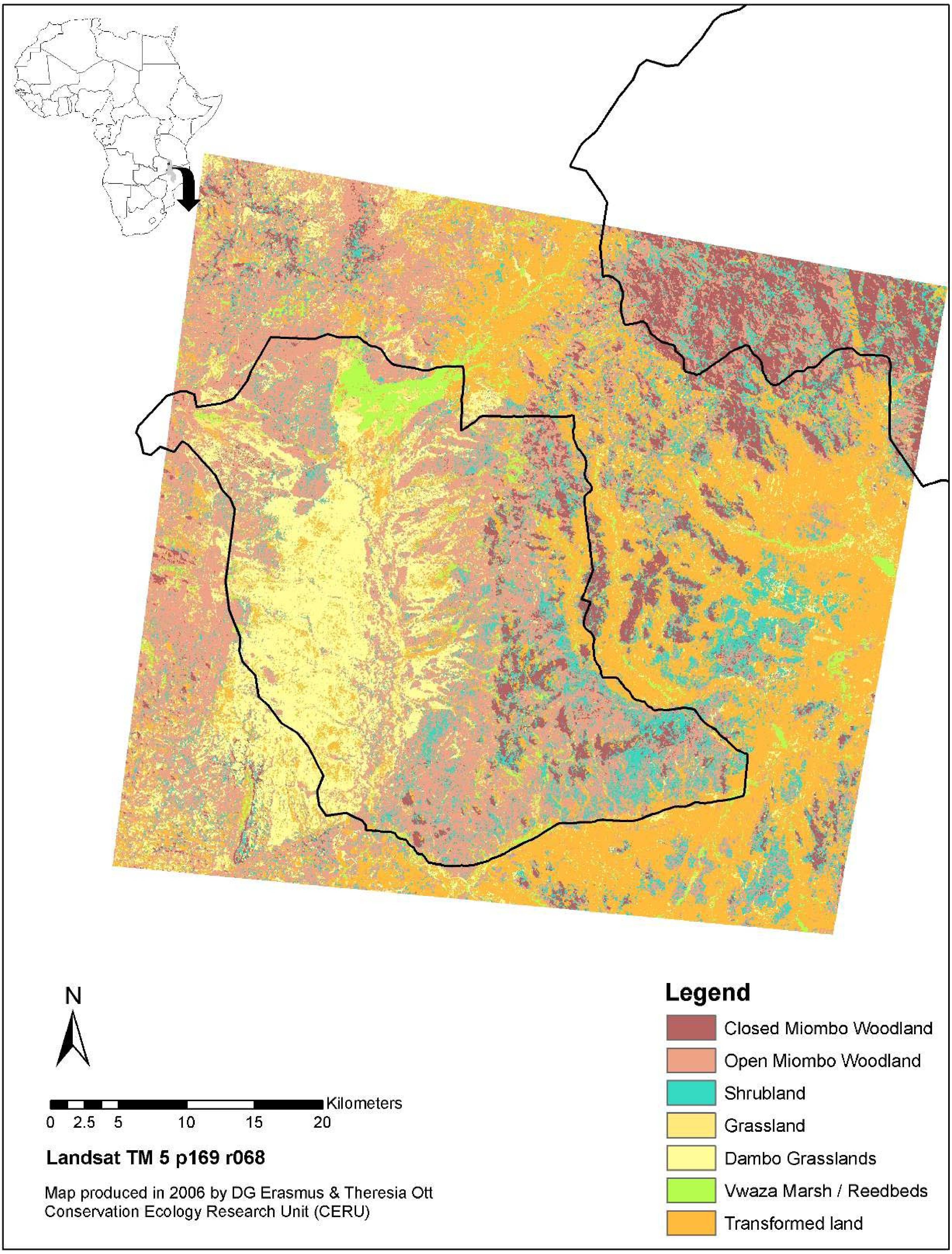


Plate 3. Landscape map of the Luangwa Valley, north-eastern Zambia. Further explanation is as given for Plate 1.

Plate 4. Landscape map of Kasungu National Park, central Malawi. Further explanation is as given for Plate 1.



Map produced in 2006 by DG Erasmus & Theresia Ott
Conservation Ecology Research Unit (CERU)

Plate 5. Landscape map of Vwaza Marsh Wildlife Reserve, north-western Malawi. Further explanation is as given for Plate 1.

Location success, Accuracy and Precision of the Satellite tracking collars

Accuracy of the collar GPS units, as measured by the mean distance between the positions and the 'true' location within each category, fell within 15m. Their accuracy also matched the range advertised by the manufacturer (10 – 15m, see page 30). However, their location precision suggested that point locations need to be corrected unless used for home range size estimates (Figure 2).

Table 8. A summary of the efficiency of the GPS units of the collars under varying canopy cover and gradients. The mean distances indicate accuracy, whilst the standard deviation (S.D.) of the mean distance indicates precision. The 'Location success' row gives an indication of the GPS units' success at recording and transmitting locations in each category. The 'open woodland' category locations were all on gentle terrain and therefore form the gentle gradient category as well. The full data set is presented as Appendix III, page 98.

Category (Total positions possible)	Forest (120)	Open Woodland / Gentle (120)	Bare ground (96)	Hill (96)	Steep (144)	Sheer (120)
Mean position distance from 'true' location ± S.D. (m)	18.3 ± 34.3	13.7 ± 13.9	10.7 ± 19.1	15.5 ± 14.6	12.5 ± 11.4	13.2 ± 33.7
Range (m) of mean position distance	3 – 172	1 – 91	0 – 107	1 - 74	1 – 71	1 – 337
Number of successful positions	23	104	88	96	116	101
Location success (%)	19	87	92	100	81	84

Accuracy was relatively low when collars were placed within forest canopies and on hill gradients (Table 8). Accuracy was higher on bare ground locations than any other canopy category (Kruskal-Wallis ANOVA $H_{(2,\ n=215)} = 13.81$, $p = 0.001$, *post-hoc* multiple comparisons tests). Whilst in the case of the landscape gradient trial, collars placed on gentle gradients, recorded significantly lower accuracies than on hill gradients, as well as a higher accuracy on steep gradients (ANOVA $H_{(3,\ n=401)} = 21.63$, $p = 0.0001$ *post-hoc* multiple comparisons tests). The variability in distance (presented by S.D. of the mean) in the forest and sheer categories suggests that positions in forest are not only inaccurate, but also imprecise. Furthermore, although the mean value of the sheer category suggests a high accuracy, positions were imprecise. For all categories, distance variability was high and suggests overall poor precision of the GPS units, irrespective of canopy cover or gradient. In addition, the location success of the collar GPS units, given as a percentage in Table 8, revealed that the dense canopy cover of forest locations reduced the number of successful position recordings. The remaining categories for both canopy cover and gradient showed a comparatively high location success, particularly hill gradients. Location success of the collars whilst deployed on elephants was high (Appendix IV, page 91), with more than 23 of the 28 collars attaining 70% success in recording locations for each of the seasons. Location success differed between study sites during one of the four seasons (see Table 9).

Table 9. Kruskal-Wallis non-parametric ANOVA H- and P-values for inter-area comparisons of location success during each season. The value in bold indicates significance at the 95% level. Source data is given in Appendix IV, page 91. Seasons are defined on page xvi.

Statistic	Dry 1	Dry 2	Wet 1	Wet 2
Kruskal-Wallis H (df, n)	3.981 (4, 26)	18.967 (4, 28)	3.930 (4, 26)	3.804 (4, 27)
P	0.4086	**0.0008**	0.4155	0.4331

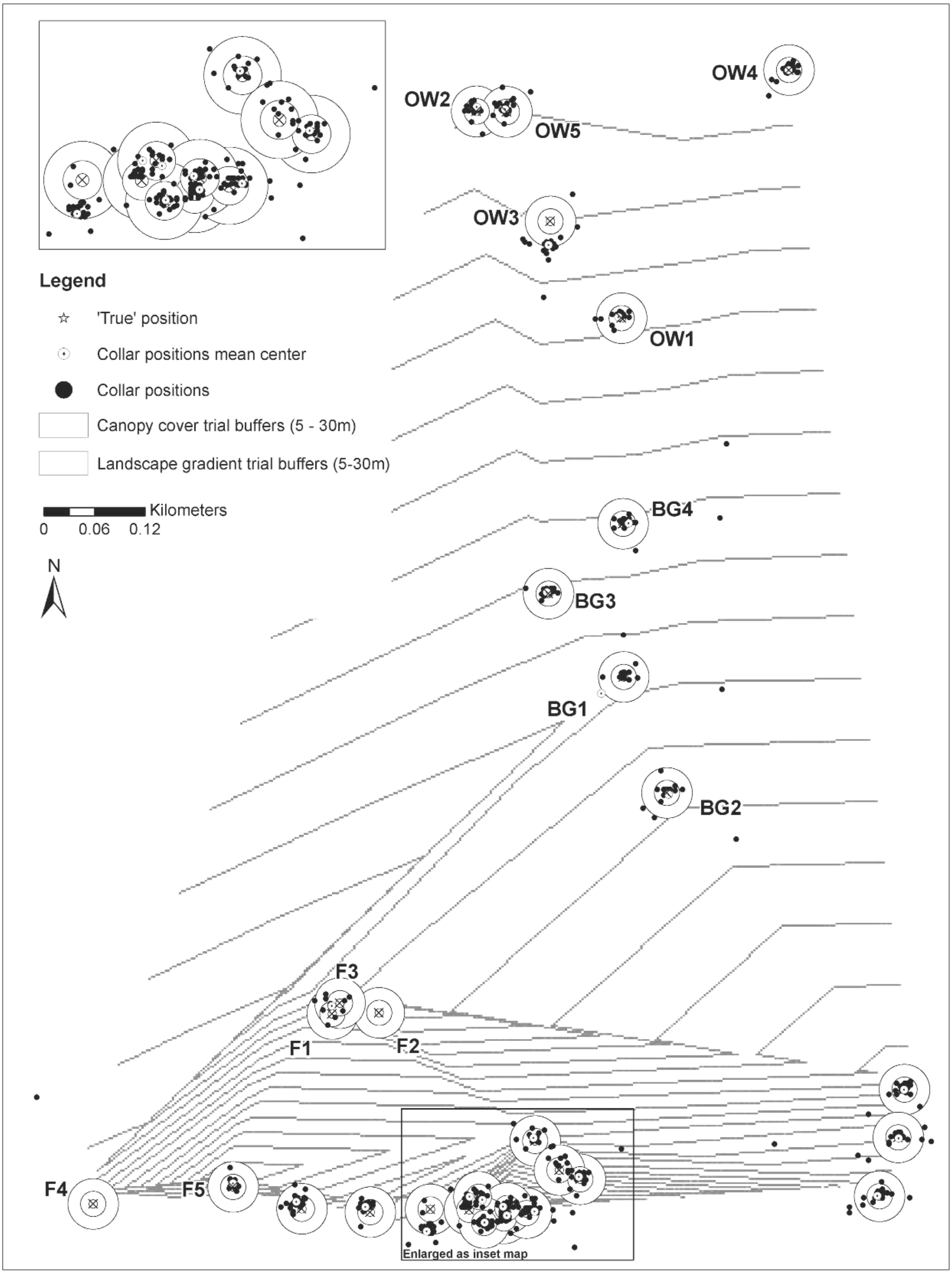


Figure 2. Map showing the spatial layout of both the canopy cover and landscape gradient trials to test the accuracy and precision of the collar GPS units. All locations are indicated by an '×' and those of the canopy cover trial are also labelled according to the category they formed part of; F = forest, OW = open woodland and BG = bare ground. The locations of the gradient trial are those that are unlabelled, their gradients are indicated by the isopleths of varying altitude at 2m intervals. Therefore, those isopleths lying closer together indicate steeper gradients. Positions recorded by each collar at each location are shown by '•' and their mean centres are indicated by '⊙'. The mean centres, together with the buffer rings, give a visual indication of the accuracy of the collars within each category.

Heterogeneity Metrics as functions of Area

My analysis suggested that Patch Density and Fractal Index change as a function of the area sampled. Linear regression slopes for all study areas showed that increases in range size resulted in decreased Patch Density, with range size accounting for up to 93% of the variability in Patch Density (see Figure 3). On the other hand, increases in range size were associated with increased Fractal Index. Range size explained 92% of the variability in Fractal Index, except in the case of Kasungu, where this value was 36%.

Interspersion and Diversity Index were barely affected by increasing range size and although in most cases slopes differed significantly from zero (see Figure 3), increasing range size accounted for a maximum of 23 and 24% of the variability, respectively. The decrease in Patch Density with increasing range size suggests that larger ranges are more likely to be homogeneous, containing fewer patches per km^2 than small ranges. These results may be an important consideration when explaining patterns of landscape utilization by elephants.

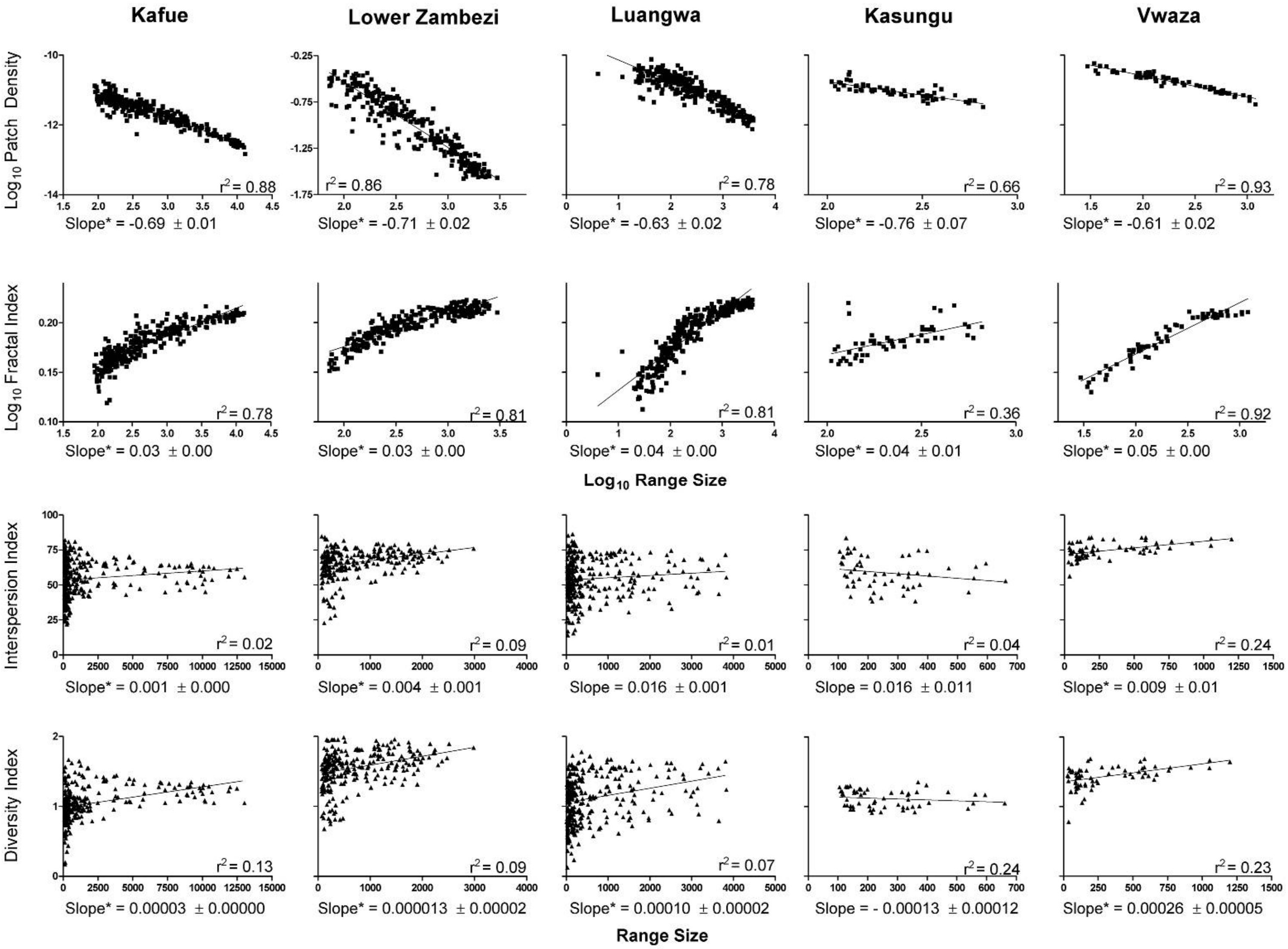


Figure 3. Landscape heterogeneity metrics plotted as functions of range size (presented in km^2) for each study area using random ranges. Both axes of Patch Density and Fractal Index are log$_{10}$ transformed to facilitate plotting a linear regression. In all cases the study areas shared common axes for each metric, except in the case of Patch Density for Lower Zambezi. The slopes (with the confidence intervals) and r^2 values of the lines are presented below each graph. The slopes indicate the apparent influence of random home range size on the metrics (asterisks '*' indicate that slope is significantly non-zero at a confidence limit of $p = 0.05$), whilst the r^2 value describes to what extent range size explains variability in each metric.

Landscape Heterogeneity of Study Areas

Landscape heterogeneity metrics differed significantly between study areas. However, *post-hoc* testing revealed that some were in fact comparable and I placed these into groups (Table 10).

Table 10. A summary of the results for the Analyses of Variance applied to compare landscape heterogeneity between the study areas. *F*-statistics indicate where I applied one-way ANOVA, whilst *H*-statistics indicate my use of the Kruskal-Wallis ANOVA for non-parametric data. I considered p-values < 0.05 as significant and presented these in bold type. Group a-d comprise comparable study areas based on the *post-hoc* tests.

	Patch Density	Fractal Index	Interspersion Index	Diversity Index
Test statistic	$F_{(4,\,140)} = 14678$	$F_{(4,\,140)} = 13.301$	$H_{(4,\,n=145)}=50.089$	$H_{(4,\,n=145)}=64.103$
p-value	$\boldsymbol{p < 0.0001}$	$\boldsymbol{p < 0.0001}$	$\boldsymbol{p < 0.0001}$	$\boldsymbol{p < 0.0001}$
Group a	Kafue	Kafue	Kafue Lower Zambezi Luangwa Kasungu	Kafue Kasungu
Group b	Lower Zambezi	Lower Zambezi Luangwa	Vwaza	Lower Zambezi Luangwa Vwaza
Group c	Luangwa Vwaza	Lower Zambezi Kasungu Vwaza	-	Luangwa Kasungu
Group d	Kasungu	-	-	-

In the analyses that followed, where I compared the landscape heterogeneity of elephant ranges between study areas, it was only possible to draw comparisons between elephant ranges for which the study areas were similar – that is, within each group assigned in Table 10. For instance, only the study areas within group c could be compared for Patch Density, whilst the other groups only contained separate study areas, precluding any comparisons (see groups a-d in Table 10).

