# Determinants of elephant spatial use, habitat selection and daily movement patterns in Hluhluwe-iMfolozi Park

by

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# Abstract

The ecological role of large herbivores is increasingly recognized due to their ability to influence ecosystem functioning and their impacts on faunal and floral assemblages. Knowledge on the determinants of spatial utilization is crucial towards the successful management of these species according to objectives set for the conservation of biodiversity. While numerous studies have investigated the factors influencing the movements and habitat preferences of large northern hemisphere herbivores, few have focused on members of the African megaherbivore guild. In the context of fenced reserves, elephants have been implicated in the degradation of habitat resulting in negative impacts on biodiversity. Using a kernel analysis approach, I calculated home range size and utilization distributions for five separate herds from an elephant population in Hluhluwe-iMfolozi Park and examined possible determinants. I explored differences in utilization intensity between herds and seasons by comparing the rugosity of utilization distributions. I used a utilization distribution-weighted composition analysis to determine seasonal habitat preferences within the home range and examined the factors influencing daily movement characteristics within different habitats in different seasons.

Substantial variation in home range size and location, utilization intensity, habitat preferences and movement responses was evident between herds. Spatial and temporal variation in resource distribution and intra-specific competition explained differences in home range size and utilization intensity. Larger herds underwent more fission-fusion events than small herds, possibly due to resource scarcity and greater competitive interactions. Elephants preferred greener habitats during the dry season and appeared to conform to optimal foraging principles. They utilized forest habitats more than others, selected larger patches with high densities of favoured food items and included greater proportions of common woody species in their diet. Large groups foraged close to rivers in the wet season and appeared to broaden foraging choices in the dry season by moving further away. Restricted displacements in the early morning and evening suggested crepuscular foraging activity while greater displacements at midday could not be explained by the need for water. This study highlights the importance of considering variation in animal movements and habitat utilization in overall conservation planning and when evaluating threats to sensitive habitats, particularly in fenced protected areas.

# Preface

The fieldwork described in this dissertation was carried out by the author in Hluhluwe-iMfolozi Park under the guidance of Ezemvelo KZN Wildlife staff. The analyses and writing were done at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, under the supervision of Prof. Kevin Duffy (Durban University of Technology) and co-supervision of Mr. Bruce Page and Dr. Abi Vanak.

This study represents original work by the author and has not otherwise been submitted in any form for any degree to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

_____                    4 March 2011

T. Bodasing                       Date

# **Declaration 1 – Plagiarism**

I, <u>Tarik Bodasing</u>, declare that

1.   The research reported in this thesis, except where otherwise indicated, is my original research.

2.   This thesis has not been submitted for any degree or examination at any other university.

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# Declaration 2 – Publications

Details of contribution to publications that form part of and/or include research presented in this thesis:

Publication 1: **Resource distribution and intra-specific competition determines range use by elephants in Hluhluwe-iMfolozi Park.** T. Bodasing, B. Page, A. Vanak & K. Duffy (in prep.).

The darting and collaring of elephants was carried out by EKZNW staff and TB. The logistics, organization and undertaking of monitoring and observing elephants were done by TB. Collation and entry of data into GIS, databases and spreadsheets, data analysis and writing of the manuscript was done by TB. The manuscript was reviewed by and received inputs from my supervisors, BP and KD and collaborator AV. AV also assisted with spatial analyses.

Publication 2: **Habitat preference and variation in daily movements by elephants determined from utilization intensity, path tortuosity and step length**. T. Bodasing, B. Page, A. Vanak & K. Duffy (in prep.).

Data on vegetation utilization that forms part of this publication was collected in three separate surveys by EKZNW staff (assisted by TB on two occasions). All other data was obtained in the same manner as detailed in Publication 1 by TB. Collation of data, data entry, analysis and writing was done by TB. The manuscript was reviewed by and received additional inputs from my supervisors, BP and KD and collaborator AV. AV assisted with spatial and statistical analyses.

TB= Tarik Bodasing
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AV= Abi Vanak
EKZNW= Ezemvelo KwaZulu-Natal Wildlife

# Acknowledgements

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# Chapter 1

# General Introduction

Large herbivores are increasingly recognized as major ecological agents in terrestrial systems due to their ability to influence ecosystem functioning and species diversity and composition (Olff & Ritchie, 1998; Fritz *et al*. 2002). They can exert a significant influence on ecosystem processes such as nutrient cycling and habitat fragmentation and are important ecological indicators (De Vires 1995; Kie *et al*. 2002). They may act as disturbance factors and substantial increases in their population densities often result in high browsing or grazing pressure that can endanger the regeneration and survival of sensitive habitat types (Barnes 1982; Du Toit & Owen-Smith 1989). This has major implications for the persistence of plant-herbivore systems (Fryxell & Sinclair 1988) especially in spatially constrained environments. As a result, substantial efforts are applied towards the management of these species around the world (Gordon *et al*. 2004). Whilst the movements, ranging behaviour and habitat preferences of large herbivores from northern temperate climates have been extensively studied (Apps *et al.* 2001; Boyce *et al*. 2003; Fortin *et al*. 2003; Anderson *et al*. 2005), fewer studies have focused on members of the African megaherbivore guild (Owen-Smith *et al*. 2010).

## 1.1 Factors influencing large herbivore spatial use and home range size and location

Environmental factors, among them temperature, elevation, rainfall and resource distribution have been identified as some of the primary determinants of large herbivore spatial use (Fischer & Cormack-Gates 2005; Kinahan *et al*. 2007; Shrader *et al*. 2010). Mueller & Fagan (2008) suggested that the major driver of home range size and occupancy of large herbivores was the spatial and temporal availability of resources. However, biotic factors such as body size, competition and predation risk clearly also play a role (Du Toit & Owen-Smith 1989; Wilmshurst *et al*. 1995; Wittemyer *et al*. 2008). Anderson *et al*. (2005) found that elk (*Cervus canadensis*) home range size and location was explained largely by the distribution of wolves (*Canis lupus*) and to a lesser extent by forage abundance. Kie *et al.* (2002) explained most of the variation in home range size of mule deer (*Odocoileus hemionus*) by aspects of landscape heterogeneity including habitat type and patch size and shape. Similar factors are known to influence the home range size and spatial use of large African species. Lewison & Carter (2004) for example, established that hippopotamus (*Hippopotamus amphibius*) ranging patterns are spatially constrained by distance to water and vegetation quality. Pienaar *et al.* (1993) deduced

that white rhino (*Ceratotherium simum*) home range size was determined by surface water availability while assessments of black rhino (*Diceros bicornis*) ranging patterns suggest that social factors influence the size of home ranges (Lent & Fike 2003). However, the vast majority of ecological studies within the African megaherbivore guild have focused on the African savanna elephant (*Loxodonta africana*).