Landscape Heterogeneity of Elephant Ranges

All the metrics increase with increasing landscape heterogeneity, this is explained on page 38. These metrics as calculated for the elephant home ranges are summarized in Table 15, the full version of which appears as Appendix XII.

Landscape heterogeneity and home range size

PREDICTION: Elephant home range size would decrease with increased Patch Density, Fractal Index, Interspersion Index and Diversity Index.

The t-tests comparing the linear regression slopes of the elephant and random ranges revealed that, contrary to my expectation, elephant home range size was independent of landscape heterogeneity as measured by the four FRAGSTATS metrics (Figure 4a-h). However, two exceptions occurred for Patch Density within group c during dry season 2 and wet season 1, and these were in line with my prediction since elephant home range size decreased with increased Patch Density.

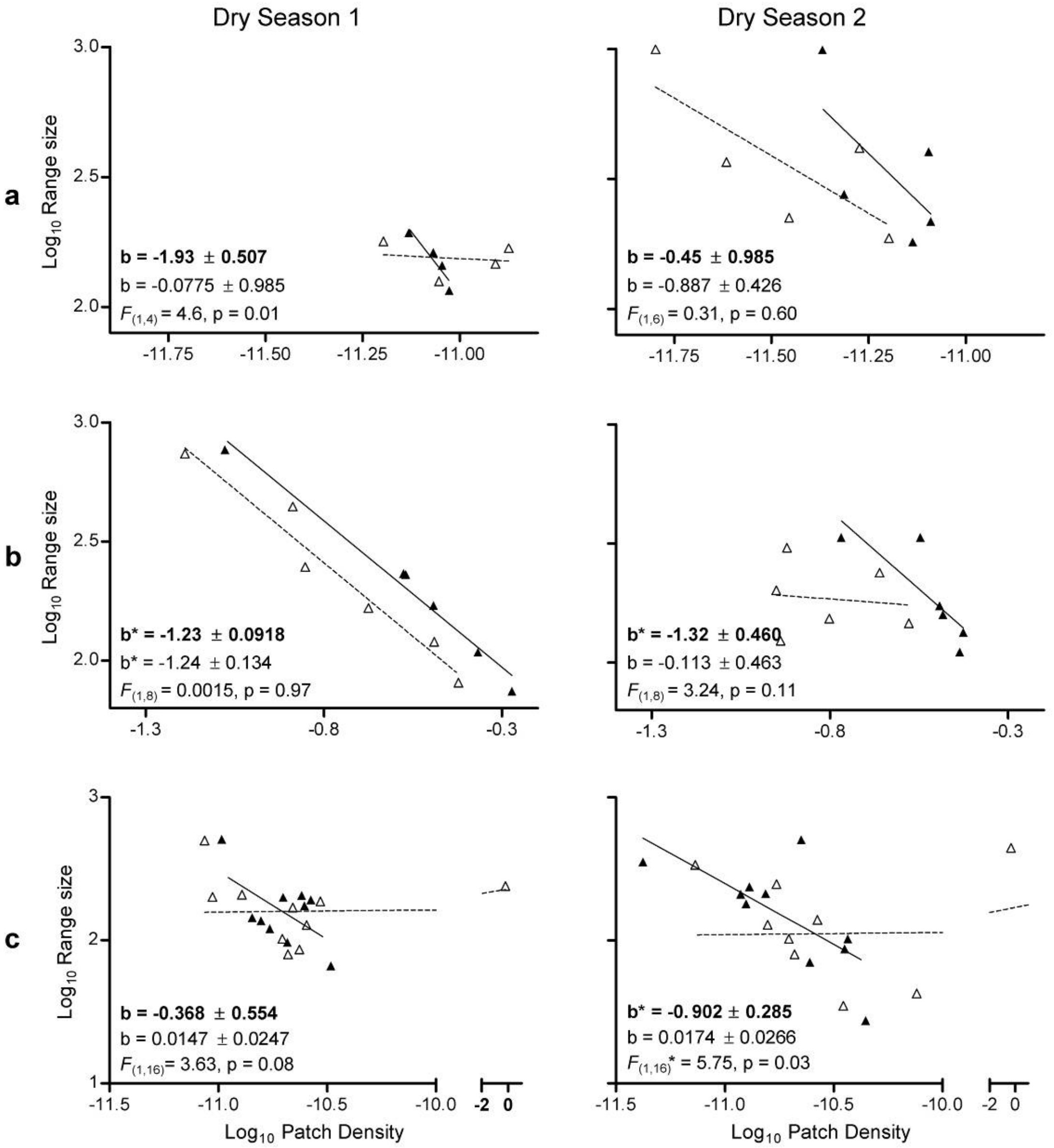


Figure 4a. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) as functions of Patch Density during two dry seasons for groups of study areas (rows a-c, see Table 10). The slope values (b) and confidence intervals are given for the elephant and random ranges (in bold and normal type, respectively) within each graph (‘*’ indicate a significantly non-zero slope at a confidence limit of p = 0.05). ‘*’ for F-values indicate that the slopes differed significantly at p = 0.05).

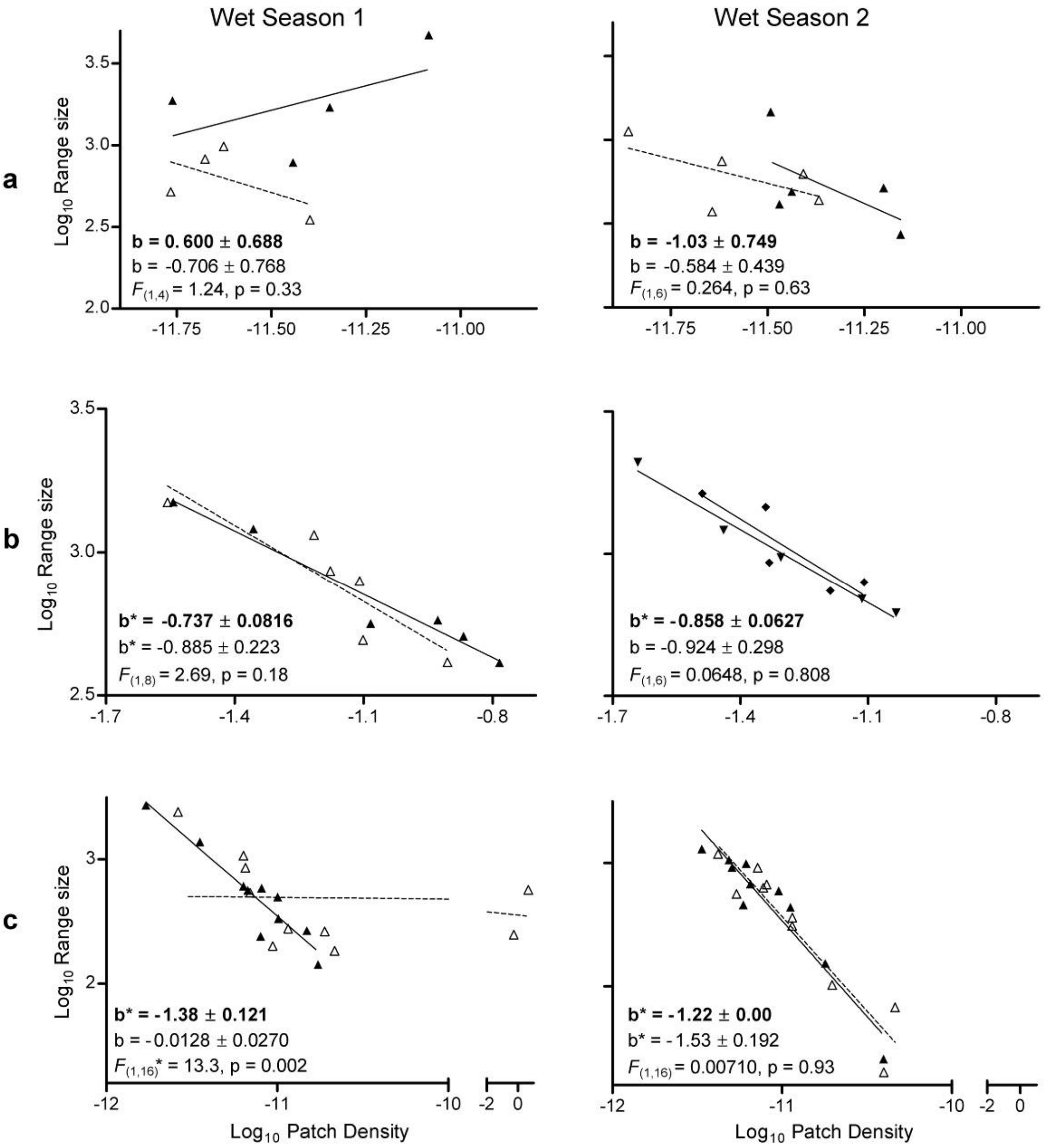


Figure 4b. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Patch Density within wet seasons for each group of study areas. Further explanation is as given for Figure 4a.

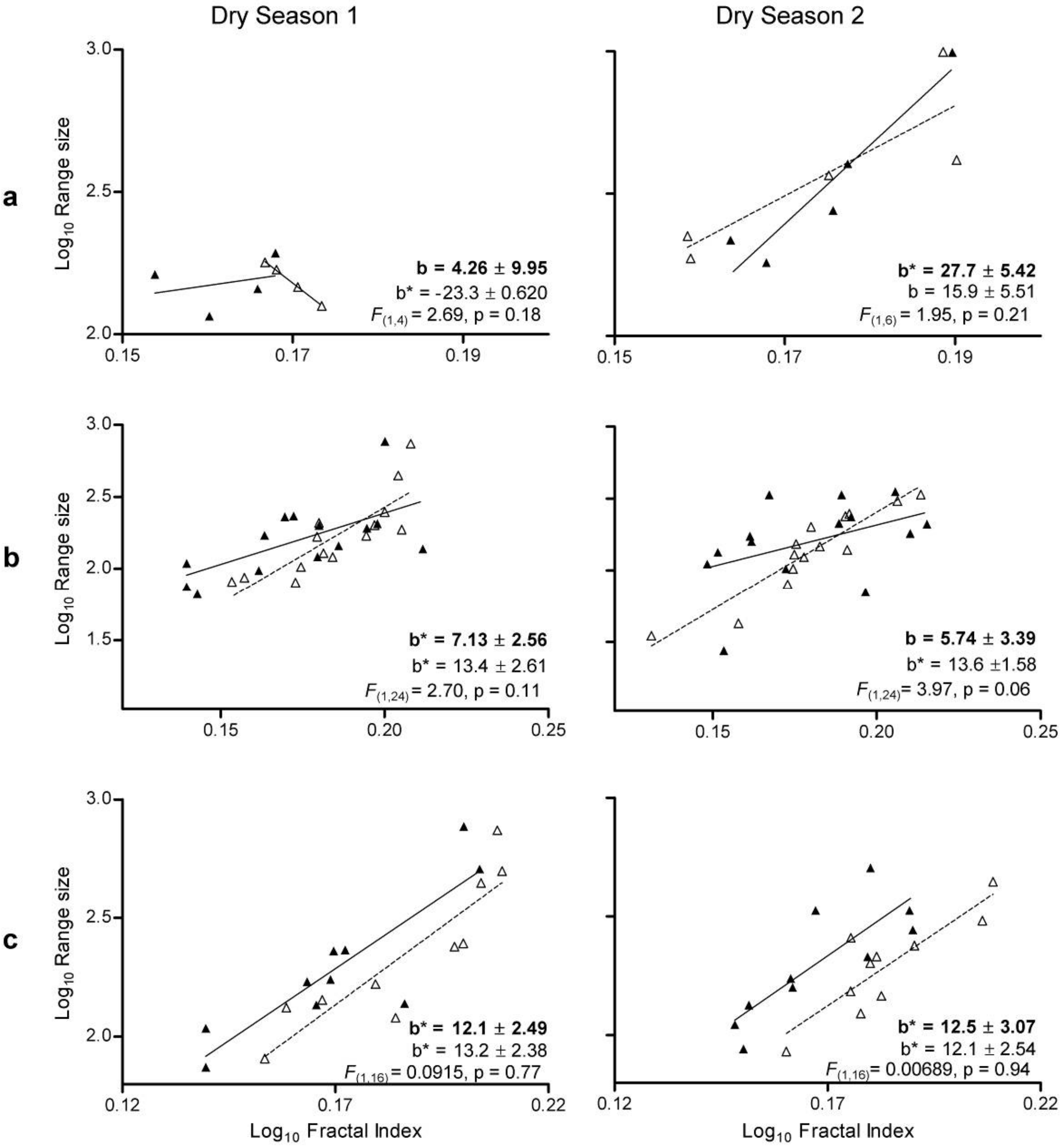


Figure 4c. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Fractal Index within dry seasons for each group of study areas. Further explanation is as given for Figure 4a.

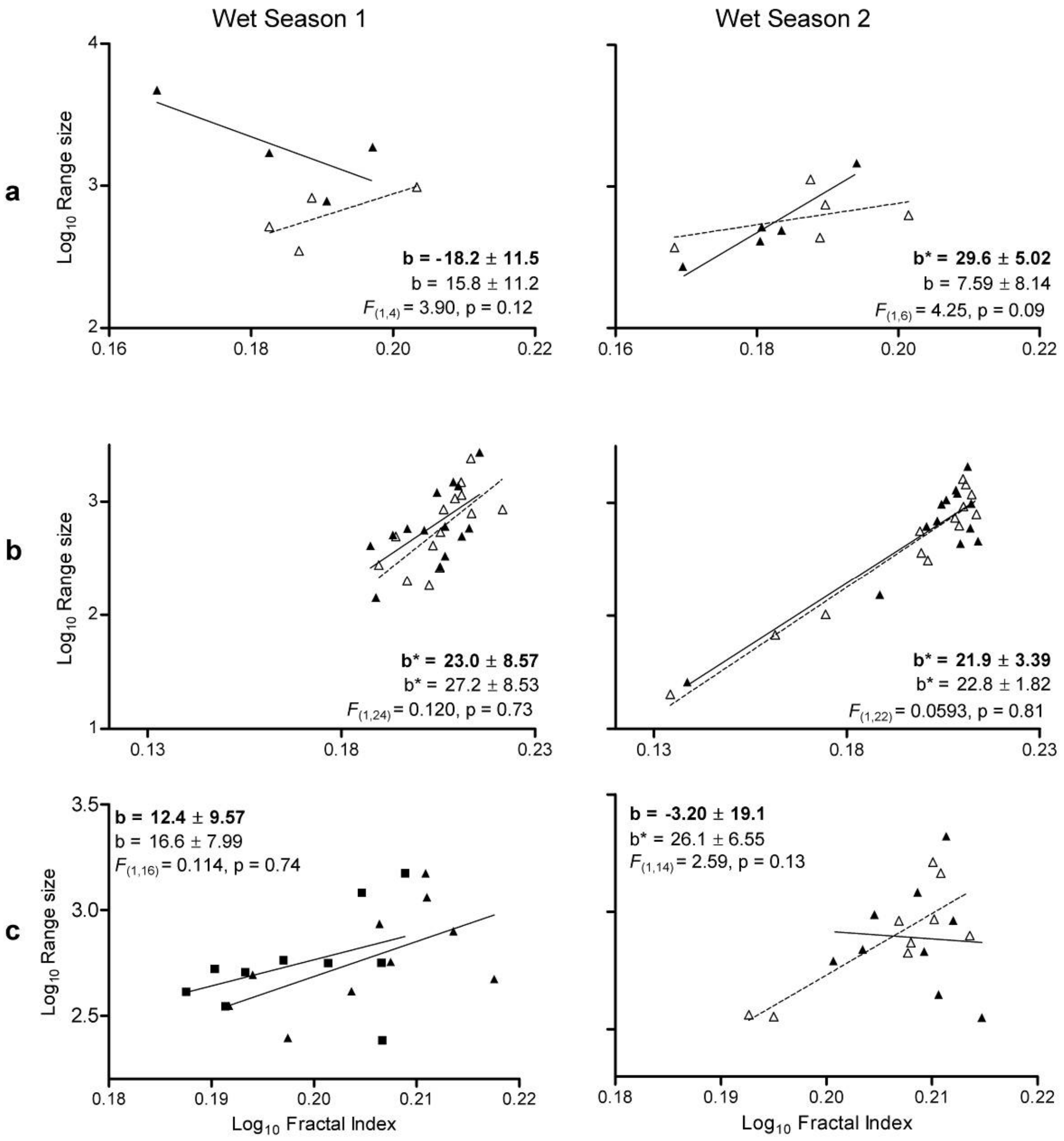


Figure 4d. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Fractal Index within wet seasons for each group of study areas. Further explanation is as given for Figure 4a.

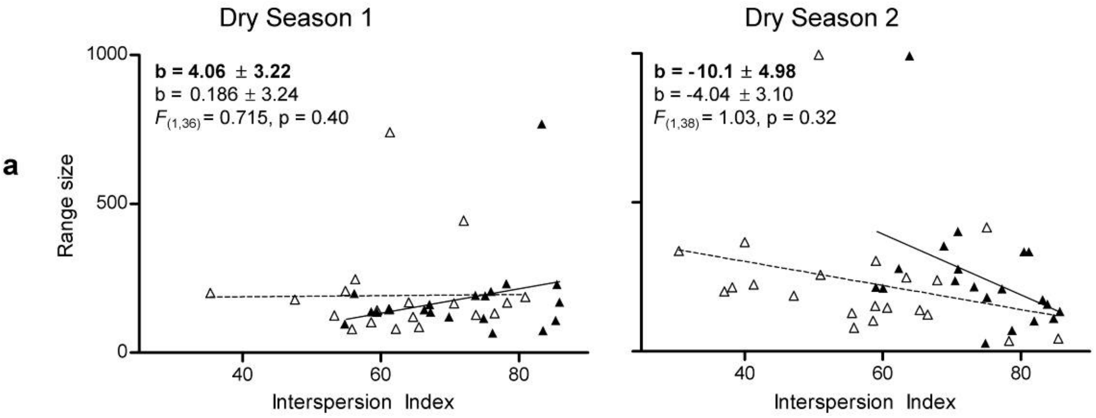


Figure 4e. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Interspersion Index within dry seasons for each group of study areas. Further explanation is as given for Figure 4a.

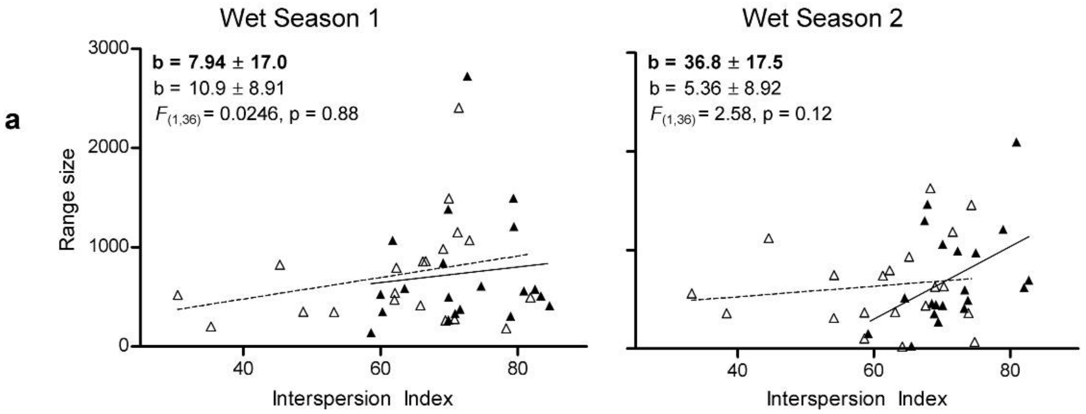


Figure 4f. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Interspersion Index within wet seasons for each group of study areas. Further explanation is as given for Figure 4a.

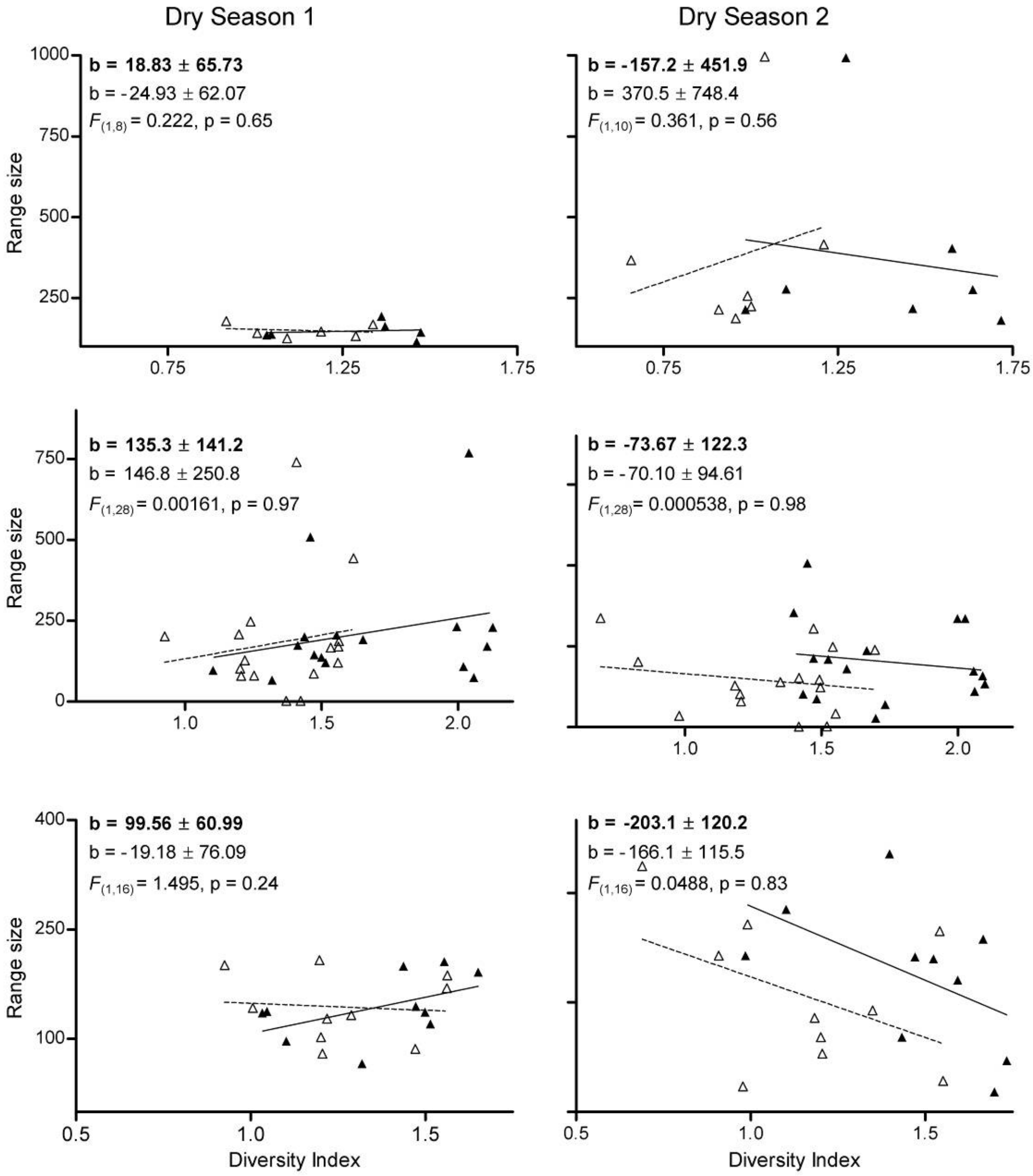


Figure 4g. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Diversity Index within dry seasons for each group of study areas. Further explanation is as given for Figure 4a.

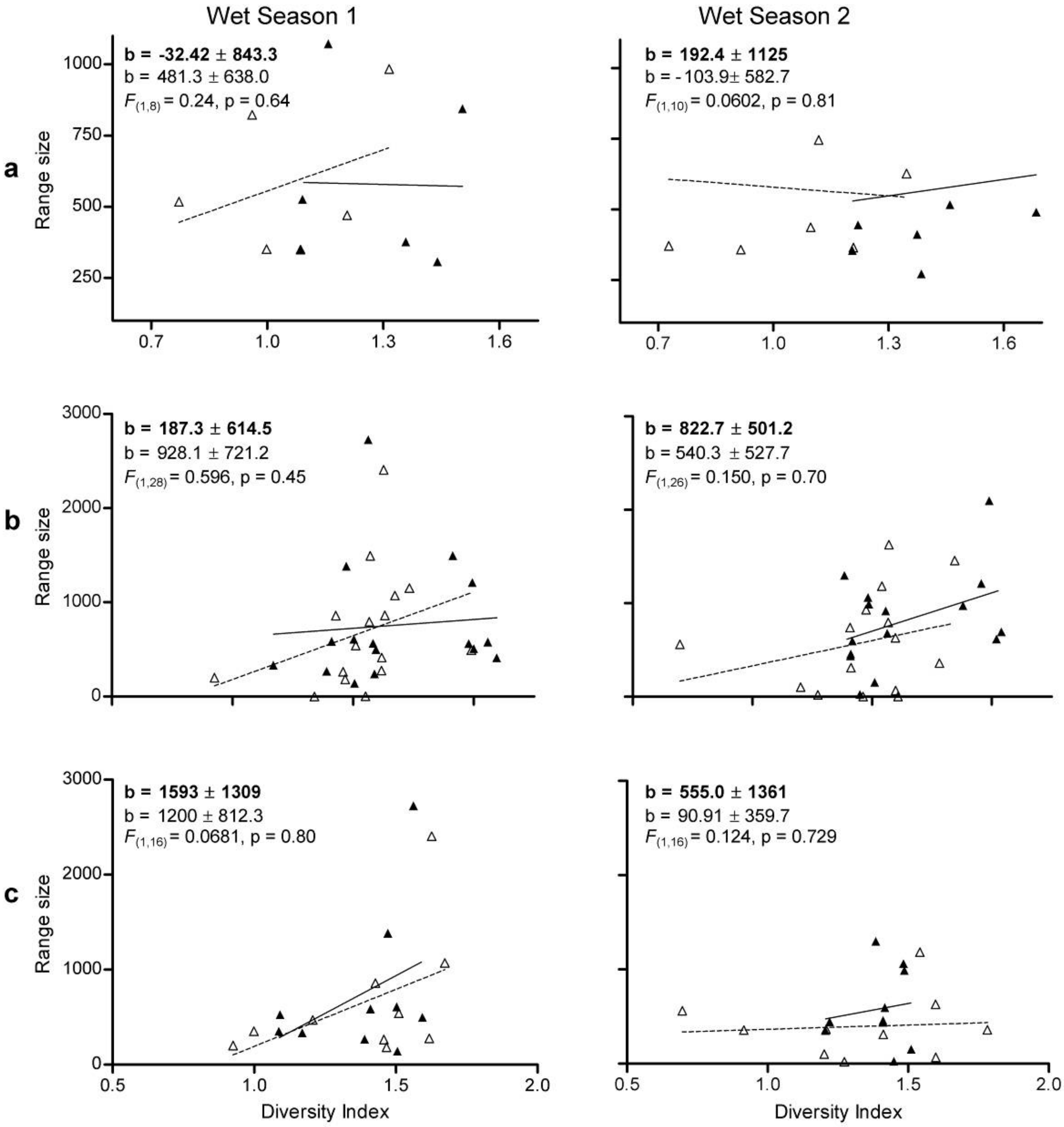


Figure 4h. Elephant home range (▲ and solid lines) and random range size (Δ and stippled lines) plotted as a function of Diversity Index within wet seasons for each group of study areas. Further explanation is as given for Figure 4a.

Between study areas

PREDICTION: The heterogeneity of elephant home ranges will differ between comparable study areas

Patch Density and Fractal Index of elephant ranges compared within groups (and seasons) were similar and therefore upheld my prediction. However, this did not hold for Interspersion and Diversity Index. However, Diversity Index did show some exceptions as Group a (Kafue and Kasungu) elephant ranges were only significantly different from one another during the dry seasons. Fractal Index showed a singular significant result for Group b (Lower Zambezi and Luangwa), where the dry season elephant ranges were different from one another.

Table 11. A summary of the results for the Analyses of Variance comparing landscape heterogeneity between elephant home ranges within similar (grouped) study areas (see Table 10). *F*-statistics indicate where I applied one-way ANOVA, whilst *H*-statistics indicate my use of the Kruskal-Wallis ANOVA for non-parametric data. I considered p-values < 0.05 as significant and presented these in bold type. Group d is not included in this table since it only exists for Patch Density, containing Kasungu and thus no comparison could be made, as indicated by dashes '-' in other groups where only one study area forms a group.

Elephants	Group	Patch Density	Fractal Index	Interspersion Index	Diversity Index
Dry Season 1	a	-	-	$H_{(3, n=20)} = 13.086$ **$p = 0.0045$**	$F_{(1,4)} = 72.281$ **$p = 0.0011$**
	b	-	$F_{(1,12)} = 2.1887$ $p = 0.1648$	-	$H_{(2, n=16)} = 10.836$ **$p = 0.0044$**
	c	$F_{(1,8)} = 0.88733$ $p = 0.3737$	$F_{(2,7)} = 0.8177$ $p = 0.\ 4796$	-	$F_{(1,8)} = 10.618$ **$p = 0.0012$**
Dry Season 2	a	-	-	$F_{(3, 17)} = 12.100$ **$p = 0.00018$**	$F_{(1, 5)} = 13.614$ **$p = 0.0142$**
	b	-	$F_{(1, 12)} = 8.2946$ **$p = 0.0138$**	-	$H_{(2, n=16)} = 10.836$ **$p = 0.0044$**
	c	$F_{(1,8)} = 0.9707$ $p = 0.3534$	$F_{(3, 7)} = 3.7131$ $p = 0.0695$	-	$F_{(1,8)} = 28.985$ **$p = 0.0006$**
Wet Season 1	a	-	-	$H_{(3, n=20)} = 13.696$ **$p = 0.0033$**	$H_{(1, n=6)} = 3.4286$ $p = 0.0641$
	b	-	$F_{(1,12)} = 3.8651$ $p = 0.0729$	-	$H_{(2, n=16)} = 11.581$ **$p = 0.0031$**
	c	$F_{(1,8)} = 0.0001$ $p = 0.9941$	$H_{(2, n=10)} = 3.9273$ $p = 0.1403$	-	$H_{(1, n=10)} = 4.3636$ **$p = 0.0367$**
Wet Season 2	a	-	-	$F_{(3,15)} = 9.4260$ **$p = 0.0010$**	$F_{(1, 4)} = 4.5385$ $p = 0.1002$
	b	-	$F_{(1,10)} = 0.1328$ $p = 0.7232$	-	$F_{(2, 6)} = 167.38$ **$p < 0.0001$**
	c	$F_{(1,7)} = 0.3336$ $p = 0.5817$	$F_{(2,6)} = 2.9438$ $p = 0.1286$	-	$F_{(1, 7)} = 40.169$ **$p = 0.0004$**

I investigated the significant cases further using *post-hoc* tests to reveal where differences lay between the elephant ranges within group a for Interspersion Index and group b for Diversity Index. In both cases, the elephant ranges of Lower Zambezi were revealed as being significantly different from those of the other study areas (see Table 11).

Table 12. Table of elephant ranges significantly different from those of the other study areas within groups (see Table 10), as revealed by *post-hoc* tests. Such tests were only necessary where groups contained more than two study areas (Interspersion Index, Group a and Diversity Index Group b), but all comparisons that yielded significant results for the ANOVA are presented here so that the elephant ranges with the largest landscape heterogeneity in terms of each metric (indicated by an asterisk '*') within each season can be shown. The study areas given in each cell are those significantly different from one another within a group during each season. 'L Zambezi' = Lower Zambezi.

	Fractal Index Group b	Interspersion Index Group a	Diversity Index Group a	Diversity Index Group b	Diversity Index Group c
Dry Season 1	-	L Zambezi Luangwa Kasungu*	Kafue* Kasungu	L Zambezi* Luangwa	Luangwa* Kasungu
Dry Season 2	L Zambezi Luangwa*	L Zambezi Kafue Luangwa Kasungu*	Kafue* Kasungu	L Zambezi* Luangwa Vwaza	Luangwa* Kasungu
Wet Season 1	-	L Zambezi Luangwa Kasungu*	-	L Zambezi* Luangwa	Luangwa* Kasungu
Wet Season 2	-	L Zambezi Kafue Luangwa*	-	L Zambezi* Luangwa Vwaza	Luangwa* Kasungu

Patch Density measures the number of structural vegetation patches per km^2. Values for elephant ranges of the study areas in Group c (Luangwa and Vwaza) never differed significantly from one another. The elephant ranges of Kafue, Lower Zambezi and Kasungu were not comparable for this metric, as they were dissimilar from each other as well as Luangwa and Vwaza.

Fractal Index expresses the complexity of patch shape within the landscape. Values for the elephant ranges between Group b (Lower Zambezi and Luangwa) only differed significantly during dry season 2 (see Table 10). The Luangwa elephant ranges had the largest mean Fractal Index during this season (Table 11). I could not compare the elephant ranges of Kafue for this metric, as they were dissimilar from those of the remaining study areas.

Interspersion Index reflects on the arrangement and distribution. This index differed significantly for all elephant ranges in Group a (Kafue, Lower Zambezi, Luangwa, Kasungu) in all seasons (see Table 10). *Post-hoc* testing revealed that the elephant ranges of Lower Zambezi and Luangwa were always different from one another as well as the ranges of one or both of the remaining study areas (Table 11). The Kasungu elephant ranges had the lowest mean Interspersion Index (highest landscape heterogeneity) for dry season 1, 2 and wet season 1, whilst the mean values for the Luangwa elephant ranges were lowest during wet season 2 – when Kasungu was not included. I could not compare the elephant ranges of Vwaza, since they were dissimilar from those of the remaining study areas.

Diversity Index is a measure of the presence of different patch types in a landscape. Values for elephant ranges differed significantly between study areas for all seasons, but not within all groups. Groups b (Lower Zambezi, Luangwa and Vwaza) and c (Luangwa and Kasungu) were significant throughout the seasons, whilst differences within Group a (Kafue and Kasungu) were only significant during the dry seasons (Table 11). However, the *post-hoc* tests revealed that the study areas responsible for significant differences in Group b were relatively consistent throughout the seasons (see Table 11), as Lower Zambezi and Luangwa.

Between seasons

PREDICTION: Landscape heterogeneity of the wet season elephant home ranges would be greater than those of the dry seasons

The landscape heterogeneity of the elephant home ranges within study areas differed significantly different between seasons for all metrics. Exceptions included Patch Density of Kasungu, Interspersion Index of Luangwa and Kasungu, and Diversity Index of Luangwa (Table 12). Table 12 also indicates where dry season ranges were more heterogeneous in terms of the metrics used than wet season ranges and *vice versa*, as extracted from Table 15.

Table 13. A summary of the results for the ANOVA comparing landscape heterogeneity between seasonal elephant home ranges within each study area. *F*-statistics indicate where I applied one-way ANOVA, whilst *H*-statistics indicate my use of the Kruskal-Wallis ANOVA for non-parametric data. I considered p-values < 0.05 as significant and presented these in bold type. Superscripts 'D' and 'W' indicate 'Dry' and 'Wet Seasons', respectively as the season that showed the highest mean landscape heterogeneity as represented by that metric.