Elephants are an important species in African savanna ecosystems but the factors influencing their movement and spatial use have not been extensively explored. Recent studies to establish the factors influencing elephant home range size have found that the distribution of water and forage, human disturbance, seasonal vegetation productivity and intraspecific competition are strong determinants (Shannon *et al*. 2006; Galanti *et al*. 2006; Chamaille-Jammes *et al*. 2007; Wittemyer *et al*. 2007a; De Beer & van Aarde 2008; Young *et al*. 2009a). However, there is a distinct paucity in the literature regarding the role of group size in determining patterns of spatial use by elephants. Thouless (1996) showed that herd size can determine the size of the home range while Wittemyer *et al.* (2005) showed that elephants may regulate group size in order to maximize space use and fitness during energetically constrained periods. Other studies have examined broad patterns of elephant spatial use across climatic gradients and found clear seasonal differences in dry savanna systems (Loarie *et al*. 2009; Young *et al*. 2009b) but not in wet ones. Crucially though, most recent studies on elephant spatial use have neglected to account for the determinants of habitat selection and how this influences patterns of use.

## 1.2 General rules of habitat selection

Any space of suitable physical or chemical conditions within which an organism searches for resources can be referred to as a habitat (Ritchie & Olff 1999). Theories of habitat selection and optimal foraging predict that animals will select habitats that offer higher energy returns compared to others and therefore enhance fitness in a shorter space of time (Stephens & Krebs 1986; Chalfoun & Martin 2007). An animal may display affinity for a particular habitat type because it contains a required resource (Law 1993; Anderson *et al*. 2005), because it offers protection against predators (Slauson *et al*. 2007; Willems & Hill 2009), for the purposes of shade (Kinahan *et al*. 2007) or all of the above. Differential habitat selection may therefore be associated with typical behavioural activities such as foraging, hiding or resting.

Animals are often referred to as 'generalists' or 'specialists' (Rosenzweig 1981) in regard to the breadth of their utilization of habitats. Use is classed as selective if a habitat is used disproportionately in relation to its natural occurrence (Johnson 1980). Habitat specialists may

be expected to be narrowly selective in their choice of habitat or to display a higher preference for specific habitat types. Polar bears (*Ursus maritimus*) as an example are known to be very selective in their use of habitats irrespective of season (Arthur *et al.* 1996) and many bird species show strong affinities for strictly riparian communities (Stauffer & Best 1980). Environmental variability influences resource selection (Alldredge & Griswold 2006) and many species may switch between general and selective behaviour during times of resource depletion (Owen-Smith 2002). Lions (*Panthera leo*) were found to adopt a more selective strategy in their choice of habitat during the dry season, specifically as higher prey abundances were associated with certain habitats over this period (Spong 2002). Black bears (*Ursa americanus*) utilized a wide variety of habitats in wetter climates but heavily favoured riparian and deciduous habitat types in drier climates (Lyons *et al.* 2003). Some animals require multiple habitats to satisfy different resource requirements (Law & Dickman 1998) and many species may in fact be less narrowly selective than predicted by optimal foraging theory (Owen-Smith 2002). Raccoons (*Procyon lotor*) and jays are well-known ecological generalists able to tolerate a diverse range of landscapes (Chamberlain *et al.* 2002; Marzluff *et al.* 2004). Elephant are expected to be more general in their choice of habitat because of their demanding food requirements in terms of bulk and nutrition (Owen-Smith 1988) but, as with other herbivores, this may change depending on the specific circumstances and location.

## 1.3 Factors influencing habitat preference within the large herbivore guild

### *1.3.1 Resource availability and predation risk*

The selection and utilization of specific habitats by large herbivores may be governed by similar criteria and associated with optimizing energy intake and minimizing predation risk (Owen-Smith 2002). They may selectively consume certain plant species and forage preferentially in favoured habitat types (Bailey *et al.* 1996). For example, habitat selection by moose (*Alces alces*) during the dry season changed according to the relative abundance of different habitats (Osko *et al.* 2004), while elk selected habitats that minimized the risk of predation by wolves (Anderson *et al.* 2005). Similarly, giraffe (*Giraffa camelopardalis*) habitat preferences may be determined by the risk of lion predation (Valeix *et al.* 2009) or by the occurrence of favourable forage species (Bond & Loffell 2001). Studies on white rhino indicate that short-term foraging patterns are related to the nutritional quality of grasses (Shrader *et al.* 2006) and that individual's shift foraging from short-grass to tall-grass patches during the dry season (Owen-Smith 1988). Thus, the nature of resources within a habitat, such as forage quality or quantity is crucial in determining the intensity of spatial utilization by large herbivores (Scoones 1995; Boone *et al.* 2006; Young *et al.* 2009a).

However, the literature presents conflicting arguments on elephant habitat preference and the factors influencing habitat utilization by elephants. Some studies have found little or no evidence of selectivity and support the theory that elephants are habitat generalists (Osborn 2005; Galanti *et al*. 2006; Roux & Bernard 2007). Conversely, others have noted that elephants may be strongly selective of specific habitats and may totally avoid others (Babassa 2000; De Boer *et al*. 2000; Steyn & Stalmans 2001). Particularly in the dry season when elephants are predominantly browsers, riparian or low-lying habitats on nutrient-rich soils can be heavily utilized (Owen-Smith 1988; Roux & Bernard 2007; Shannon *et al*. 2006) and adult females may forage more selectively than adult males (Stokke & du Toit 2002). Vegetation density, food availability and distance to water have previously been identified as determinants of habitat selection by elephants (Viljoen 1989; Babaasa 2000; De Boer *et al*. 2000; Harris *et al*. 2008).

### 1.3.2 Competition

Habitat selection may be regulated by density-dependent mechanisms such as territoriality leading to dominant individuals settling in the most suitable habitat (Fretwell & Lucas 1968). Among large herbivores, this process may be driven by competition between individuals or groups for heterogeneously distributed resources (Jarman 1972; Fritz *et al*. 1996). Animals may be forced to become more selective or territorial during periods of resource scarcity and as competition for available resources increases (Fritz *et al*. 1996). Fischer & Cormack-Gates (2005) showed that bison (*Bison bison*) and woodland caribou (*Rangifer tarangus caribou*) had distinctly separate diets at the height of the dry season thus reducing the chance of interspecific competition. Competition can limit both group size and the distribution of individuals or groups across space and time (Jarman 1974). It may become necessary for herd animals in particular to regulate their group size through fission-fusion events in order to satisfy nutritional demands (Wittenberger 1980; Wittemyer *et al*. 2005).