Elephants	Patch Density	Fractal Index	Interspersion Index	Diversity Index
Kafue males	$F_{(1,16)} = 20.432$ $\boldsymbol{p = 0.0003}^{\mathrm{D}}$	$H_{(1,\, n=18)} = 7.7368$ $\boldsymbol{p = 0.0054}^{\mathrm{W}}$	$F_{(1,\, 16)} = 19.982$ $\boldsymbol{p = 0.0004}^{\mathrm{W}}$	$F_{(1,\, 16)} = 8.6484$ $\boldsymbol{p = 0.0096}^{\mathrm{W}}$
Kafue females	$F_{(1,15)} = 9.8975$ $\boldsymbol{p = 0.0067}^{\mathrm{D}}$	$F_{(1,\, 15)} = 7.1783$ $\boldsymbol{p = 0.0172}^{\mathrm{W}}$	$F_{(1,\, 15)} = 0.0010$ $p = 0.9758$	$F_{(1,\, 15)} = 0.00096$ $p = 0.9758$
Lower Zambezi	$F_{(1,\, 21)} = 39.426$ $\boldsymbol{p < 0.0001}^{\mathrm{D}}$	$H_{(1,\, n=23)} = 14.568$ $\boldsymbol{p = 0.0001}^{\mathrm{W}}$	$F_{(1,\, 21)} = 5.6047$ $\boldsymbol{p = 0.0276}^{\mathrm{W}}$	$F_{(1,\, 21)} = 8.2525$ $\boldsymbol{p = 0.0091}^{\mathrm{D}}$
Luangwa	$F_{(1,\, 29)} = 17.743$ $\boldsymbol{p = 0.0002}^{\mathrm{D}}$	$H_{(1,\, n=31)} = 9.0268$ $\boldsymbol{p = 0.0027}^{\mathrm{W}}$	$H_{(1,\, n=31)} = 1.1391$ $p = 0.2859$	$F_{(1,\, 29)} = 1.4214$ $p = 0.2428$
Kasungu	$H_{(1,\, n=8)} = 0.3333$ $p = 0.5637$	$F_{(1,\, 6)} = 6.6113$ $\boldsymbol{p < 0.0423}^{\mathrm{W}}$	$F_{(1,\, 6)} = 3.1187$ $p = 0.1278$	$F_{(1,\, 6)} = 6.4296$ $\boldsymbol{p = 0.0443}^{\mathrm{W}}$
Vwaza	$F_{(1,\, 6)} = 18.543$ $\boldsymbol{p = 0.0051}^{\mathrm{D}}$	$H_{(1,\, n=8)} = 5.3333$ $\boldsymbol{p = 0.0209}^{\mathrm{W}}$	$F_{(1,\, 6)} = 70.938$ $\boldsymbol{p = 0.0002}^{\mathrm{D}}$	$F_{(1,\, 6)} = 55.486$ $\boldsymbol{p = 0.0003}^{\mathrm{W}}$

Dry season ranges were consistently more heterogeneous than wet seasons in terms of Patch Density, whilst the opposite held for Fractal Index (Table 12). No clear patterns emerged for Interspersion and Diversity Index.

Between sexes

PREDICTION: Landscape heterogeneity of the female elephant home ranges would be greater than those of male home ranges

All landscape heterogeneity metrics differed significantly between the sexes for the wet seasons, but only for Patch Density during the dry seasons (Table 13). Table 13 also indicates whether male or female home ranges showed greater landscape heterogeneity per metric, as indicated by the metric mean values presented in Table 15.

Table 14. A summary of the results for the Analyses of Variance comparing landscape heterogeneity between male and female elephant home ranges of Kafue National Park within the dry and wet seasons. *F*-statistics indicate where I applied one-way ANOVA, whilst *H*-statistics indicate my use of the Kruskal-Wallis ANOVA for non-parametric data. I considered p-values < 0.05 as significant and presented these in bold type. Superscripts ‘M’ and ‘F’ indicate ‘Male’ and ‘Female home ranges’, respectively as the sex that showed the greatest landscape heterogeneity, as indicated by the mean value of the metric.

Comparison	Patch Density	Fractal Index	Interspersion Index	Diversity Index
Dry Seasons	$H_{(1,\, n=18)} = 2.6741$ $\mathbf{p = 0.0002}^{F}$	$F_{(1,16)} = 1.4405$ $p = 0.2475$	$F_{(1,16)} = 1.3874$ $p = 0.2561$	$H_{(1,\, n=18)} = 2.2557$ $p = 0.1331$
Wet Seasons	$F_{(1,15)} = 24.041$ $\mathbf{p = 0.0001}^{F}$	$F_{(1,15)} = 13.746$ $\mathbf{p = 0.0021}^{M}$	$F_{(1,15)} = 32.217$ $\mathbf{p < 0.0001}^{F}$	$F_{(1,16)} = 10.120$ $\mathbf{p = 0.0062}^{F}$

In significant cases, female home ranges showed a greater Patch Density, Interspersion Index and Diversity Index than those of males during both seasons. However, male home ranges had greater Fractal Index than females during the wet seasons.

Table 15. Mean values of landscape heterogeneity metrics for the elephant home ranges. The calculation of these metrics is explained in the text (see page 42). 'S.D.' = standard deviation of the mean value. Shaded cells indicate study areas where the mean value for the elephant ranges is significantly larger when compared between seasons within a study area. Bold cells indicate study areas where the mean value is significantly larger when compared between study areas (within groups indicated by 'Group' row) within seasons. The Kafue males were only compared with the Kafue females. Where a study area belonged to more than one group (indicated by '/'), and multiple comparisons are drawn, superscript letters indicate which group comparison is indicated by bold text. Italic cells indicate where elephant ranges of Kafue have significantly larger landscape heterogeneity between sexes, within dry and wet seasons. Full table appears as Appendix XII.

Metric		Patch Density				Fractal Index				Interspersion Index				Diversity Index			
Study Area	Season	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2
Kafue Males	*Mean*	-11.28	-11.23	-11.92	-12.11	1.49	1.50	*1.57*	*1.58*	67.85	68.29	*57.56*	*59.59*	1.36	1.47	1.09	1.27
	S.D.	0.32	0.15	0.28	0.32	0.05	0.04	*0.01*	*0.01*	6.58	4.46	*3.41*	*4.02*	0.15	0.22	0.04	0.14
Kafue Females	*Mean*	-11.07	-11.20	*-11.41*	*-11.39*	1.45	1.50	1.53	1.52	70.48	70.80	70.37	69.77	**1.42**	**1.53**	*1.37*	*1.46*
	S.D.	0.05	0.13	*0.28*	*0.16*	0.02	0.03	0.05	0.04	4.44	4.25	7.09	3.87	**0.06**	**0.17**	*0.15*	*0.13*
	Group	a				a				a				a			
Lower Zambezi	*Mean*	-0.56	-0.53	-1.09	-1.31	1.46	1.46	1.58	**1.61**	**83.61**	**83.17**	**81.71**	**79.92**	**2.06**	**2.06**	**2.01**	**1.98**
	S.D.	0.28	0.13	0.30	0.24	0.08	0.05	0.03	**0.02**	**2.88**	**2.03**	**2.16**	**3.12**	**0.05**	**0.04**	**0.06**	**0.06**
	Group	b				b/c				a				b			
Luangwa	*Mean*	-10.68	-10.79	-11.14	-11.13	1.52	1.56	1.61	1.61	67.05	73.40	68.76	68.70	**1.44**^{c}	**1.56**^{c}	**1.45**^{c}	**1.44**^{c}
	S.D.	0.12	0.32	0.33	0.25	0.07	0.07	0.03	0.03	8.78	6.85	5.20	4.67	**0.17**	**0.13**	**0.13**	**0.05**
	Group	c				b				a				b/c			
Kasungu	*Mean**	-23.67	-11.02	-11.19	-10.96	1.50	1.53	1.55	1.63	59.02	60.66	60.17	68.99	1.04	1.04	1.09	1.21
	*S.D.**	0.00	0.11	0.02	0.01	0.05	0.03	0.00	0.01	0.61	2.33	0.21	0.19	0.01	0.08	0.00	0.01
	Group	d				c				a				a/c			
Vwaza	*Mean**	-10.79	-10.55	-11.13	-11.24	1.54	1.46	1.61	1.62	70.52	69.20	78.63	78.23	1.44	1.46	1.59	1.56
	*S.D.**	0.27	0.14	0.05	0.08	0.09	0.07	0.00	0.01	2.89	1.21	0.64	0.57	0.03	0.02	0.00	0.01
	Group	c				c				b				b			

*These are presented only for comparative purposes, although the small sample sizes limit such calculations.

Landscape heterogeneity and home range location

PREDICTION: Elephant home ranges would be located in more heterogeneous areas than randomly located ranges of similar size and shape in the same study area

The observed mean and individual values (Table 15) of each of the metrics for the elephant ranges of each study area are presented as a point on the corresponding normal curves formed by the random ranges (predicted mean values) (Figure 5). The points beyond the two-tailed 95% confidence limit suggest selection for that metric of landscape heterogeneity. The observed variance for each metric of the elephant ranges is presented on the relevant gamma curve formed by the random ranges (Figure 6). The variance confirmed that elephants select for landscape heterogeneity as suggested by the mean when the points of the elephant ranges representing both the mean and variance values fall beyond the two-tailed 95% confidence limit. However, when the variance points did not fall outside the 95% confidence limits, but the mean values do, selection is implied but not confirmed. These results are summarized in Table 16.

Aside from Interspersion Index and Diversity Index, there was little consistency within seasons between study areas and between seasons within study areas for each of the metrics. Patch Density played a major, though inconsistent role in landscape selection by Kafue elephants, but was important in Lower Zambezi for both dry seasons and only during wet season 2 for Luangwa elephants. Fractal Index was important during all seasons for Lower Zambezi elephants, but only in wet season 2 for the Kafue male elephants and dry and wet season 2 for Luangwa. Both Interspersion Index and Diversity Index were important throughout all seasons and study areas, with the exception of the Kafue males, only showing selection in the dry seasons (Table 16). However, consistent selection for Interspersion and Diversity Index was in line with their importance as suggested by the inter-area comparisons (page 66). None of the elephants from my study areas selected against (avoided) any of the four landscape metrics I used to express heterogeneity. Furthermore, Kafue males apparently did not select, nor avoid these metrics. Only the female elephants demonstrate instances where both the mean values and variances for their home ranges fell outside the two-tailed confidence limits. These results, together with those of inter-area comparisons suggested that Interspersion and Diversity Index were consistently important to the elephants of Lower Zambezi and Luangwa when selecting the location home ranges.

Table 16. A summary of results for the comparison of random and elephant range landscape heterogeneity as expressed by FRAGSTATS metrics, shown in Figures 5 and 6. Arrows indicate positive (⇧) and negative (⇩) selection by elephants of the relevant metric. Open arrows indicate where the position of the elephant range mean (Figure 5) fell outside the two-tail 95% confidence limit, but the corresponding variance (Figure 6) did not. Closed arrows indicate where both the mean and variance fell outside the two-tailed confidence limit. The mean values appear in Table 15. These cells therefore infer which features of landscape heterogeneity are selected for by elephants. Empty cells indicate no selection.

Study Area	Season*	Log_{10} Patch Density	Fractal Index	Interspersion Index	Diversity Index
Kafue (male)	Dry 1			⇧	⇧
	Dry 2	⇧		⇧	⇧
	Wet 1				
	Wet 2	⇧	⇩		
Kafue (female)	Dry 1	⇧		⇧	⇧
	Dry 2			⬆	⇧
	Wet 1	⇧		⇧	⇧
	Wet 2	⇧		⬆	⇧
Lower Zambezi	Dry 1	⇧	⇩	⬆	⬆
	Dry 2	⇧	⇩	⬆	⬆
	Wet 1		⇩	⬆	⬆
	Wet 2		⇩	⇧	⬆
Luangwa	Dry 1			⬆	⬆
	Dry 2		⇧	⬆	⬆
	Wet 1			⬆	⬆
	Wet 2	⇩	⬆	⬆	⬆

*Defined fully in Glossary of Terminology, Acronyms and Contractions, page i.

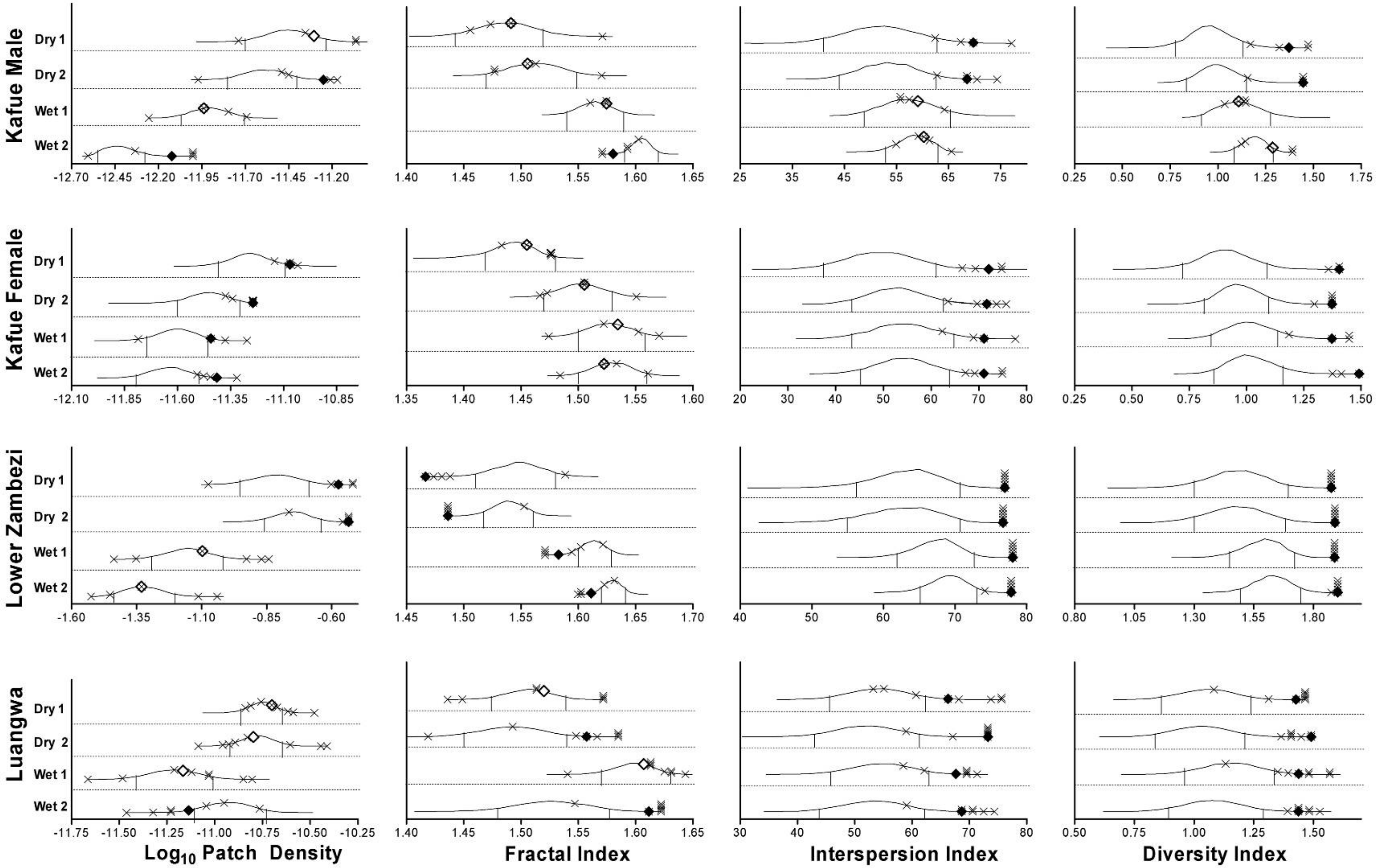


Figure 5. Landscape heterogeneity of the random ranges modelled and fitted to a normal distribution. The position of the mean values of the elephant home ranges are marked on the relevant curve with a ◆ symbol. Mean values of the elephant home ranges beyond the two-tailed 95% (vertical lines) confidence limit imply selection and are marked by closed symbols, whilst those falling within confidence limit (no selection) are marked by open symbols. Individual observed values are marked with × for all seasons and study areas, these were stacked when multiple observations fell at the same point.

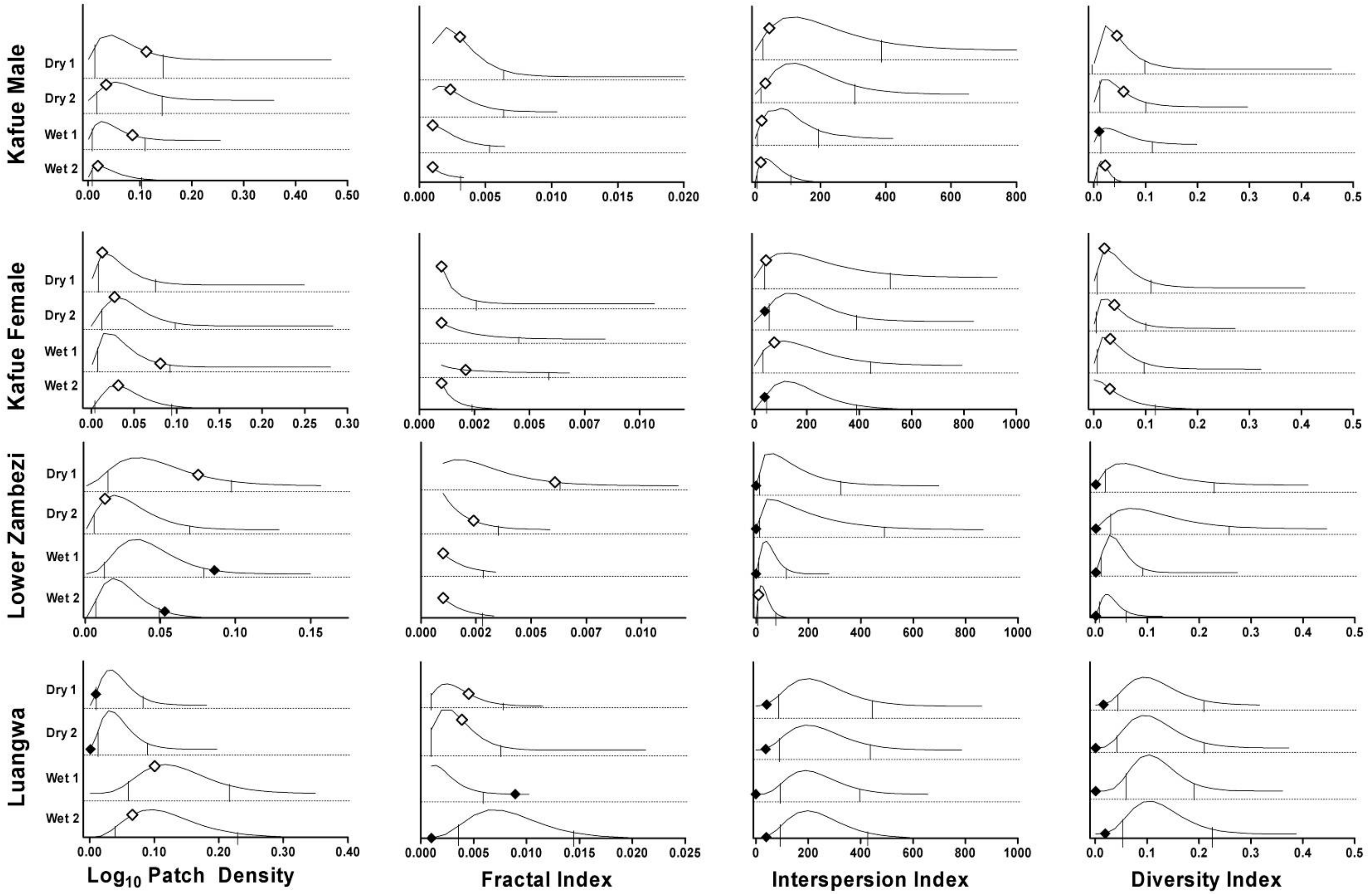


Figure 6. The variance of landscape heterogeneity of random ranges modelled and fitted to a Gamma distribution. The position of the variance values of the elephant home ranges are marked on the relevant curve with a ◆ symbol. Variances falling outside the two-tailed 95% (vertical lines) for the same metric and season as in Figure 5, emphasize significance shown by the mean values of the random and elephant ranges. Such instances are marked by closed symbols, whilst those falling within the confidence limits are marked by open symbols.

CHAPTER 5

DISCUSSION

My study aimed to determine whether landscape heterogeneity can explain variability in elephant home range size and location. Published information on optimal foraging theory and elephant range utilization patterns suggests that at the landscape scale, elephants may select areas with a more heterogeneous vegetation structure (see Introduction).

My research was based on the premise that landscape heterogeneity[22] reflects on resource quality and quantity, since areas of relatively high heterogeneity are sought after by animals as a superior source of beneficial resources (Tufto et al. 1996; Saïd and Servanty 2005). This follows my reasoning as presented in Chapter 1. In this thesis, I focussed on searching for apparent relations between the location and size of home ranges and the underlying heterogeneity of landscapes where the home ranges occurred. I showed that when roaming freely, elephants in the miombo woodlands located their home ranges in areas with greater landscape heterogeneity than in surrounding areas. However, landscape heterogeneity was not a determinant of the size of home ranges. Thus, only one of my original hypotheses was supported. From this, I conclude that the selection of home range locations by elephants based on landscape heterogeneity may be the result of elephants foraging optimally for resources within such landscapes. This presents an avenue for further study.

My analyses relied on classified landscape maps that depicted heterogeneity in terms of vegetation structure. The classification accuracy of these maps was relatively high, albeit not for all of the individual landscape types. Lower accuracies were not necessarily a symptom of poor methodology, as accuracies below 50% corresponded to those landscapes with few verification points (Table 7, page 46). For example, in Lower Zambezi, the random selection

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[22] In some cases in the Discussion, I have referred to each of the metrics of landscape heterogeneity using descriptive phrases (see Glossary of Terminology, Acronyms and Contractions page xvi) for explanatory purposes.

of verification points included only three points for miombo woodlands. These all fell beyond the miombo woodlands, resulting in a Kappa statistic of 0%. In the future, this limitation may be overcome with relative ease by increasing the number of verification points. Furthermore, in a few instances, differences between the verification points and the classified maps suggested that the points may carry a spatial error. In some cases, unintentional drift of the helicopter may have induced spatial error due to the time delay in recording the waypoint. This holds for all the maps that I develop but for Kafue, where all sampling took place during ground surveys and where landscape specific accuracies always exceeded 50%. Thus, spatial error could be related to GPS error (see Chapter 3, page 30), helicopter drift during sampling or a combination of both. Future studies should therefore be based on as many verification points as possible, since Kappa statistics are based on the percentage of verification points matching the vegetation type in which they fall. Furthermore, a camera linked to a GPS unit for helicopter surveys, where images are captured as the GPS records the location, would prevent error introduced by helicopter drift.

While all my study areas fell within the dry miombo region, they varied in patch density, patch shape complexity, landscape complexity and landscape diversity metrics (see Table 10). Geological and topographical differences across the region may be responsible for these differences since both vegetation structure and habitat diversity (e.g. Johnson et al. 2003) reflect on substrate characteristics. To enhance the interpretation of the consequences of heterogeneity for home range size and location, I opted to compare home ranges within comparable study areas. I then compared the heterogeneity of elephant ranges within these.

Trials to determine how efficient the GPS units of the collars used in the present study were, showed that canopy cover influences their accuracy and precision. In agreement with Moen et al. (1996), forest landscapes resulted in the least locations successfully recorded by the unit, due to the dense cover. Furthermore, locations from such landscapes were relatively inaccurate and imprecise (see Table 8). This would result in underestimating the presence of elephants in such landscapes (Dussault et al. 1999). This kind of bias may be more of a problem when using the locations directly, rather than when using them to estimate 95% Kernel home range (Dussault et al. 1999). Positions recorded by the GPS units on gentle gradients were more accurate than those recorded on steep terrain. This is in line with other studies (e.g. Dussault et al. 1999; D'Eon et al. 2002) suggesting that mountainous terrain induces bias since slopes block portions of the sky and therefore affect satellite geometry. Unexpectedly though, I found that positions recorded on gentle terrain were less accurate than those from hilly terrain. This may have been an effect of the hilly landscapes on which the collars were placed, being higher (up to 10 m), therefore improving the line-of-sight capability of the GPS unit. Finally, whilst deployed on the elephants within the various study areas, the collars showed impressive success, with more than three quarters being more than 70% successful at recording a location (see Appendix IV). Furthermore, all but one season's location success were similar between study areas. Therefore, no particular study area has a tendency to provide better access between the satellites and the GPS receiver. It seems that the cause of there being a difference during the second dry season was all the Kafue collars having attained a location success of greater than 98% during this season.

Elephants are dependant on water (Redfern et al. 2005; de Beer et al. 2006), while nutrition (Western and Lindsay 1984; Osborn 2004a; 2004b), indices of environmental greenness (e.g. Normalized Difference Vegetation Index (NDVI), Young et al. in review), terrain (Wall et al. 2006), thermoregulatory constraints (De Villiers and Kok 1988; Kinahan et al. 2007) and the presence of people (Parker and Graham 1989; Hoare and du Toit 1999; Murwira and Skidmore 2005; Ntumi et al. 2005), further influence their movements. Considering these constraints, I hypothesized that the location and size of elephant home ranges would be determined by landscape heterogeneity throughout mesic savannas.

Unlike mule deer *Odocoileus hemionus* (Ogilby 1839) (Kie et al. 2002) and contrary to my prediction, differences in elephant home range size could in general not be explained by landscape heterogeneity. My findings are also in contrast to those of Grainger et al. (2005) who found that home range sizes of elephants in Kruger National Park decreased with an increase in the number of patches. However, fences restrict the movement of elephants in Kruger and therefore their opportunity to select, which was not the case for my study areas. However, Tufto et al. (1996) found that access to diverse landscapes did not affect the home range size of female roe deer *Capreolus capreolus* (Linnaeus 1758). They suggested that this was because variation in heterogeneity between different home ranges was too low, which may also be the case for my study. In line with Tufto et al. (1996) as well as Mitchell and Powell (2004), my results also imply that home ranges in areas with greater heterogeneity are not necessarily smaller than those in less heterogeneous areas. Therefore, factors other than landscape heterogeneity, such as the availability of water (e.g. de Beer et al. 2006) and primary productivity (e.g. Murwira and Skidmore 2005), or a combination of these, may govern the size of elephant home ranges.

In line with my expectation, the heterogeneity of elephant home ranges within groups of study areas with similar heterogeneity was alike for metrics not corrected for area (Patch Density and Fractal Index). However, the area-corrected metrics (Interspersion and Diversity Index) differed between elephant home ranges within groups of similar study areas. These results suggest that Interspersion and Diversity Index characterize aspects of landscape heterogeneity important to elephant home range location.

At the onset of a wet season, elephants in my study region expanded and shifted their ranges to include areas away from rivers and other perennial water sources as water became widely available in ephemeral streams and waterholes (see Jackson & Erasmus 2005). These shifts and expansions were also reflected in seasonal changes in landscape heterogeneity. As predicted, heterogeneity was greater for wet season ranges than for dry ranges for Fractal, Interspersion and Diversity Indices. It therefore seems that elephants optimize their foraging during the wet season by roaming in areas with relatively higher heterogeneity than during the dry season. This may be explained by water requirements constraining elephant ranging (see Introduction) to sub-optimal areas during the dry season. After all, de Beer et al. (2006), amongst others, showed that water availability is a likely driver of home range locality. On the other hand, areas with permanent water may also be naturally more heterogeneous than surrounding areas (e.g. Gaylard et al. 2003).

Landscape heterogeneity within elephant ranges differed between the sexes, though mostly during wet seasons. Again, this may result from elephant home range utilization only satisfying optimal foraging needs when water does not limit roaming, as breeding herds usually concentrate their foraging to areas in the proximity of water (Caughley and Goddard 1975; Western and Lindsay 1984; Lindeque and Lindeque 1991; Verlinden and Gavor 1998; Stokke and du Toit 2002). Furthermore, females were more selective than males for all aspects of landscape heterogeneity except patch shape complexity. Similarly, the research of Stokke (1999) and Stokke and du Toit (2002) also suggests that females are more selective than males.

Different to my study, Grainger et al. (2005) could not illustrate a difference in landscape heterogeneity between the home ranges of bulls and cows living in the Kruger National Park where the home ranges of bulls and cows were of similar size. In addition, management actions such as park fences and the large number of artificial watering points maintained in Kruger at the time of their study would also have influenced elephant ranging. However, similar management is not practiced in Kafue and in line with my predictions, patch density and landscape diversity of the female ranges were greater than those of the bulls, despite the ranges of bulls being two orders of magnitude greater than those of cows. On the contrary, patch shape complexity and landscape complexity of male ranges were greater than for those of cows. Since cows are more selective of habitat than bulls (see Stokke 1999, Shannon et al. 2006a, 2006b) my illustration of them also being more selective for landscape heterogeneity than bulls suggests that landscape heterogeneity may present some sought after benefit (see Introduction).

In this part of my study, I investigated whether elephants locate their ranges in areas with greater heterogeneity than typical for the landscapes in which they lived. Landscape complexity and diversity (represented by Interspersion and Diversity Index, respectively) emerged as measures of landscape heterogeneity that may explain the non-random location of elephant ranges. These two metrics are corrected for area. Though elephants do select for aspects of landscape heterogeneity, the mechanisms involved can only be speculated upon. Among the free ranging elephant cows that I studied, those from Lower Zambezi and Luangwa generally selected for landscape complexity and diversity, while those from Kafue only selected for heterogeneity in terms of landscape complexity during the second dry and wet seasons. This suggests that factors other than landscape heterogeneity govern the location of home ranges by elephants here. In the case of Kafue, the apparent lack of preference for relatively heterogeneous landscapes can be explained by the construction of the Itezhi-tezhi dam that resulted in the development of massive floodplains that support a green lawn of palatable grass for most of the year.

In general, it seems that elephant cows select for landscape complexity and diversity. They therefore seem to prefer areas with high diversity as is also known for female roe deer (Tufto et al. 1996). In support of my findings, Verlinden and Gavor (1998) as well as Murwira and Skidmore (2005), show that elephants select for landscape heterogeneity, though they measured heterogeneity very different to the way that I did. What now remains, is to search for mechanisms (processes) that underlie the pattern of landscape utilisation that is in favour of heterogeneity, especially during the wet season.

CHAPTER 6

SYNTHESIS

Published information suggests that the positioning and size of elephant home ranges may be determined by unevenly distributed resources (see Introduction). Landscape heterogeneity reflects on the distribution of these resources. Using vegetation structure as a surrogate, I investigated whether landscape heterogeneity explains the variability home range size and location of elephants occurring in the mesic savannas of Zambia and Malawi.

Saïd and Servanty (2005) suggest that landscape heterogeneity may be an important factor influencing the distribution, local population density and home range areas of herbivores. In support of this, I showed that elephants select ranges that are significantly more heterogeneous than those of the surrounding matrix. Landscape complexity and diversity metrics appear particularly powerful in explaining range selection in elephants. However, factors other than landscape heterogeneity may explain differences in elephant home range size (see Introduction). Some of these may co-vary with, or even be determined by landscape heterogeneity. Selecting for heterogeneous landscapes, for instance, could optimize feeding opportunities by reducing foraging time (Tufto et al. 1996). Heterogeneous landscapes may also provide for the thermoregulatory requirements of elephants (Kinahan et al. 2007), as well as drinking water in areas relatively close to feeding grounds (de Beer et al. 2006). Such landscapes may be complex and diverse, thereby explaining my findings.

Optimal foraging may provide for the mechanism(s) through which elephants select for areas of relatively greater landscape heterogeneity. This may be addressed in future studies using Resource Selection Functions (e.g. Manly et al. 2002; Chetkiewicz et al. 2006). Water availability may be another factor that may cause the inability of heterogeneity to explain landscape selection during the drier months, as it seems to play an overriding role in landscape utilization. However, this will also have to be explored in further studies within this region by incorporating climatic data.

In some parts of southern Africa, conservation authorities are attempting to solve the apparent problem of burgeoning elephant populations and their threat to biodiversity (see Whyte et al. 2003; van Aarde et al. 2006). Culling, translocation, and contraception have all been ruled out as long-term solutions for free-ranging populations (van Aarde et al. 1999; Pimm and van Aarde 2001). However, other populations such as those in my study region are declining (e.g. Guldemond et al. 2005). Recently, the metapopulation paradigm has been introduced as a possible ecological framework for the conservation management of elephants across southern Africa (see van Aarde and Jackson 2007). The functioning of the elephant metapopulation may rely on source-sink dynamics facilitated by linkages in the form of megaparks (van Aarde et al. 2006). The planning for such parks needs to make ecological sense by providing elephants with the mechanism to disperse.

Chetkiewicz et al. (2006) amongst others, urge that research should incorporate spatial and temporal aspects of the landscape with the animals’ needs in order to achieve ecologically sound conservation planning. As I have shown in my study, landscape heterogeneity may have consequences for the spatial dynamics of populations and that its relevance differs between seasons and sexes. The functioning of a metapopulation relies on such heterogeneity, particularly on factors that may induce differences in demographic parameters. Such factors may include the vacancy of suitable landscapes and the incentive for dispersal and migration between them (see review by van Aarde and Jackson 2007). The provision of space will also make more heterogeneous landscapes available for selection by elephants. When driven by season, this in itself may also ameliorate impact by providing vegetation the opportunity to recover (see van Aarde et al. 2006).

The landscape metrics that I used allow for the large-scale application across the sub-continent when searching for linkages that may meet the dispersal needs of elephants. Within the mesic savannas the distributional range of elephants in southern Africa is dominated by the miombo woodlands. My focus on this region therefore contributes to conservation management planning.

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Landscape heterogeneity as a determinant of range utilization by African elephants
(*Loxodonta africana*) in mesic savannas

by

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SUMMARY

I investigated landscape heterogeneity as a determinant of elephant landscape utilization. This study was conducted in five conservation areas within the mesic savannas of Zambia and Malawi. My first step was to generate a classified landscape map for each area. These maps were used to quantify landscape heterogeneity of the study areas, elephant home ranges and randomly located ranges within each study area. The quantification was done using four FRAGSTATS landscape heterogeneity metrics.

The maps that I generated were all accurate to >50%, as measured by Kappa statistics. To control for variability in the landscapes between study areas I placed them into comparable groups based on heterogeneity metrics. Within these groups, I investigated whether elephant

home range size was influenced by landscape heterogeneity and compared the landscape heterogeneity of the elephant ranges within seasons.

I examined the influence of season and sex on elephant range location within study areas. Finally, I used randomization procedures to infer selection by elephants for landscape heterogeneity, by comparing the heterogeneity of their ranges to similarly-sized randomly located ranges.

Landscape heterogeneity was not a determinant of elephant home range size, but did explain variability in the location of elephant home ranges. Elephant home range heterogeneity varied within groups of study areas. In most cases, wet season elephant home ranges encapsulated greater landscape heterogeneity than dry season home ranges. Female elephant home ranges often showed greater landscape heterogeneity than male home ranges during the wet seasons. Elephant home ranges also were more heterogeneous than the randomly located home ranges and this suggested selection for landscape complexity and diversity by elephants. Therefore, elephants favoured complex landscapes with more vegetation types in patches arranged irregularly across the landscape. Ideally, further research would benefit from more collared elephants to better understand mechanisms of landscape utilization.

A metapopulation framework has been suggested as an innovative solution to manage southern Africa's elephants. Landscape heterogeneity may underlie the functioning of such a metapopulation, particularly factors that give rise to differences in demographic parameters and that allow for dispersal. Megapark planning should thus focus on the inclusion of complex and diverse landscapes. The relatively simple nature of the metrics I used allows for their application at a large scale. This should enable conservation planners to identify areas that may fulfil the ranging and dispersal needs of elephants. Within the mesic savannas of southern Africa, the distributional range of elephants is largely comprised of miombo woodlands. My focus on this region therefore provides an opportunity for landscape utilization and selection patterns to be included in conservation management planning.

OPSOMMING

Ek het landskapsheterogeniteit as ‘n bepaler van landskapgebruik deur olifante ondersoek. Hierdie studie is in vyf bewaringsgebiede in die mesiese savannas van Zambia en Malawi onderneem. My eerste stap was om vir elke studiegebied ‘n geklassifiseerde landskapskaart te ontwikkel. Die kaarte was gebruik om landskapsheterogeniteit vir die studiegebiede te beskryf, en om die heterogeneniteit in beide die olifant- en ewe-kansige geplaasde tuisgebiede te ondersoek. Die onderskeie landskappe is met vier FRAGSTATS heterogeniteitsindekse gekwantifiseer.

Gebaseer op die Kappa statistiek was die onderskeie landskapskaarte meer as 50% akkuraat. Verskille in die landskapsheterogeniteits maatstawwe tussen die studiegebiede het my genoodsaak om vergelykbare groeperings te vorm alvorens ek die onderskeie olifant tuisgebiede met mekaar kon vergelyk. Vir elke groep het ek ook die invloed van landskapsheterogeniteit op die grootte van olifant tuisgebiede bepaal. Ek het ook die verband tussen landskapsheterogeniteit binne die tuisgebiede van olifante, seisoene en die geslagte bepaal. Ten laaste het ek die landskapsheterogeniteit maatstawwe van die tuisgebiede van olifante en ewekansig geleë gebiede van soortgelyk grotes, vergelyk..