Smaller groups may be more efficient foraging units (Jacobs 2010) whereas larger groups have to traverse larger expanses of land to reduce competitive interactions (Wrangham *et al*. 1993). Studies examining the manner in which competition shapes habitat use and population structure of large African herbivores have mainly focused on ungulate species (Sinclair 1985; Sinclair & Arcese 1995). Page & Walker (1978) found clear separation in habitat use between four large savanna herbivores driven by differences in feeding height and Fritz *et al*. (1996) found evidence for seasonal interspecific competition between impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and cattle (*Bos taurus*). More recently, an assessment of black rhino

spatial use by Morgan *et al.* (2009) suggests that competition between individuals may promote differential habitat selection.

### 1.3.3 Body size

The metabolic demands associated with body size and digestive physiology play a key role in determining the dietary and habitat requirements for many herbivore species. This has given rise to a concept known as the Jarman–Bell principle which states that large-bodied mammalian herbivores can subsist on lower quality diets because of their lower metabolism requirement/gut capacity ratio (Bell 1971; Jarman 1974). Within the African savanna guild, species belonging to smaller size classes such as klipspringer (*Oreotragus oreotragus*) or suni (*Neotragus moschatus*) are restricted by the quality of plants they can consume and therefore have very specific habitat requirements such as rocky slopes or evergreen forest patches (Du Toit & Owen-Smith 1989; Skinner & Chimimba 2005). These species have become habitat specialists due to their lower energy demands and narrow dietary tolerance. Large herbivores, as a consequence of mass-specific metabolic requirements and the passage rate of food, do not tend to display such habitat selectivity (Du Toit & Owen-Smith 1989) and are more restricted by the availability of food and not the quality (Jarman 1974; Geist 1974). Instead, habitat selection among large herbivores often shifts or broadens over time due to their wider dietary tolerance (Owen-Smith 2002). These strategies are more evident in areas where resource availability differs markedly between seasons (Fritz *et al*. 1996) and are used to optimize energy intake.

### 1.3.4 Scale

Johnson (1980) identified four orders of selection each related to use at different spatial scales. First order selection represents the geographical range of the species while second order determines the home range of the individual or population under study. Third order selection reflects the use of habitats within the home range and fourth order selection the actual consumption of specific food items available within the habitat. Whether a species is a generalist or specialist may therefore also vary according to the spatial or temporal scale at which selection is viewed. An understanding of why selection may change at different scales is crucial towards the effective conservation of large herbivores (Kie *et al*. 2002). This is because patterns of habitat use can reveal how different parts of the environment vary in quality based on the costs and benefits of using each habitat (Boyce *et al*. 2003; Druce *et al*. 2009). Schaefer & Messier (1995) revealed that over the winter period, muskoxen (*Ovibos moschatus*) selected the same habitats across a hierarchy of spatial scales but broadened their dietary choice. At a temporal scale use may range from daily requirements for adjacent habitats

to seasonal use of geographically distinct patches (Law & Dickman 1998). Seasonal habitat preferences by mountain caribou (*Rangifer tarandus*) can vary greatly at different spatial scales (Apps *et al*. 2001) whereas klipspringers are known to alternate their utilization of habitats in the dry season and depending on the time of day (Druce *et al*. 2009). Consequently, multiple-scale studies of habitat selection can be more accurate in predicting general patterns of spatial or resource use compared to a single scale (Fortin *et al*. 2003).

## 1.4 Factors influencing movements by large herbivores (Path tortuosity and step length)

The movement of organisms is a crucial component of many ecological processes (Nathan 2009). Resource heterogeneity within ecosystems influences animal behaviour (Turner 1989) and movement may be employed as a foraging strategy to meet daily nutritional requirements and to alleviate the effects of resource scarcity in the environment (Fryxell & Sinclair 1988). On a daily basis, animals forage and travel within and between patches of resources (Owen-Smith 1988) and larger herbivores in particular may cover greater distances in order to find suitable foraging areas (Johnson *et al*. 1992). Changes in behavioural activity (e.g. foraging and travelling) can be inferred from variation in the distribution of movement parameters (Johnson *et al*. 2002; Morales *et al*. 2004) such as step length, turn angle and path tortuosity. Such variation can also reflect the intensity of the search for food by an animal (Nams 2005). More tortuous paths and lower displacements for instance, can indicate repeated use and possibly area-restricted searching patterns (Nams & Bourgeois 2004).

Using such techniques, Fryxell *et al.* (2008) found that elk movements were linked to the distribution of habitats and the search for food, at different spatial and temporal scales. Forester *et al.* (2007) found that elk displacements were strongly dependent on time of day, forage abundance and predator density, while Laporte *et al.* (2010) linked elk path sinuosity to the presence of predators. Within the African large herbivore context, some researchers have employed movement metrics such as net displacement, turn angles and step lengths to show how fine-scale movement responses by elephants are associated with foraging patterns, habitat occupancy and fences (Dai *et al*. 2007; Wittemyer *et al*. 2008; Vanak *et al*. 2010). Few studies have attempted to link herbivore movement to behavioural activities centred on fitness-maximizing principles (Owen-Smith *et al*. 2010). In one such study, Shannon *et al.* (2008) assessed elephant behavioural patterns over a day and suggested that daily activities may be influenced by social and environmental factors. The nature of animal movements therefore remains a key but poorly understood factor affecting the vulnerability of habitats and species to

landscape change (Law & Dickman 1998) and relatively little is known about the factors driving the movements of large African herbivores between resource patches (Owen-Smith 2002).

## 1.5 Elephant as ecosystem engineers: landscape utilization in the context of South African reserves

The southern African sub-region supports the highest density of elephants compared to other African regions (Blanc *et al*. 2007). However, the movements of all elephant populations in South Africa have been restricted due to confinement within fenced protected areas (Slotow *et al*. 2008; Vanak *et al*. 2010) often less than a thousand square kilometres in size (Slotow *et al*. 2005). South African elephant populations have thus experienced higher growth rates due to increased protection and the provision of water (Mackey *et al*. 2006; Van Aarde *et al*. 2008; Shrader *et al*. 2010). This steady increase in elephant numbers has fuelled concern within conservation circles regarding the impact of high elephant densities on the environment (Kerley *et al*. 2008; Van Aarde *et al*. 2008). These are mainly focused around the complex relationship between elephants and natural resources and the uncertainty surrounding the impact of elephants on the ecosystem (Owen-Smith *et al*. 2006; Biggs *et al*. 2008).

The African elephant is the largest terrestrial mammal and is classed as a megaherbivore with a total mass in excess of one ton (Owen-Smith 1988). Their large body size and greater food requirements coupled with high mobility make the scale of their impacts on the ecosystem disproportionately larger than many other species (Laws 1970; Kerley *et al*. 2008). Elephants are therefore considered as agents of significant influence and change and are often referred to as 'ecological engineers' (Jones *et al*. 2004). They can significantly alter their surrounding environment by changing vegetation structure and composition (Cumming *et al*. 1997; Skarpe *et al*. 2004), assisting tree recruitment through seed dispersion (Kerley & Landman 2006), promoting landscape level fragmentation (Hoft & Hoft 1995) and by influencing the composition of faunal assemblages both positively and negatively (Herremans 1995; Govender 2005; Pringle 2008). The nature and direction of influence thus remains equivocal in the literature (Gillson & Lindsay 2003) and there is a crucial need for more concise data on elephant-associated impacts and influence.

Elephants may rely heavily on key resource patches containing food and water during stressful times (e.g. De Beer *et al*. 2006; Smit *et al*. 2007) and clumped or isolated resource patches can experience a higher degree of utilization than the surrounding landscape. Additionally, seasonal

resource variation causes shifts in broad patterns of spatial use (migration between wet and dry season home ranges (Wittemyer *et al*. 2008) and at a finer scale, changes in diet composition from predominantly grass in the wet season to mainly browse in the dry (Owen-Smith 1988; Estes 1991). The patchy distribution of resources in savanna ecosystems and the nutritional requirements of elephants may determine the rate of foraging pressure and competitive interactions within herds (Wittemyer *et al*. 2005). Elephant impacts may therefore be associated with the number of individuals as well as with variation in the intensity of spatial utilization (Young *et al*. 2009b).

Elephants are able to alter their utilization of space and change their movement patterns in order to maximize energy gains and optimize fitness (Scholes *et al*. 2003). This, together with their often destructive feeding behaviour, has large-scale implications for the preservation of spatial heterogeneity. Unchecked increases in elephant numbers may intensify undesirable effects, an unavoidable occurrence in fenced areas where spatial and temporal variation in utilization is reduced (Kerley *et al*. 2008; Grant *et al*. 2008; Vanak *et al*. 2010). Such effects may be compounded in wetter savanna systems where seasonal home ranges are typically smaller and utilization more persistent (Young *et al*. 2009b) and in small reserves with high elephant densities (Shannon *et al*. 2006). Habitat degradation and the loss of faunal and botanical diversity are among the negative processes linked with high elephant densities in many fenced reserves throughout southern Africa (Cumming *et al*. 1997; Wiseman *et al*. 2004; De Beer *et al*. 2006).

Thus, the confinement of elephants within fenced areas has lead to more actively managed populations. This has included actions such as the creation of artificial water sources (Redfern *et al*. 2005), culling and contraception (Naeve & Tanton 1989; Delsink *et al*. 2007) and the erection of fences around sensitive habitat types (Lombard *et al*. 2001). These interventions may ultimately restrict or alter movement patterns and change the way elephants utilize the landscape. Physical barriers for instance, can impair movement by severing habitat connectivity (Beier & Noss 1998; McDonald & St Clair 2004). This can result in the reduction of immigration and emigration rates (Turner 1996) and ultimately affect the persistence of faunal and floral assemblages that reside in patches of suitable habitat (Severns 2003). Alterations in the intensity of spatial use by elephants may be in direct conflict with targets set for the conservation of ecosystem biodiversity. Knowledge of the factors affecting animal movements and habitat preference is therefore vital in order to understand the ecology of a species (Ben-

Shahar & Skinner 1988; Chamberlain *et al.* 2002) and its influence on ecosystem diversity and processes.

## 1.6 Aims and objectives of the study

While studies agree that rainfall, resource (food and water) heterogeneity and fences are among the major drivers of elephant spatial use (Chamaille-Jammes *et al.* 2007; De Beer & van Aarde 2008; Loarie *et al.* 2009; Young *et al.* 2009b; Shrader *et al.* 2010; Vanak *et al.* 2010), the effects of competition, and the factors influencing habitat selection within elephant populations remains uncertain. Furthermore, very few studies have attempted to determine the drivers of variation in short-term movements by elephant. The link between daily movement patterns and foraging-related activity is therefore unclear. The aim of this study was to determine the factors influencing seasonal home range size and habitat preferences and daily movement patterns of elephant herds in Hluhluwe-iMfolozi Park. More specifically, the objectives of the study were to:

i) describe seasonal home range use for separate female herds and establish the factors that influence home range size, location and the intensity of use within the home range

ii) determine the occupancy rates of different habitat types in different seasons by elephants

iii) determine the influence of vegetation productivity in different habitat types on habitat preference by elephants

iv) establish whether movement patterns (in terms of step length and tortuosity) are different in different habitats

v) assess whether time of day, habitat availability and the density of woody vegetation could explain variation in daily movement

I expected that resource distribution and intra-specific competition could explain differences in spatial use and habitat preference of separate female herds within the same population. In this regard I tested the hypotheses that spatial variation in rainfall, vegetation productivity and surface water and variation in group size determines seasonal home range size and utilization intensity. I further expected that elephants would prefer greener habitats and that daily movement patterns were dependent on the time of day, habitat type and availability and the density of woody vegetation within a habitat. I therefore tested the hypothesis that greater habitat productivity and higher densities of certain species would determine habitat selection. I also hypothesized that daily movements would differ according to the time of day and the amount of habitat available.

## 1.7 Thesis layout

The thesis is divided into the following chapters:

Chapter 1 – Introduction to the topic and the context and aims of the study (given above)

Chapter 2 – Examines and describes differential spatial use by separate female herds at the home range scale within Hluhluwe-iMfolozi Park. The results are discussed with regards to the potential drivers of variation in the intensity of spatial utilization within the home range and the relevance of this to the preservation of spatial heterogeneity. Resource distribution and intra-specific competition are presented as the most likely explanatory factors of variable spatial use.

Chapter 3 – Investigates and compares habitat preference within the home range for all female groups by quantifying the utilization intensity for each habitat type. Also examined are daily movements in different habitat types using path tortuosity and step length as response variables. The results are discussed in terms of the factors influencing seasonal habitat preference and daily movements by elephants, and the importance of this to ecosystem conservation.

Chapter 4 – Conclusions and discussions of the importance of understanding factors governing animal movements and habitat choices in order to successfully manage ecosystems. Also discussed is how knowledge on animal movements can demonstrate the conservation value of habitats and the importance of preserving habitat heterogeneity.