My voorspellings het as volg gevaar: landskapsheterogeniteit was nie 'n aanduiding van olifant tuisgebied groottes nie, maar het wel die posisie van tuisgebiede bepaal. Landskapsheterogeniteit maatstawwe in die olifant tuisgebiede het ook in die vergelykbare studiegebiede gevarieer. In die meeste gevalle was die landskapsheterogeniteit in nat seisoen tuisgebiede van olifante hoër as gedurende die droeë seisoen. Gedurende die nat seisoen was die landskapsheterogeniteit in die tuisgebiede van olifant koeie dikwels ook hoër in as dié van bulle. Olifant tuisgebiede was ook meer heterogenies as die ewekansig geplaasde tuisgebiede - dit impliseer dat olifante vir komplekse en diverse landskappe selekteer. Skynbaar verkies olifante landskappe waar verskillende plantegroeitipes onreëlmatig gerangskik en versprei is.

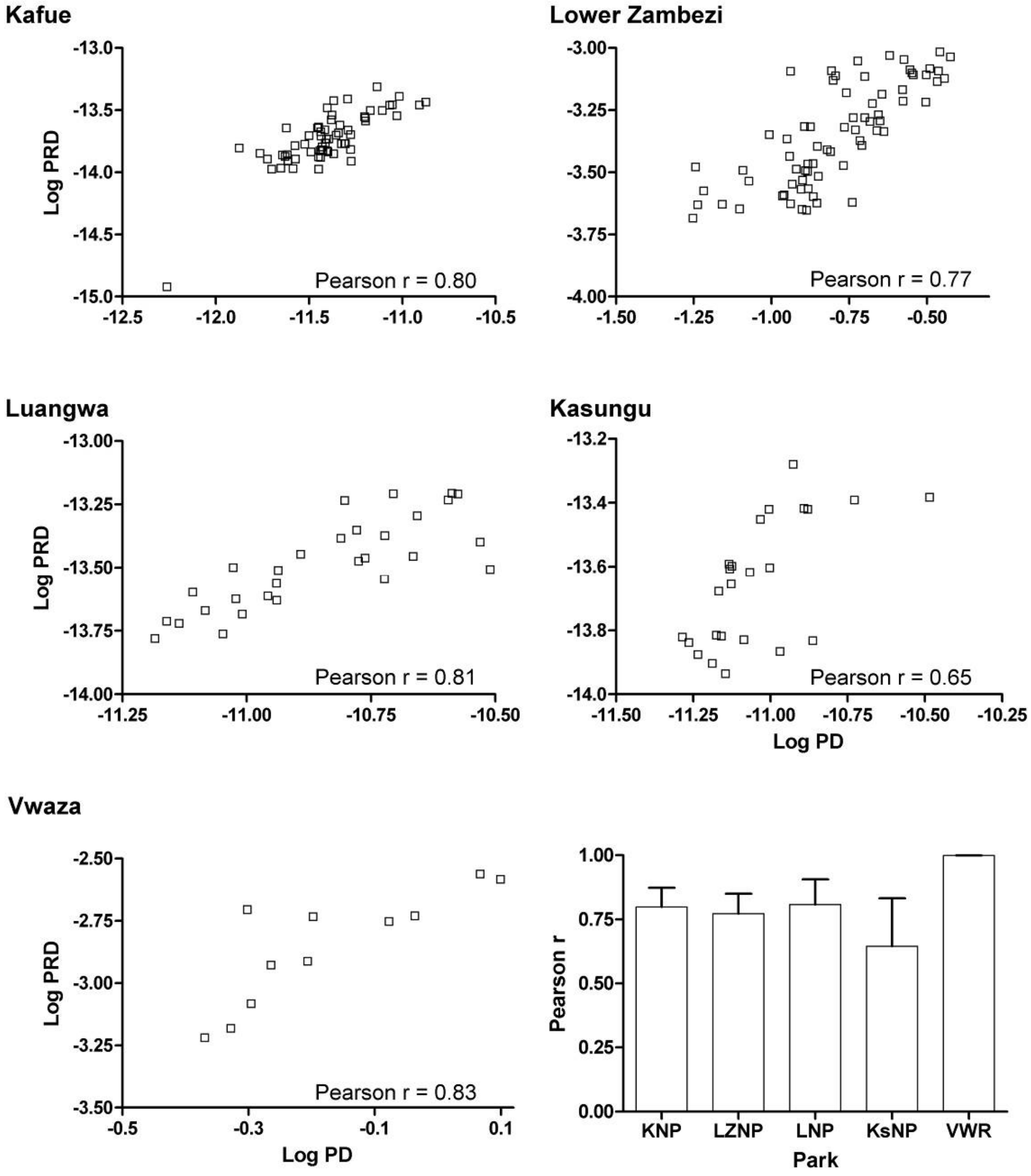
Voorkeur vir landskapsheterogeniteit is dus 'n belangrike faktor wat die posisie van tuisgebiede en dus ook vir die gebruik van die landskappe en die verspreidings dinamika van olifantbevolkings, bepaal. Onder ideale omstandighede, sou verdere navorsing bevoordeel word deur die landskapsgebruik van meer olifante na te speur..

'n Metabevolkingsraamwerk word tans voorgestel as ʼn nuwe oplossing om die olifante van suidelike Afrika te bestuur. Landskapsheterogeniteit mag ʼn bepalende rol speel in die funksionering van 'n metabevolking, veral die aspekte wat verskille in demografiese veranderlikes veroorsaak, soos byvoorbeeld migrasie en verstrooiing. Die beplanning van ʼn megaparksbenadering tot bewaring behoort dus op komplekse en diverse landskappe te fokus. Die relatief eenvoudige heterogenitieits maatstawwe wat ek gebruik het laat dit toe dat dié oor 'n weie skaal en verskeidenheid van toestande gebruik kan word. Bewaringsbestuur kan gevolglik gebiede identifiseer wat aan die bewegings en migrasie vereistes van olifante voldoen. Die grootste gedeelte van die mesiese savannas van suidelike Afrika beslaan miombo woude. My klem op die landstreek is dus belangrik vir bewaringsbestuur en beplanning.

Appendix I. Comparative matrix showing statistics of paired t-tests comparing dry season 1 and 2 home range sizes for the elephants of each study area (*p*-values < 0.05 were considered significant, df = degrees of freedom). Although the former were estimated from incomplete data and were expected to have smaller home ranges than the latter from complete data, this was clearly not the case. The columns for the Kafue ranges are shaded as their data sets were complete. The elephant ranges of Luangwa, however were estimated from the most incomplete data sets (particularly for South Luangwa). This test could not be carried out for Kasungu and Vwaza due to their small sample sizes.

Statistic	Kafue males	Kafue females	Lower Zambezi	Luangwa	North Luangwa	South Luangwa
t-value	0.71	1.69	0.95	0.51	0.43	1.065
df	3	3	5	7	2	4
p-value	0.529	0.189	0.384	0.698	0.711	0.347

Appendix II. Patch Richness Density (PRD) as a function of Patch Density (PD) for each study area. All values have been transformed to Log_{10} for reasons given in the text (page 39). Pearson correlation coefficients (bottom right) show that these variables co-varied significantly where the confidence limit was set as $p = 0.05$.



Appendix III. A comparative matrix of the distances between the 'true' location and the positions recorded by the collars within each category. Values in brackets indicate the total number of possible positions for each category. The mean distance, total number of positions recorded (n), standard deviation (S.D.) and range are also presented for each category. The ‘open woodland’ category locations were all on gentle terrain and therefore form the gentle gradient category as well. The mean values indicate accuracy, whilst the S.D. indicates precision.

Summary statistics	Forest (120)	Open Woodland / Gentle (120)	Bare Ground (96)	Hill (96)	Steep (144)	Sheer (120)
	distance from ‘true’ location (m)					
	172	1	3	12	2	1
	3	1	5	18	7	4
	5	1	3	18	10	3
	3	1	4	19	7	4
	4	1	3	20	9	3
	3	1	3	21	7	4
	3	2	8	21	8	4
	8	3	6	22	13	3
	6	4	7	23	12	2
	7	4	9	24	12	3
	9	5	10	23	10	3
	10	4	23	23	12	7
	23	6	22	23	12	7
	6	6	24	23	11	6
	10	9	25	25	13	6
	13	6	27	27	13	6
	10	13	27	25	14	7
	18	12	27	27	17	5
	16	11	29	29	17	8
	20	11	29	29	22	14
	18	14	29	40	23	18
	29	35	27	48	29	21
	27	104	30	74	6	28
		1	30	65	9	37
		3	30	4	7	3
		3	33	4	6	3
		1	31	2	7	1
		1	35	4	6	1
		1	38	4	7	5
		2	46	4	9	6
		4	35	2	6	6
		4	37	4	8	6
		5	36	7	8	8
		9	40	5	12	7
		6	91	8	13	6
		7	2	8	13	6
		7	2	9	12	6
		6	5	9	11	6
		7	3	6	11	6
		7	5	5	12	13
		5	3	10	12	11
		7	3	10	14	11
		10	2	12	18	11
		11	6	11	20	23
		25	6	17	2	31
		0	9	26	2	32
		0	8	41	4	3
		2	8	48	5	4
		2	8	2	6	8
		4	14	4	6	9
		2	12	4	7	9
		1	12	4	9	8
		2	11	2	9	6
		3	13	1	9	8
		4	13	3	7	8
		4	22	3	6	7
		3	27	5	11	9
		5	40	6	12	9
		7	3	7	12	5
		8	3	5	12	8
		5	3	5	16	11
		15	3	5	18	11
		20	3	8	20	15
		22	4	6	21	14
		50	4	11	21	16

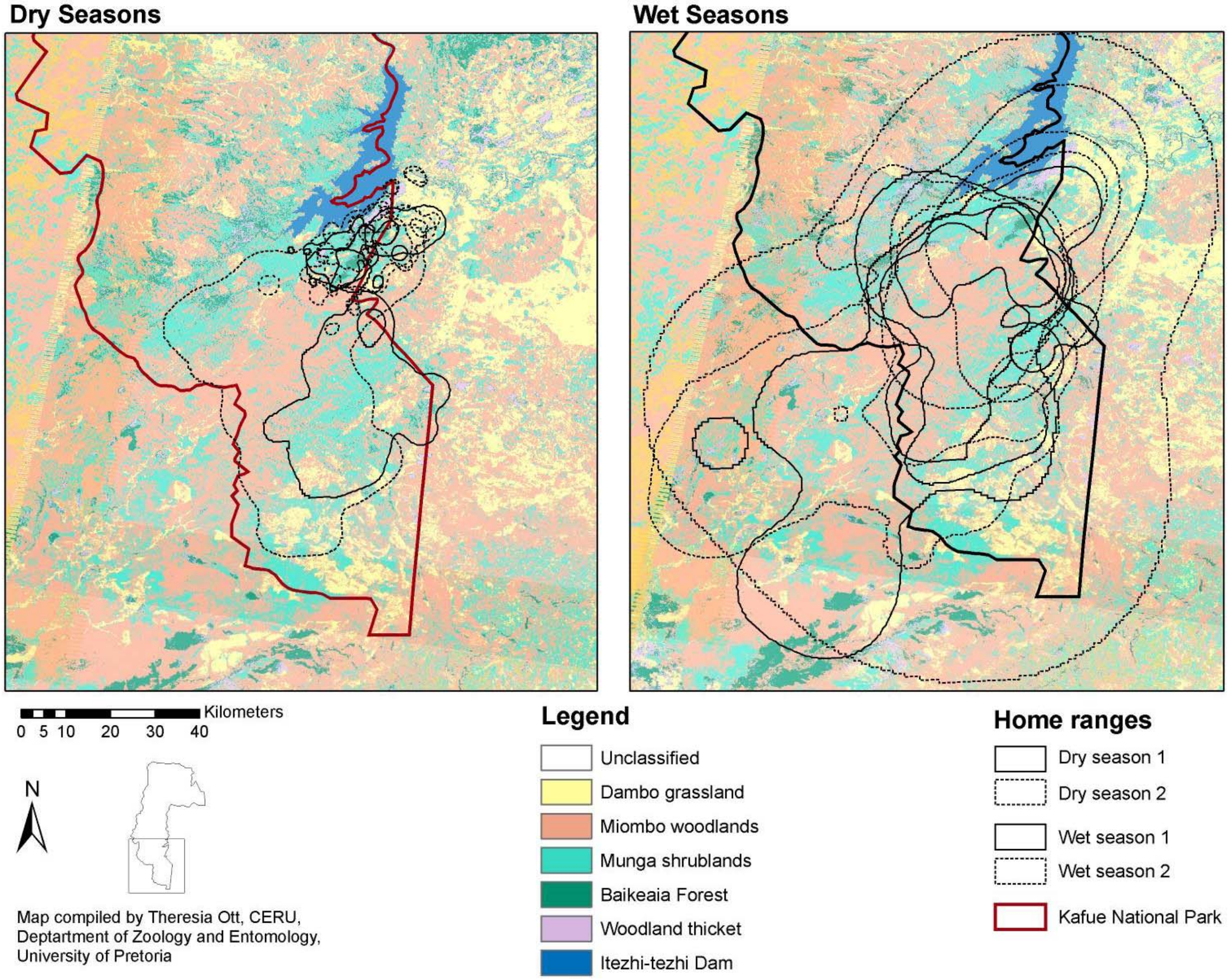
		107 3 3 4 4 3 3 3 3 2 4 4 5 5 9 12 12 11 17 27 32 31 92	4 4 7 5 5 7 8 6 6 5 9 12 11 10 19 22 1 1 2 5 5 3 3 4 2 2 3 3 3 7 8 7 8 11 14 11 17 22 28	11 13 26 31 36 42 48 3 3 4 4 2 4 3 4 3 6 9 7 9 5 6 6 10 14 17 17 21 32 34 37	29 50 66 2 4 4 4 4 5 2 2 5 3 3 5 7 9 10 14 15 16 19 20 31 1 2 4 8 9 7 5 6 7 7 9 12 15 20 24 5 9 10 14 12 14 12 17 18 29 71 61	19 22 26 31 337 4 4 5 4 2 2 2 5 7 7 7 9 9 8 6 6 9 11 11 15 15 27 31 5 5 5 5 7 10 19 63
Mean (m)	18.3	13.7	10.7	15.5	12.5	13.2
n	23	104	88	96	116	101
S.D.	34.3	13.9	19.1	14.6	11.4	33.9
Location success (%)	19	87	92	100	81	84
Range	3 -34	1 – 91	0 – 107	1 -74	1 – 71	1 – 337

Appendix IV. Location success of satellite GPS collars whilst deployed on the elephants during all seasons for all study areas, presented as a percentage of locations recorded out of the total possible. 'No data' denotes incomplete data (<10 locations recorded throughout a season) due to collar failure. The ' Elephant ID' column identifies the elephant and 'f' or 'm' denotes its sex as female or male, respectively. The 'Collar Code' column provides the collar code as stored in the CERU archive. Seasons (Dry 1, 2 and Wet 1, 2) are defined on page xvi.

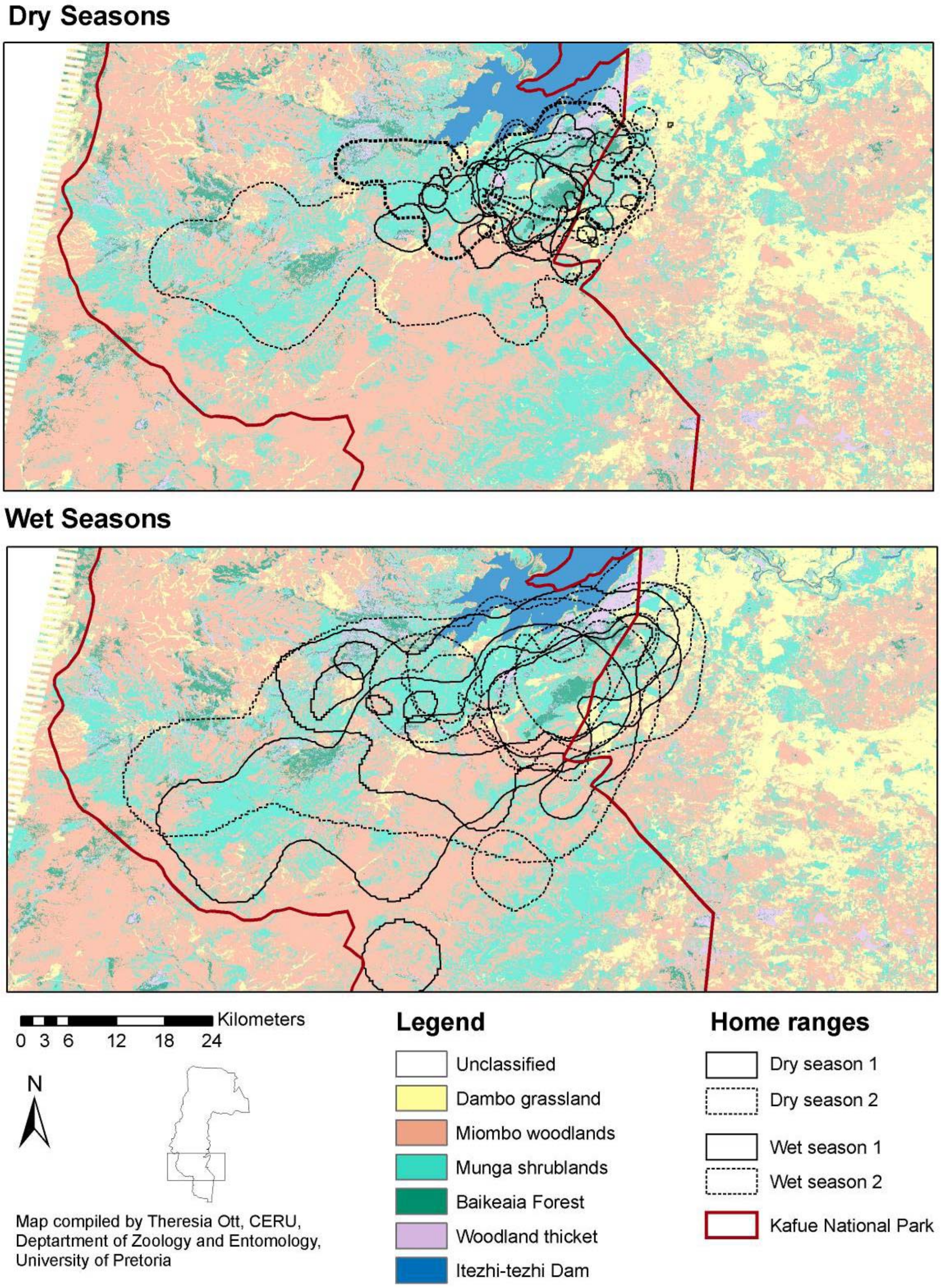
Study Area	Collar Code	Elephant ID	Location Success (%)			
			Dry 1	Dry 2	Wet 1	Wet 2
Kafue	00036543VTI33F8	K2m	88.9	99.4	83.3	84.4
	00036573VTIAC8E	K4m	90.0	99.4	92.6	97.2
	00036523VTIE394	K7m	87.2	100.0	80.8	93.3
	00036506VTI1F3F	K9m	No data	99.4	No data	77.7
	00036722VTI8377	K10m	88.3	98.8	74.7	96.7
	00036480VTIB6BD	K1f	92.8	99.4	75.3	97.8
	00036491VTI62F4	K3f	81.1	99.4	97.3	97.8
	00036489VTI5AEA	K5f	47.9	100.0	35.1	97.2
	00036481VTI3AC2	K6f	No data	98.2	No data	15.0
	00036473VTI1A9A	K8f	86.6	98.8	74.3	98.3
		Mean	*82.9*	*99.7*	*76.7*	*85.5*
		Min	*47.9*	*98.2*	*35.1*	*15.0*
		Max	*92.8*	*100.0*	*97.3*	*98.3*
		S.D.	*14.50*	*0.57*	*18.82*	*25.73*
Lower Zambezi	39973VTI0EF6	LZ 1f	75.0	78.9	70.0	89.4
	55789VTI63DE	LZ 2f	82.8	81.7	72.8	91.7
	55833VTI14BA	LZ 3f	85.1	88.9	81.1	96.1
	38081VTI5A02	LZ 4f	86.4	75.6	78.3	88.3
	39984VTIBB2D	LZ 5f	79.1	93.2	55.6	No data
	55805VTIA42E	LZ 6f	85.1	87.2	74.4	89.3
		Mean	*82.2*	*84.2*	*72.0*	*91.0*
		Min	*75.0*	*75.6*	*55.6*	*88.2*
		Max	*86.4*	*93.2*	*81.1*	*96.1*
		S.D.	*4.37*	*6.65*	*8.99*	*3.13*
North Luangwa	55799VTI8C10	NL 1f	64.7	54.2	37.4	18.4
	56218VTIA03F	NL 2f	83.9	85.0	81.7	90.0
	38168VTI37B5	NL 3f	86.1	75.7	86.7	88.8
South Luangwa	00039748VTI0691	SL 1f	100.0	92.2	77.8	94.4
	00039759VTIB2C8	SL 2f	100.0	69.3	65.4	83.0
	00039784VTI9745	SL 3f	70.6	83.2	82.8	90.6
	00039991VTI5750	SL 4f	94.7	87.8	80.0	60.0
	00055103VTI9E78	SL 5f	94.7	87.8	78.9	95.0
		Mean	*86.8*	*79.4*	*73.8*	*77.5*
		Min	*64.7*	*54.2*	*37.4*	*18.4*
		Max	*100.0*	*92.2*	*86.7*	*95.0*
		S.D.	*13.28*	*12.5*	*15.96*	*26.39*
Kasungu*	56211VTI041C	KS 2f	84.9	91.1	68.9	93.3
	55131VTI0F04	KS 3f	86.1	83.9	77.2	80.0
		Mean	*85.5*	*87.5*	*68.7*	*86.7*
		Min	*76.7*	*83.9*	*68.9*	*60.0*
		Max	*86.1*	*91.1*	*77.2*	*93.3*
		S.D.	*0.82*	*5.11*	*5.89*	*9.43*
Vwaza*	39983VTI3728	V 2f	76.7	83.9	71.7	91.0
	55097VTI865A	V 4f	84.15	84.2	72.2	90.0
		Mean	*80.5*	*84.0*	*71.9*	*90.5*
		Min	*76.7*	*83.9*	*71.7*	*90.0*
		Max	*84.2*	*84.2*	*72.7*	*91.0*
		S.D.	*5.24*	*0.21*	*0.39*	*0.72*

* Mean, Standard Deviation and Variance presented here for illustrative purposes only, the sample size is not large enough to calculate these statistics

Appendix V. An enlarged portion of the landscape map of Kafue National Park, depicting the area over which the male elephants range. Inset map indicates relative position within the park. Contrast of the landscape map is reduced to enhance the visibility of the home ranges over the map. The 95% Kernel estimations of their home ranges during the dry and wet seasons are shown. Further information is depicted by the map legends.



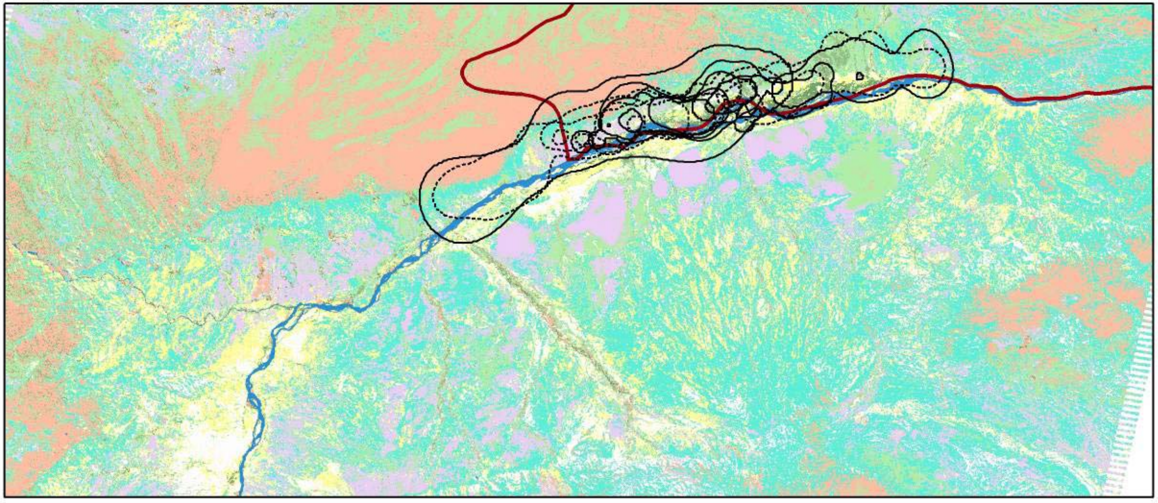
Appendix VI. An enlarged portion of the landscape map of Kafue National Park, depicting the area over which the female elephants range. Inset map indicates relative position within the park. The contrast of the map is reduced to enhance the visibility of the 95% Kernel home ranges over the map, for the dry and wet seasons. Further information is given by the map legends.



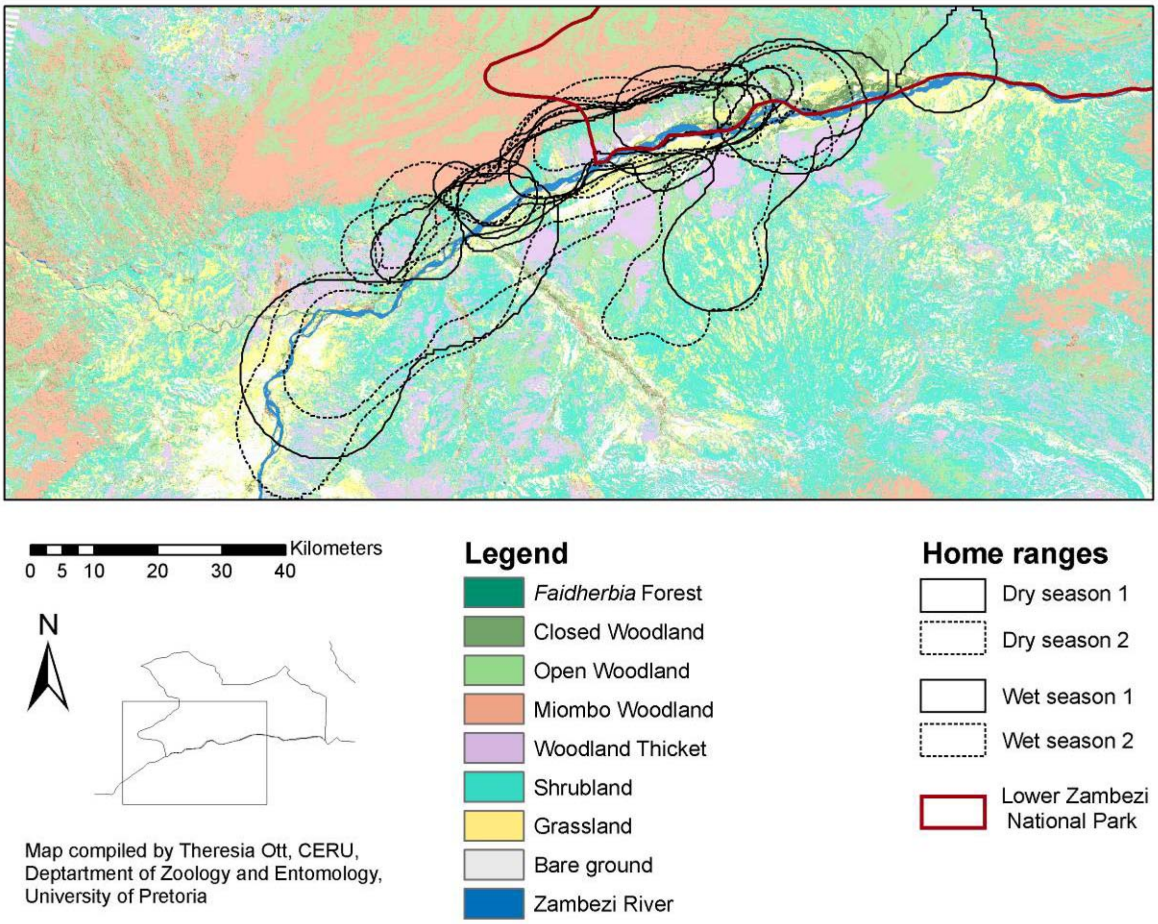
Map compiled by Theresia Ott, CERU, Deptartment of Zoology and Entomology, University of Pretoria

Appendix VII. An enlarged portion of the landscape map of Lower Zambezi National Park, depicting the area over which the elephants (all females) range. Inset map indicates relative position within the park. The contrast of the map is reduced to enhance the visibility of the 95% Kernel home ranges over the map, for the dry and wet seasons. Further information is given by the map legends.

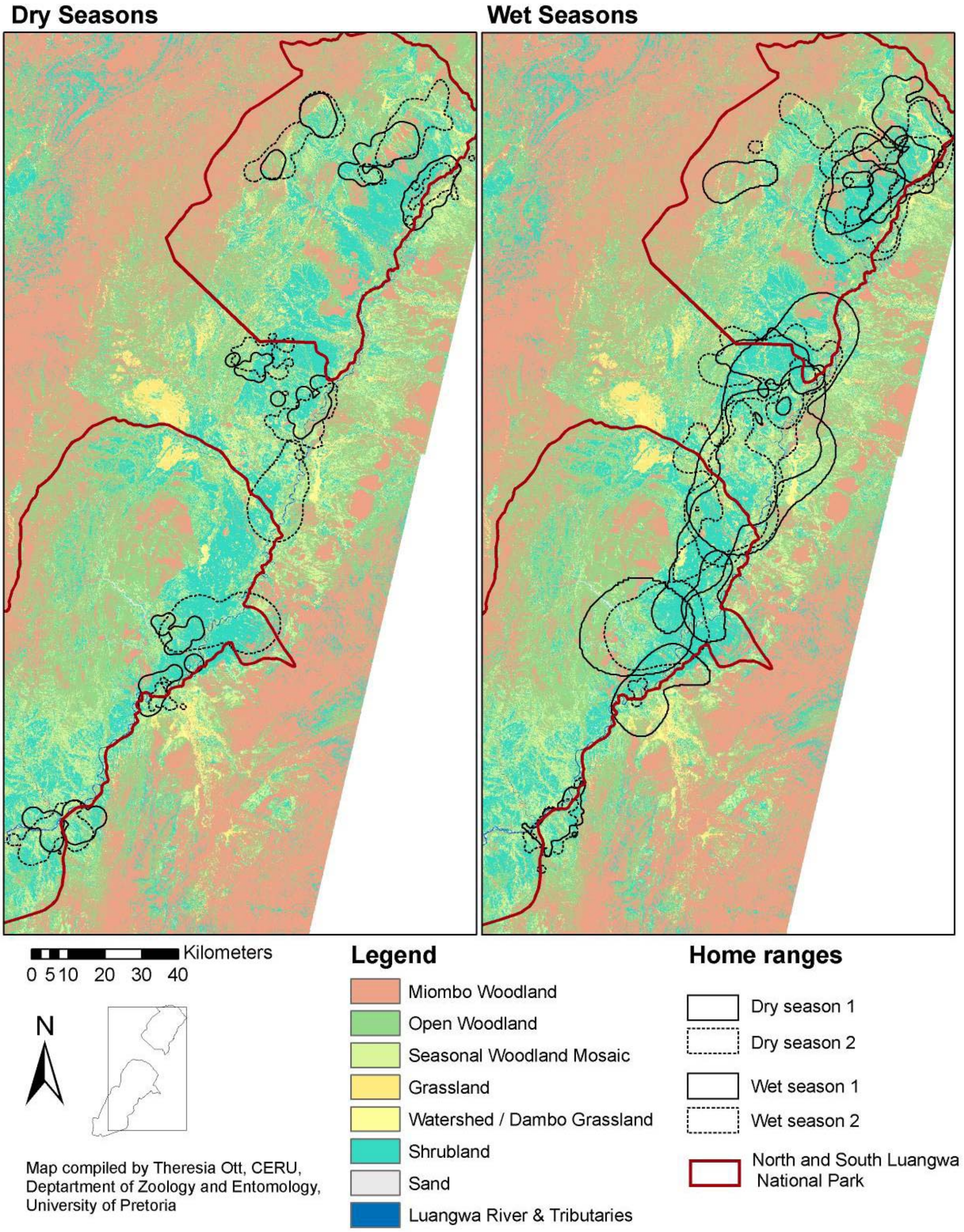
Dry Seasons



Wet Seasons

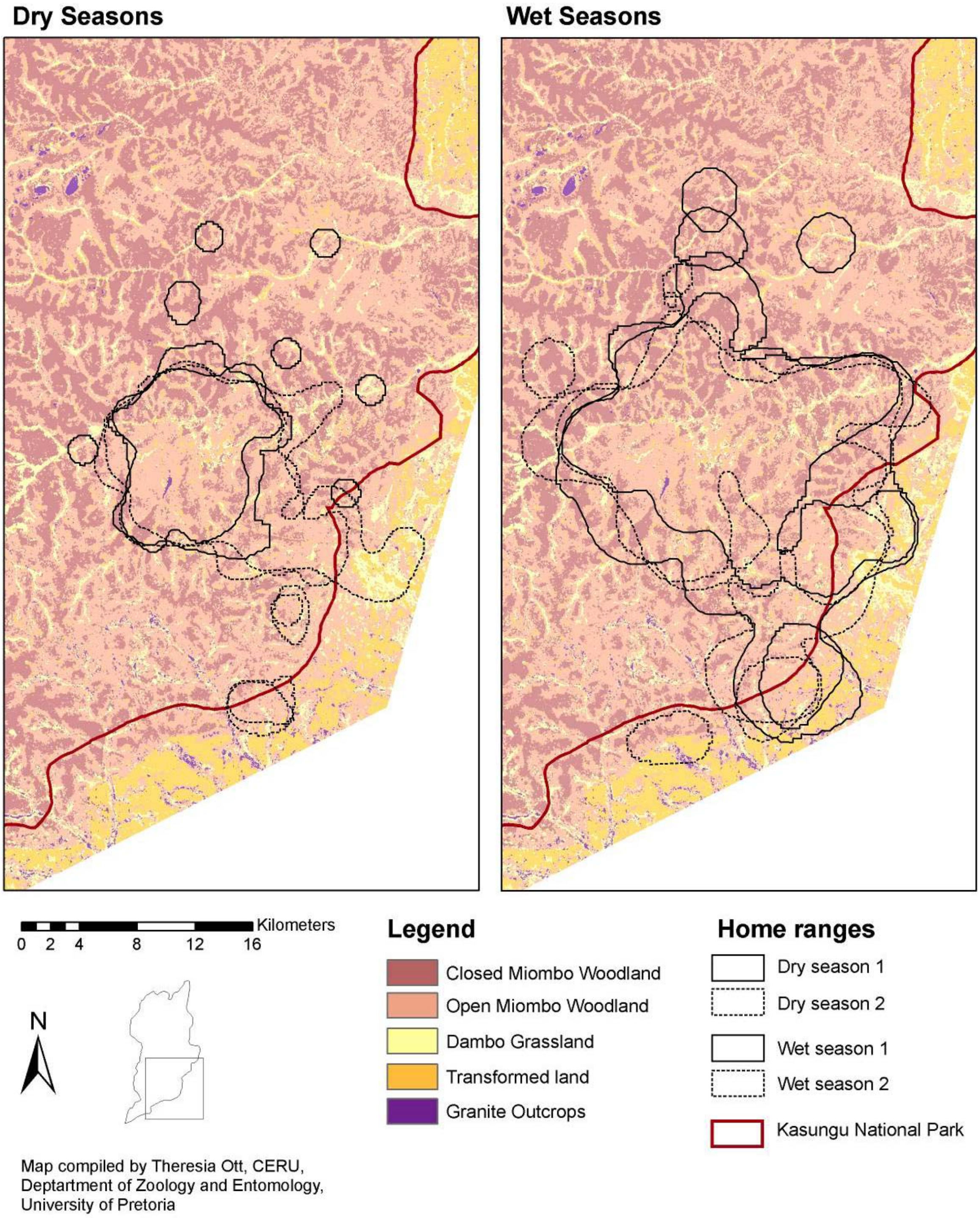


Appendix VIII. An enlarged portion of the landscape map of the Luangwa Valley, depicting the area over which the elephants (all females) range. Inset map indicates relative position within the parks. The contrast of the map is reduced to enhance the visibility of the 95% Kernel home ranges over the map, for the dry and wet seasons. Further information is given by the map legends.