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# Chapter 2

# Resource distribution and intra-specific competition determines range use by elephants in Hluhluwe-iMfolozi Park

## 2.1 Summary

Knowledge of how an animal utilizes its environment over space and time is essential in directing conservation and management efforts. I quantified the extent and intensity of spatial use by separate female herds of an elephant population and examined possible determinants. I hypothesize that intra-specific competition, inferred from variation in group size, the amount of rainfall, and vegetation patch heterogeneity can explain seasonal differences in home range size. Additionally, I hypothesize that the intensity of spatial utilization will increase in close proximity to water and in areas with greener vegetation, particularly in the dry season. The results reflect a seasonal and spatial differentiation in home range size and utilization intensity among herds. Rugosity values were higher in the dry season compared to the wet, suggesting a greater intensity of use. Some herds displayed contraction in home range size during the dry season but expanded their home ranges in the wet season, while other herds were less mobile. Home range size was significantly correlated with mean total rainfall and mean group size in the wet season but not in the dry. Fission-fusion events were more common in larger herds all year indicating possible trade-offs in terms of group size. Utilization intensity was inversely related to proximity to rivers, significantly so in the wet season but was not associated with greener vegetation in either season. I suggest that herds may forage more selectively close to rivers during the wet season and broaden their foraging choices in the dry season as they move further away. Home range size was also inversely correlated with aspects of vegetation patch heterogeneity in the dry season. This study highlights the presence of variation in spatial use within an elephant population, driven largely by resource distribution and intra-group competition.

## 2.2 Introduction

An understanding of the determinants of spatial distribution of individuals in a population is central to the study of animal ecology and is essential in directing conservation efforts (Pinaud 2008). This is especially important when dealing with high-impact species such as large herbivores that are able to influence ecosystem functioning (Fritz *et al*. 2002). Within the large herbivore guild spatial use may be constrained by rainfall and surface water distribution (Chamaille-Jammes *et al*. 2008; Redfern *et al*. 2003), elevation (Boyce *et al*. 2003), temperature

(Olff *et al*. 2002), the distribution of forage (Fortin *et al*. 2003) or by heterogeneity in the properties of the landscape (Morales *et al*. 2005). The role of density-dependent factors such as competition (Wittemyer *et al*. 2007a) and predation risk (Anderson *et al*. 2005) has also been documented. The degree of influence of these determinants however, remains uncertain for many behaviourally complex species.

Researchers studying patterns of spatial use have frequently employed kernel-based techniques to determine variation in space use and to relate this to specific resources (Kie *et al*. 2002; Willems & Hill 2009). Kernel methods provide a direct density estimate as a probability of occurrence at a specific location (Silverman 1986; Leggett 2006). Least Squares Cross Validation (LSCV) has recently been the method of choice for kernel-based analysis (Seaman *et al*. 1999; Gitzen *et al*. 2006; Willems & Hill 2009) due to the accuracy of home range estimates. Alternatively, the utilization distribution (Worton 1989) provides a measure of the intensity of probable use at any point within the home range (Kernohan *et al*. 2001; Marzluff *et al*. 2004; Gitzen *et al*. 2006) that can be related to resource distribution (Millspaugh *et al*. 2006). The use of utilization distributions in establishing spatial use assumes that the animal is the primary sampling unit and reduces the effects of spatial autocorrelation (Aebischer *et al*. 1993). Integrating Global Positioning Systems (GPS) technology into animal movement studies has considerably improved our ability to accurately model the movements of free-ranging animals (Frair *et al.* 2004).

African elephants show an extremely wide range of tolerance and adaptation to ecological conditions, from deserts (Viljoen & Bothma 1990) to forests (Tchamba 1995). They are a water-dependent species (Western 1975; Smit *et al*. 2007) and are known to drink on a daily basis in some areas (De Beer *et al*. 2006). Studies of elephant populations have revealed extensive seasonal and spatial variation in home range size (Leuthold 1977; Thouless 1995; Lindeque & Lindeque 1991; Shannon *et al*. 2006). In some cases smaller home ranges occur in the dry season compared to the wet (Thouless 1996; De Villiers & Kok 1997) whilst others have larger dry season ranges (Jachmann 1983; Shannon *et al*. 2006). Consequently different populations vary widely in terms of group size and ranging behaviour (Owen-Smith 1988).

The regulation of group size through the temporary fission and fusion of groups in order to maximize fitness has been well documented in a number of species including some primates (Wittenberger 1980) and elephants (Wittemyer *et al*. 2005). Potential benefits favouring larger group sizes include more effective defences against predators, more efficient acquisition of

resources and cooperative rearing of young (Chapman & Chapman 2000), while low group cohesion may allow individuals to better exploit preferred food items during times of resource scarcity (Jacobs 2010). The patchy distribution of resources in savanna ecosystems and the foraging requirements of elephant make them susceptible to intraspecific competition (Wittemyer *et al*. 2005). Intraspecific competition can limit group size and can influence the spatial proximity of one group to one another (Jarman 1974). Bigger groups may increase their food-encounter rates by foraging over larger areas than smaller groups, in order to support their higher per-capita costs due to intra-specific competition (Wrangham *et al*. 1993). Although elephant group size can vary significantly between herds in a population (Thouless 1996) few studies have examined this as a driver of spatial use.

The distribution of vegetation of different quality and quantity strongly influences animal movements and dynamics (Pettorelli *et al.* 2005). The dispersion of food in savannas is linked to differences in rates of primary productivity in different places, which is determined by differences in rainfall (Scholes *et al.* 2003; Chamaille-Jammes 2008) and soil conditions (Illius & O'Connor 2000; Fritz *et al*. 2002). Although long-term rainfall patterns are fairly regular and thus predictable, short-term irregularities may cause changes to water availability and primary productivity. Such variable ecological conditions may require an equally dynamic strategy of space use by elephants, centered on long-term patterns but flexible enough to accommodate short-term variation (Leuthold 1977). The Normalized Differential Vegetation Index (NDVI) is an index of primary productivity and can be used to quantify the relationship between animal distributions and vegetation greenness (Pettorelli *et al.* 2005). Previous studies have used the NDVI to link the distribution patterns of herbivores with changes in forage quality (Boone *et al*. 1994; Leimgruber *et al*. 2001) or with selection for vegetation patches of higher productivity (Young *et al*. 2009a).

The distribution of surface-water may also influence herbivore distribution patterns in semi-arid ecosystems (Western 1975; Bergstrom & Skarpe 1999; Redfern *et al*. 2003). A number of herbivore species including elephant are especially dependent on water during the dry season when resources may be depleted. Furthermore, the establishment of artificial water sources has resulted in changes in the intensity of herbivore spatial use particularly within fenced protected areas (Smit & Grant 2009). This has created distinct gradients in utilization intensity around water points in many areas a term known as the "piosphere" effect (Lange 1969). In areas where surface water distribution is highly seasonal elephants are known to concentrate near perennial water sources during the dry season (Western & Lindsay 1984; Lindeque & Lindeque 1991;

Osborn & Parker 2003; Wittemyer *et al*. 2007; Smit *et al*. 2007). Fewer studies however, have explored elephant spatial use as a function of distance to water in wetter areas where artificial water is not provided.