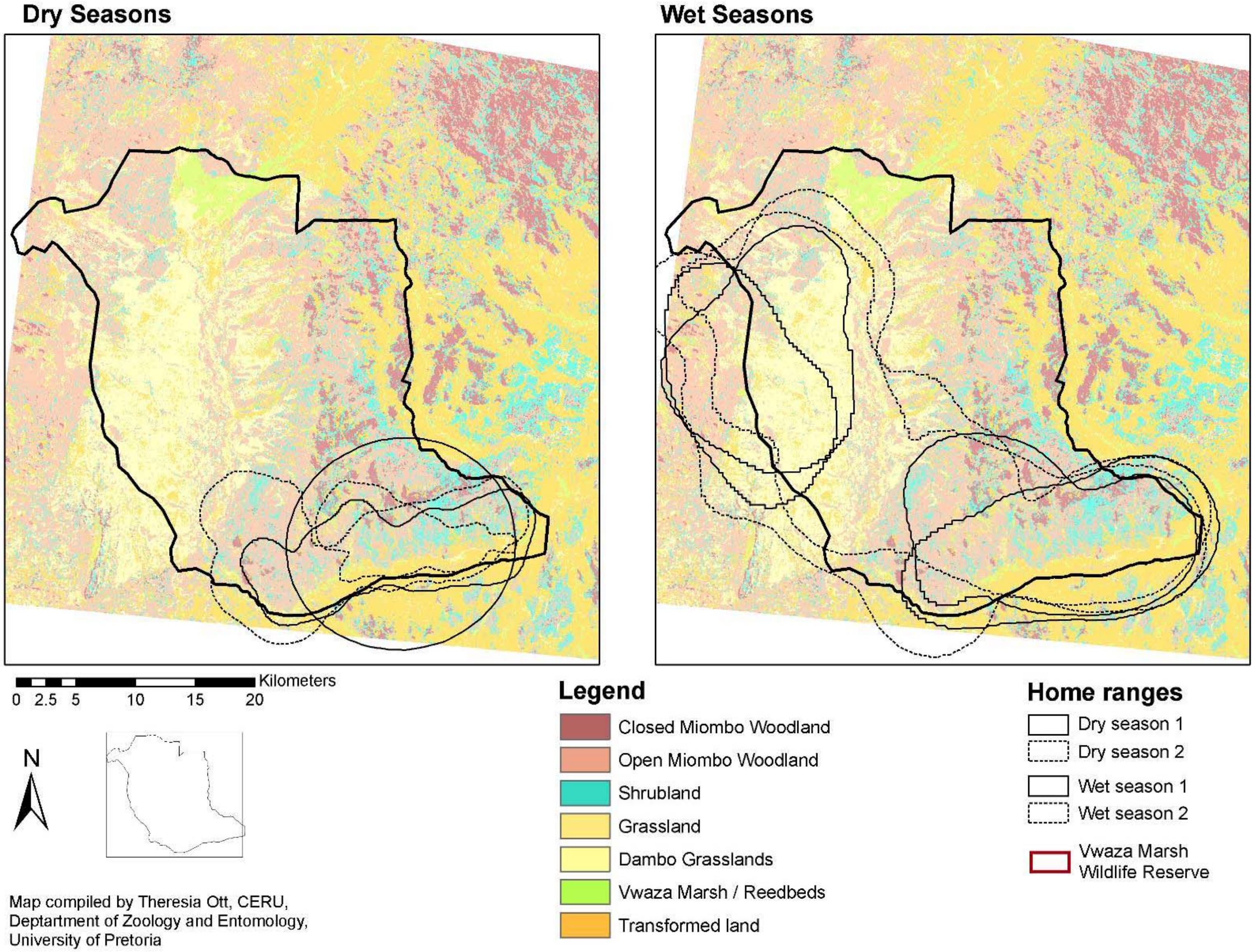
Map compiled by Theresia Ott, CERU, Deptartment of Zoology and Entomology, University of Pretoria

Appendix IX. An enlarged portion of the landscape map of Kasungu National Park, depicting the area over which the elephants (all females) range. Inset map indicates relative position within the park. The contrast of the map is reduced to enhance the visibility of the 95% Kernel home ranges over the map, for the dry and wet seasons. Further information is given by the map legends.



Map compiled by Theresia Ott, CERU,
Deptartment of Zoology and Entomology,
University of Pretoria

Appendix X. An enlarged portion of the landscape map of Vwaza Marsh Wildlife Reserve, depicting the area over which the elephants (all females) range. Inset map indicates relative position within the reserve. The contrast of the map is reduced to enhance the visibility of the 95% Kernel home ranges over the map, for the dry and wet seasons. Further information is given by the map legends.



Map compiled by Theresia Ott, CERU,
Deptartment of Zoology and Entomology,
University of Pretoria

Appendix XI. Normality test results for each set of random ranges selected to compare the landscape heterogeneity of the study areas (see text page 39). Kolmogorov-Smirnov d ('K-S d') and p-values ('p') are presented. A significant result indicates deviation from normal distribution. '–' indicates that normality could not be calculated as discussed in text (page 40).

Metric	Statistic	Kafue	Lower Zambezi	Luangwa	Kasungu	Vwaza
Patch Density	K-S d	–	0.11	–	–	–
	p-value	–	> 0.20	–	–	–
Log10 Patch Density	K-S d	0.10	0.09	0.11	0.16	0.07
	p-value	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
Fractal Index	K-S d	0.18	0.09	0.14	0.16	0.16417
	p-value	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
Interspersion Index	K-S d	0.14	0.16	0.11	0.07	0.14
	p-value	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
Diversity Index	K-S d	0.12	0.19	0.14	0.19	0.10
	p-value	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20

Appendix XII. Normality test results (Kolmogorov-Smirnov d and p-values, indicated by ‘K-S d’ and ‘p’, respectively) within seasons (‘Season’ column) for random and elephant ranges (‘Range’ column) of each study area. A significant result would indicate deviation from a normal distribution, there was no instance of this in these results. ‘–‘ indicates that normality could not be calculated as discussed in text (page 40).

Range	Season		Dry Season 1						Dry Season 2					
	Metric	Statistic	Kafue Male	Kafue Female	Lower Zambezi	Luangwa	Kasungu	Vwaza	Kafue Male	Kafue Female	Lower Zambezi	Luangwa	Kasungu	Vwaza
Random	Patch Density	K-S d	–	–	0.24	–	–	0.33	–	–	0.11	–	–	0.40
		p	–	–	> 0.20	–	–	> 0.20	–	–	> 0.20	–	–	< 0.10
	Log10 Patch Density	K-S d	0.12	0.13	0.16	0.13	0.28	0.49	0.15	0.21	0.11	0.25	0.33	0.28
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	< 0.10	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Fractal Index	K-S d	0.18	0.17	0.18	0.10	0.30	0.25	0.31	0.20	0.18	0.12	0.26	0.30
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Interspersion Index	K-S d	0.17	0.16	0.16	0.17	0.26	0.24	0.17	0.25	0.33	0.19	0.15	0.22
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Diversity Index	K-S d	0.18	0.25	0.24	0.27	0.32	0.15	0.22	0.16	0.28	0.20	0.16	0.23
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
Elephant	Patch Density	K-S d	–	–	0.20	–	–	–	–	–	0.24	–	–	–
		p	–	–	> 0.20	–	–	–	–	–	> 0.20	–	–	–
	Log10 Patch Density	K-S d	0.27	0.25	0.31	0.12	0.26	0.26	0.27	0.29	0.27	0.21	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Fractal Index	K-S d	0.29	0.23	0.20	0.20	0.26	0.26	0.29	0.20	0.23	0.18	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Interspersion Index	K–S d	0.26	0.28	0.29	0.20	0.26	0.26	0.27	0.31	0.17	0.21	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Diversity Index	K–S d	0.28	0.28	0.17	0.23	0.26	0.26	0.22	0.20	0.19	0.16	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20

Continued on next page

			Wet Season 1						Wet Season 2					
Random	Patch Density	K-S d	–	–	0.26	–	–	0.41	–	–	0.24	–	–	–
		p	–	–	> 0.20	–	–	< 0.15	–	–	> 0.20	–	–	–
	Log10 Patch Density	K-S d	0.19	0.17	0.20	0.25	0.22	0.47	0.18	0.16	0.24	0.20	0.20	0.25
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	< 0.10	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Fractal Index	K-S d	0.17	0.14	0.18	0.29	0.25	0.31	0.29	0.21	0.19	0.26	0.28	0.37
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Interspersion Index	K-S d	0.18	0.16	0.28	0.25	0.12	0.23	0.28	0.12	0.10	0.14	0.23	0.24
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Diversity Index	K-S d	0.17	0.22	0.25	0.33	0.20	0.14	0.12	0.20	0.12	0.22	0.20	0.15
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
Elephant	Patch Density	K-S d	–	–	0.17	–	–	–	–	–	0.18	–	–	–
		p	–	–	> 0.20	–	–	–	–	–	> 0.20	–	–	–
	Log10 Patch Density	K-S d	0.23	0.20	0.21	0.18	0.26	0.26	0.29	0.31	0.18	0.19	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Fractal Index	K-S d	0.25	0.20	0.13	0.29	0.26	0.26	0.25	0.24	0.21	0.36	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Interspersion Index	K-S d	0.23	0.18	0.19	0.34	0.26	0.26	0.23	0.22	0.22	0.18	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20
	Diversity Index	K-S d	0.24	0.23	0.21	0.20	0.26	0.26	0.24	0.31	0.18	0.22	0.26	0.26
		p	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20	> 0.20

Appendix XIII. Season specific landscape heterogeneity metrics for individual elephant home ranges. The calculation of these metrics is explained in the text (page 39). ID = individual collar codes, where f denotes a female and m a male elephant. S.D. = standard deviation of the mean value. Only the Kafue females were used for comparison with the other study areas. Shaded cells indicate study areas where the mean value for the elephant ranges is significantly larger when compared between seasons within a study area. Bold cells indicate study areas where the mean value is significantly larger when compared between study areas (within groups indicated by 'Group' row) within seasons. Only the Kafue females were used for comparison with the other study areas. Where a study area belonged to more than one group (indicated by '/'), and multiple comparisons are drawn, superscript letters specify which group comparison is indicated by bold text. Italic cells indicate where elephant ranges of Kafue have significantly larger landscape heterogeneity between sexes, within seasons (dry and wet seasons were pooled). NOTE: 'largest mean values', as presented here refer to landscape heterogeneity as represented by that metric. Summary table appears as Table 15.

Metric		Patch Density				Fractal Index				Interspersion Index				Diversity Index			
Study Area	ID	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2	Dry Season 1	Dry Season 2	Wet Season 1	Wet Season 2
Kafue	K2m	-11.73	-11.46	-11.77	-12.58	1.57	1.51	1.57	1.60	60.81	68.62	56.44	60.35	1.17	1.52	1.03	1.26
	K4m	-11.05	-11.14	-11.67	-11.81	1.47	1.47	1.57	1.56	66.30	75.10	62.64	58.30	1.47	1.72	1.11	1.41
	K7m	-11.04	-11.42	-11.93	-11.95	1.45	1.50	1.56	1.59	76.68	66.73	55.58	65.48	1.48	1.55	1.12	1.41
	K9m	–	-11.97	–	-11.92	–	1.57	–	1.59	–	62.75	–	59.50	–	1.12	–	1.13
	K10m	-11.31	-11.18	-12.30	-12.32	1.49	1.47	1.57	1.57	67.61	68.26	55.57	54.34	1.31	1.42	1.10	1.12
	Mean	-11.28	-11.23	-11.92	-12.11	1.49	1.50	1.57	1.58	67.85	68.29	57.56	59.59	1.36	1.47	1.09	1.27
	S.D.	0.32	0.15	0.28	0.32	0.05	0.04	0.01	0.01	6.58	4.46	3.41	4.02	0.15	0.22	0.04	0.14
	K1f	-11.03	-11.09	-11.35	-11.47	1.45	1.46	1.52	1.52	74.89	73.23	71.61	73.25	1.46	1.46	1.36	1.37
	K3f	-11.05	-11.14	-11.44	-11.44	1.47	1.47	1.55	1.53	66.30	75.10	69.14	73.79	1.47	1.72	1.50	1.69
	K5f	-11.13	-11.37	-11.76	-11.49	1.47	1.55	1.57	1.56	73.70	63.89	61.78	67.85	1.36	1.27	1.16	1.38
	K6f	–	-11.31	–	–	–	1.50	–	–	–	70.91	–	–	–	1.64	–	–
	K8f	-11.07	-11.10	-11.08	-11.16	1.43	1.50	1.47	1.48	67.04	70.89	78.97	69.43	1.37	1.58	1.44	1.39
	Mean	-11.07	-11.20	-11.41	-11.39	1.45	1.50	1.53	1.52	70.48	70.80	70.37	71.08	**1.42**	**1.53**	1.37	1.46
	S.D.	0.05	0.13	0.28	0.16	0.02	0.03	0.05	0.04	4.44	4.25	7.09	2.90	**0.06**	**0.17**	0.15	0.15
	Group	a				a				a				a			
Lower Zambezi	LZ 1	-0.27	-0.49	-0.93	-1.44	1.38	1.45	1.57	1.62	83.50	83.14	82.52	78.98	2.06	2.06	2.06	1.96
	LZ 2	-0.49	-0.43	-0.78	-1.11	1.46	1.42	1.54	1.60	85.86	85.67	84.64	82.72	2.11	2.10	2.09	2.04
	LZ 3	-0.37	-0.44	-1.54	-1.64	1.38	1.41	1.62	1.63	85.33	84.74	79.38	80.91	2.02	2.06	1.91	1.99
	LZ 4	-0.57	-0.48	-0.87	-1.03	1.48	1.45	1.56	1.59	85.49	83.84	83.38	82.05	2.13	2.09	2.00	2.02
	LZ 5	-1.08	-0.77	-1.08	–	1.59	1.55	1.59	–	83.29	81.18	80.88	–	2.04	2.00	1.98	–
	LZ 6	-0.58	-0.55	-1.36	-1.31	1.49	1.47	1.60	1.60	78.16	80.44	79.45	74.94	2.00	2.03	1.99	1.88
	Mean	-0.56	-0.53	-1.09	-1.31	1.46	1.46	1.58	**1.61**	83.61	83.17	81.71	79.92	**2.06**	**2.06**	**2.01**	**1.98**
	S.D.	0.28	0.13	0.30	0.24	0.08	0.05	0.03	**0.02**	2.88	2.03	2.16	3.12	**0.05**	**0.04**	**0.06**	**0.06**
	Group	b				b/c				a				b			

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Luangwa	NL 1	-10.62	-10.90	-11.00	-11.21	1.58	1.62	1.63	1.63	75.95	75.05	69.94	72.29	1.55	1.59	1.59	1.49
	NL 2	-10.57	-10.61	-10.83	-10.95	1.57	1.57	1.61	1.62	75.12	78.73	69.92	70.08	1.65	1.73	1.39	1.41
	NL 3	-10.80	-10.93	-11.09	-11.23	1.63	1.64	1.63	1.64	67.18	77.26	63.50	68.48	1.50	1.52	1.41	1.41
	SL 1	-10.48	-10.44	-10.99	-11.02	1.39	1.49	1.61	1.63	76.18	81.94	70.88	73.33	1.32	1.43	1.17	1.42
	SL 2	-10.84	-10.89	-11.45	-11.31	1.53	1.56	1.62	1.61	61.20	70.48	69.87	70.09	1.47	1.67	1.47	1.48
	SL 3	-10.70	-10.81	-10.76	-10.74	1.51	1.54	1.54	1.54	56.14	60.04	58.63	59.15	1.44	1.47	1.51	1.51
	SL 4	-10.76	-10.35	-11.20	–	1.51	1.42	1.61	–	69.86	74.85	74.68	–	1.51	1.70	1.50	–
	SL 5	-10.68	-11.38	-11.77	-11.47	1.45	1.61	1.64	1.62	54.77	68.86	72.65	67.47	1.10	1.40	1.56	1.38
	Mean	-10.68	-10.79	-11.14	-11.13	1.52	1.56	1.61	1.61	67.05	73.40	68.76	**68.70**	**1.44**	**1.56**	**1.45**	**1.44**
	S.D.	0.12	0.32	0.33	0.25	0.07	0.07	0.03	0.03	8.78	6.85	5.20	**4.67**	**0.17**	**0.13**	**0.13**	**0.05**
	Group	c				b				a				b/c			
Kasungu	KS 2	-23.67	-10.95	-11.18	-10.96	1.54	1.51	1.55	1.64	58.59	59.02	60.31	68.86	1.05	0.99	1.09	1.21
	KS 3	-23.67	-11.10	-11.20	-10.97	1.46	1.55	1.55	1.62	59.44	62.31	60.02	69.13	1.03	1.10	1.09	1.22
	Mean*	-23.67	-11.02	-11.19	-10.96	1.50	1.53	1.55	1.63	**59.02**	**60.66**	**60.17**	68.99	1.04	1.04	1.09	1.21
	*S.D.**	0.00	0.11	0.02	0.01	0.05	0.03	0.00	0.01	**0.61**	**2.33**	**0.21**	0.19	0.01	0.08	0.00	0.01
	Group	d				c				a				a/c			
Vwaza	V 2	-10.98	-10.45	-11.17	-11.19	1.60	1.41	1.61	1.62	72.56	68.35	78.18	77.83	1.46	1.48	1.58	1.56
	V 4	-10.61	-10.65	-11.10	-11.29	1.48	1.51	1.61	1.63	68.48	70.06	79.08	78.63	1.41	1.45	1.59	1.56
	Mean*	-10.79	-10.55	-11.13	-11.24	1.54	1.46	1.61	1.62	70.52	69.20	78.63	78.23	1.44	1.46	1.59	1.56
	*S.D.**	0.27	0.14	0.05	0.08	0.09	0.07	0.00	0.01	2.89	1.21	0.64	0.57	0.03	0.02	0.00	0.01
	Group	e				c				b				b			

*These are only presented for comparative purposes, although the small sample sizes limit such calculations.