The manner in which an animal uses space may also be influenced by environmental heterogeneity at differing scales (Johnson *et al*. 2002). To date studies of how the spatial arrangement of resources influences animal distributions have been neglected, especially with reference to large mammals (Kie *et al*. 2002; Grainger *et al*. 2005). Heterogeneity in habitat structure and composition for example, has been shown to influence habitat selection (Boyce *et al*. 2003) and home range use (Said & Servanty 2005) by large herbivores. Variation in the composition and spatial arrangement of vegetation patches can also represent landscape heterogeneity (Turner *et al*. 2001). This in turn may be linked to resource distribution and can influence elephant spatial use (De Beer & van Aarde 2008). Elephant home range size and variation in use has been associated with vegetation patch density and with the scale of spatial heterogeneity (Grainger *et al*. 2005; Murwira & Skidmore 2005).

While ecologists recognize that elephant space use is determined primarily by the distribution of resources in a landscape, differential utilization patterns within populations have not been thoroughly explored in spatially constrained environments. The aim of this study was to determine whether the distribution of specific resources and intra-specific competition influenced elephant spatial use in a fenced protected area. I predicted that utilization intensity would be higher in the dry season when resources were scarce and lower in the wet season when resources were more abundant. I hypothesized that seasonal variation in rainfall, vegetation greenness and the distribution of perennial water, intra-group competition (inferred from changes in group size), and the inherent patchiness of vegetation, could explain heterogeneity in home range size and utilization intensity of different breeding herds. My first objective was to determine whether differential spatial use was evident between seasons and herds. Secondly, I examined the role of intra-group competition in determining group size and the influence of this on home range size. Thereafter, I examined how spatial and temporal differences in rainfall, the distribution of vegetation of varying primary productivity and distance to perennial rivers influenced the intensity of spatial use. Lastly, I questioned whether home range size was related to the spatial heterogeneity of vegetation.

## 2.3 Methods

### 2.3.1 Study Area

Hluhluwe-iMfolozi Park covers an area of roughly 900 km$^2$ (90 000 ha) in northern Kwa-Zulu Natal between 28°00 - 28°26 S and 31°43 - 32°09 E. The topography of the park ranges from hilly in the north to gently undulating in the south. Altitudes range from 60 m/asl in the large river courses to 750 m/asl in the northern hills. Shales and sandstones from the Ecca and Dwyka groups and belonging to the Volkrust, Vryheid and Pietermaritzburg formations characterize the geology of most of the park, while some dolerite, basalt and alluvium is also present in the south (King 1970; Downing 1980). Swartland and Shortland are the main soil types in the north and centre of the park, while shallow Mispah and Glenrosa forms dominate most of the south (Mucina & Rutherford 2006). About 500 elephant are found in the area together with most of the mammalian fauna typically associated with South African savannas. These include large herbivore species indigenous to the area such as white (2312) and black rhino (198), buffalo (4789), zebra (2749), blue wildebeest (3002), impala (14 074), hippopotamus (20) and kudu (717) as well as introduced herbivore species such as giraffe (874) and nyala (4082). Estimates from the annual game count in 2010 are given in brackets.

### 2.3.2 Rainfall and surface water

Rainfall is highest in the far north at 990 mm/pa and lowest in the far south at 635 mm/pa (Balfour & Howison 2002). Wet and dry seasons are defined by mean rainfall across the park with the April-September period being the drier part of the year and October-March the wetter part of the year, based on long-term averages for four stations (Fig. 2.1). Mean rainfall totals for the first and second wet seasons were 87.62 mm ± 16.2 SD and 87.36 mm ± 25.9 SD respectively, while totals for the first and second dry season were 38.33 mm ± 10.1 SD and 30.08 mm ± 6.0 SD. Unseasonal rainfall events did occur, indicated by the notably above average rainfall (10-year short-term) in the mid-dry season of 2007 as compared to the slightly above average in the mid-dry season of 2008 (Fig. 2.1). Three main rivers flow through the park: The Hluhluwe River in the north and the Black and White iMfolozi Rivers in the south. The Hluhluwe River was the main perennial river in the park. Numerous ephemeral water bodies hold water during the wet season across the entire park. There are no artificial water sources in the park.

### 2.3.3 Vegetation

Mucina & Rutherford (2006) described 3 large-scale vegetation units that comprise the area of Kwa-Zulu Natal in which Hluhluwe-iMfolozi is located, namely: Scarp Forest, Northern

Zululand Sourveld and Zululand Lowveld. Scarp forest patches occur at higher altitudes in the far north on wetter south-facing slopes. Much of the north of the park falls within Northern Zululand Sourveld. The majority of iMfolozi and the corridor area of the park fall into the Zululand Lowveld vegetation unit. Whateley & Porter (1983) recognized and mapped 16 distinct woody plant communities across the park. Due to the high level of detail in this map I combined their communities into six structural types: open and closed woodland, riparian forest, scarp forest, thicket and wooded grassland.

## 2.3.4 Home range size and the utilization distributions within the home range

GPS collars were fitted to five adult matriarchs in different herds during October 2006. The first study year therefore ran from October 2006 to September 2007 and the second from October 2007 to September 2008. Matriarchs were defined based on their age and the level of dominance in interactions with other adult females in the group (Archie *et al*. 2006). Two of these females (hereafter identified as Herd 1 and 2) were collared in the south of iMfolozi while the other three (identified as Herd 3, 4 and 5) were collared in the north of Hluhluwe. This ensured that the sample of collared females covered all known breeding herds within the park at the time of darting. Subsequently, Herd 4 and 5 were observed to occasionally merge and split during the study period. As matriarchs primarily dictate movement and spatial use (Moss 1988), collaring an older, dominant matriarch in a herd ensures that any location data obtained is representative of the entire herd (Wittemyer *et al*. 2007a).

Fixes of positions were obtained every 30 minutes for the two-year period and the accuracy was within 10 metres. The locations for each female were highly spatially autocorrelated (Global Moran's $I > 0.5$) at the smallest time intervals (30 minutes). To reduce autocorrelation, five locations were selected each day, at the same times of day (4 am, 9 am, 2 pm, 7 pm and 11.30 pm) and at approximately regular (4.5-5 hr) intervals (Swihart & Slade 1997) for the entire dataset. The selected times covered a 24 hr timeframe and ensured that the locations were not biased towards a specific time of day. Although this did not remove autocorrelation totally, it considerably reduced the Global Moran's $I$ value thus increasing spatial independence between points. Complete removal of spatial autocorrelation from data has been shown to incur a loss of crucial information and compromise the accuracy and validity of interpretation of data depicting space use (De Solla *et al*. 1999; Cushman *et al*. 2005). Furthermore, the use of short sampling intervals over a seasonally defined study period is advocated for home range estimates and quantification of the intensity of spatial use (Rooney *et al*. 1998; Wittemyer *et al*. 2007a).

ArcGIS Version 9.3 was used to overlay the five daily locations for each animal for the season on surface water, NDVI (see section 2.3.7.2 for source of data and time period selected) and vegetation type layers. I used the LSCV fixed kernel density estimator within the Home Range Tools Version 1.1 (Rodgers *et al*. 2007) package to determine 50% and 95% isopleths and the utilization distributions for each of the collared elephants in each of the breeding herds in each season. The LSCV home range estimator converts Cartesian point locations into a three-dimensional probability density surface known as the utilization distribution (Willems & Hill 2009). The height of the utilization distribution at a given point indicates the relative probability of use of space within the home range and is determined by the concentration of location points (Marzluff *et al*. 2004) at a particular spot.

### 2.3.5 Differences in the size, location and use intensity of home ranges

I calculated 95% home range kernels (hereafter referred to as 'home range') for each of five herds for the 2-year study, in each year and in two wet and two dry seasons. 50% kernels (hereafter referred to as 'core') were calculated for each herd in two wet and two dry seasons. For the purposes of this study, Herd 1 and 2 are referred to as range-restricted herds (hereafter 'RR') and Herd 3,4 and 5 as wide-ranging herds (hereafter 'WR') due to differences in home range and core size, location and use intensity (Table. 2.1/Figs.2.2 & 2.3). To examine use intensity within the home range, the Benthic Terrain Modeler tool for ArcGIS (Wright *et al*. 2005) was used to calculate rugosity of use data. Rugosity represents a measure of the ruggedness of a surface where low values indicate flatter, even surfaces and high values indicate increasingly rougher surfaces (Wright *et al*. 2005; Gratwicke & Speight 2005). I used it to determine the ruggedness of seasonal LSCV utilization distributions in order to gain a measure of use intensity within the home range. It was expected that wet season utilization distributions would contain shallower peaks indicative of an even intensity of use due to a homogenous distribution of resources. Conversely, dry season distributions were expected to consist of fewer, high peaks indicating concentrated use due to a more heterogeneous distribution of resources. As these data were not normally distributed, I used a Mann-Whitney U Test to test for differences in rugosity of utilization distributions and included season (wet/dry), herd I.D (WR/RR) and season-herd interaction as factors.

### 2.3.6 Influence of group size on home range size

Larger herds are expected to move further and occupy a greater area because of competition between individuals for food. Herd sizes were accurately determined from total counts whenever they were observed directly and by viewing video playbacks. Each herd was observed

and counted on ten or more occasions during each season (6-month block). I calculated the mean group size for each herd in each wet and dry season separately. Pearson correlation statistical tests were used to examine the relationship between herd size and home range size by plotting the mean group size against home range size in separate wet and dry seasons. Fission-fusion events within herds were examined by plotting the mean group size for each herd over two wet and two dry seasons. A parametric analysis of variance (ANOVA) was used on these data to test variance in group size, with season, herd I.D and season-herd interaction included as factors.

### 2.3.7 Influence of water and vegetation quality on home range size and within range use

### 2.3.7.1 Effect of rainfall on home range size

Monthly data were obtained from four rainfall stations, two in the north and two in the south of the park. I was interested in seasonal effects and therefore determined the mean total rainfall in each season for the two stations in the north and for the two in the south separately, and calculated an average for the whole park in each season. This was done by averaging the cumulative monthly rainfall at each station over a 6-month period from Oct-Mar for the wet season and Apr-Sep for the dry season. The values used reflected the location of each herd during that season (north, south or park). I hypothesized that home range sizes would increase during wetter periods due to an abundance of resources and contract during drier periods due to a paucity of resources. Regression plots and Pearson correlations were employed to test the relationship between home range size and mean total rainfall within and between season.

### 2.3.7.2 Effect of vegetation quality on within range use

To investigate the extent to which herds actively select areas of greener vegetation, NDVI data was used (http://LPDAAC.usgs.gov). NDVI at a resolution of 250m x 250 m, calculated using 16-day composite images from the MODIS 13 SPOT4 and SPOT5 satellites was obtained for the three years covering the study period (2006-2008). Seasonal NDVI values were obtained by calculating the mean NDVI for each raster grid square within the home range (250m x 250m) for the six 16 day composite images over the 3 driest months (May/June/July) and 3 wettest months (Nov/Dec/Jan) in each season. The images were standardized (Boone *et al*. 2006) to contain values from -3 to 10. Values were then divided by 10 in order to bring them into the range normally associated with NDVI (-1 to 1). Values between -1 and 0 indicate a low chlorophyll content or inactive primary production while those increasingly > 0 indicate higher net primary productivity (Leimgruber *et al*. 2001). The range of NDVI values for HIP fell

between 0.3 and 0.8 where values closer to 0.3 represented less green vegetation and values closer to 0.8 more green vegetation. The proportion of location fixes within each NDVI category in each of the home ranges was determined for each herd separately. As data were not normally distributed, I used a Kruskal-Wallis test, to test whether the proportion of location fixes varied according to NDVI category. I included season and herd I.D (WR and RR) as factors and examined associated interaction effects between NDVI category-season, NDVI category-herd and season-herd.

### 2.3.7.3 Effect of surface water distribution on within range use

I considered elephant occupancy relative to distance from three major perennial rivers by calculating the proportion of location fixes within five distance categories (0-2; 2-4; 4-6; 6-8 and > 8 km from rivers) for all herds combined in both seasons. I expected that spatial use would be higher closer to perennial rivers in the dry season particularly in the absence of artificial water sources. I focused on the three wettest and three driest months in each season and used the complete dataset (48 points per day) for the analysis in order to assess total proportions. I employed an ANOVA to test whether the proportion of herd location fixes varied according to distance from rivers. I included season and herd I.D (WR and RR) as factors and examined associated interaction effects between distance category-season, distance category-herd and season-herd. Proportions were arcsine-root transformed to meet the assumptions of a parametric analysis.

### 2.3.8 Influence of spatial heterogeneity of vegetation on home range size

I hypothesized that vegetation patch heterogeneity influenced elephant home range size. Patch heterogeneity was assessed separately for each breeding herd in each season in those areas of the park most frequented by that herd. A patch was defined from the vegetation layer in ArcGIS, as an area of a specific vegetation type surrounded by other vegetation types (Grainger *et al.* 2005). The indices patch richness density (PRD), Shannon diversity index (SD), largest patch index (LPI), mean shape index (MSI) and mean nearest neighbour distance (MNND) were calculated using VLATE (Vector-based Landscape Analysis Tools Extension) for ArcGIS Version 9 (Lang & Tiede 2003) (Table. 2.2). Indices were selected to represent biologically meaningful aspects of vegetation structure and composition (size, shape, diversity and density) that are known to influence elephant foraging patterns and therefore spatial use. I expected that elephant would favour larger, irregularly shaped patches that were in close proximity and to select areas of higher patch diversity, in order to optimize foraging. The relationship between home range size and the chosen metrics was tested using Pearson correlations. All statistical and

spatial analysis was carried out using SPSS Version 18.0 and ArcGIS 9.3 software package with Hawth's Tools (Beyer *et al*. 2004), XTools Pro and Spatial Analyst animal movement extensions.

## 2.4 Results

I was able to differentiate two distinct patterns of movement. RR herds maintained small home ranges in the south of the park in both seasons while WR herds used the north and south in the wet season and mostly the north in the dry season.

### 2.4.1 Intensity of spatial use

The intensity of spatial use as measured by the rugosity of the utilization distributions was found to be significantly different between seasons (Mann-Whitney $p<0.0001$). An example of a typical utilization distribution in a wet and dry season is given for a WR herd (Fig. 2.2A & B) and a RR herd (Fig. 2.3A & B). For WR herds specifically wet season utilization distributions in both years consisted of collectively larger cores (Table. 2.1), often connected and of high rugosity (use intensity), while dry season distributions in both years consisted of collectively smaller cores (Table. 2.1), often isolated from each other and of higher rugosity (use intensity). For RR herds, the rugosity (use intensity) within the home range was higher in the dry season in both years but to a slightly lesser degree compared to WR herds. Herd main effects and herd-season interaction effects were non-significant.

### 2.4.2 Influence of group size on spatial use

Mean group size was significantly correlated with home range size in Wet Season 1 (Pearson $r=0.960$; $p=0.009$) and Wet Season 2 (Pearson $r=0.918$; $p=0.028$), with home range size increasing considerably as mean group size increased (Fig. 2.4a & b). There was a non-significant inverse relationship between group size and home range size in Dry Season 1 (Pearson $r=-0.656$; $p=0.230$) and Dry Season 2 (Pearson $r=-0.559$; $p=0.327$) (Fig 2.4c & d). Mean group size within larger, WR herds was significantly more variable than within smaller, RR herds (ANOVA $F=42.079$; $df=4$; $p<0.0001$); however, there was no difference in the variance of mean group size between seasons (Fig. 2.5). Season-herd interaction effects were also non-significant.

### 2.4.3 Influence of rainfall on spatial use

*Within season*

Home range size was significantly positively correlated to mean rainfall in both the first (Pearson $r=0.963$; $p=0.009$) and second (Pearson $r=0.876$; $p=0.050$) wet season indicating an expansion in home range size with higher rainfall (Fig. 2.6a & b). By contrast, home range size was not significantly associated with mean rainfall in either the first (Pearson $r= -0.873$; $p=0.054$) or second (Pearson $r= -0.591$; $p=0.294$) dry season indicating that rainfall did not affect home range size (Fig. 2.6c & d).

*Between season*

The difference in home range size between Dry Season 1 and 2 was not significantly associated with the difference in mean total rainfall between these seasons (Pearson $r=0.834$; $p=0.079$) (Fig. 2.7a) or with the difference in mean rainfall between seasons as a percentage of rainfall in the first dry season (Pearson $r=0.781$; $p=0.119$) (Fig. 2.7b). The difference in home range size between Wet Season 1 and 2 was also not significantly related to the difference in mean rainfall between each wet season (Pearson $r= -0.165$; $p=0.791$).

### 2.4.4 Influence of vegetation productivity on spatial use

The intensity of use based on the proportion of location fixes varied significantly across NDVI categories (Kruskal-Wallis $F =60.391$; $df=5$; $p<0.0001$) but not between season or herd. Preferential use of vegetation patches of intermediate productivity (0.5-0.7 NDVI) but not the highest (0.8 NDVI), was evident in both seasons for all herds (Fig. 2.8). A significant interaction effect between NDVI category and season was apparent (Kruskal-Wallis $F =6.523$; $df=5$; $p<0.0001$). In the wet season, the intensity of use was significantly higher within moderately green patches (0.6 NDVI) compared to the dry season when use was more evenly spread (Fig. 2.8). Post-hoc tests with Bonferroni correction revealed significant pairwise differences ($p<0.0001$) between the middle NDVI categories and the lowest and highest categories, suggesting that herds chose moderately green vegetation, but not the greenest or least green, in both seasons. Areas with the lowest primary productivity (0.3 NDVI) were not utilized in either season (Fig. 2.8). Other interaction effects were not significant and therefore removed from the analysis.

### 2.4.5 Influence of surface water distribution on spatial use

The intensity of use as reflected by the proportions of location points varied significantly across distance to river categories (ANOVA $F=102.29$; $df=4$; $p<0.0001$). Use intensity decreased with

increasing distance from perennial rivers in both seasons for all herds (Fig. 2.9). An interaction effect between distance to river category and season was evident ($F$=4.985; $df$=4; $p$=0.003) indicating differential use within certain distance categories between seasons. Pairwise testing with Bonferroni correction indicated that spatial use was significantly higher closer to rivers (0-2 km) in the wet season compared to the dry season ($p$<0.0001), in which a greater proportion of locations were found further away (Fig. 2.9). Season (ANOVA $F$=2.249; $p$=0.142) and herd (ANOVA $F$=0.105; $p$=0.980) main effects were not significant. Interaction effects between season and herd were also not significant and were removed from the analysis.

### 2.4.6 Patch heterogeneity

The Largest Patch Index was inversely correlated with home range size in the wet (Pearson $r$= -0.753; $p$=0.012) and the dry season (Pearson $r$= -0.824; $p$=0.003). This indicates that home range size decreased with increasing patch size (Fig. 2.10a & b). Mean Shape Index (Pearson $r$= -0.737; $p$=0.015) and Mean Nearest Neighbour Distance (Pearson $r$= -0.683; $p$=0.029) were inversely correlated with home range size in the dry season only. This indicated that home range size decreased as patch shape became more irregular and patches of the same vegetation type were further apart (Fig. 2.11a & b). No significant correlations were evident between home range size and patch richness density in either the wet (Pearson $r$= -0.420; $p$=0.227) or the dry season (Pearson $r$= -0.192; $p$=0.595). There was also no significant correlation between home range size and Shannon diversity in the wet (Pearson $r$= 0.355; $p$=0.315) or the dry season (Pearson $r$= -0.517; $p$=0.126).

## 2.5 Discussion

Elephant spatial use has previously been linked with rainfall, forage preference and resource availability (Tchamba 1993; Western & Lindsay 1984; White 1994; Babaasa 2000). In the context of this study, resource distribution and intra-specific competition played a major role in determining elephant spatial use. Seasonal variation in home range size and utilization intensity was evident between breeding herds and influenced by rainfall variation, the distribution of green vegetation and surface water, vegetation patch heterogeneity and intra-group competition. In support of my prediction, dry season utilization intensities were higher and use more concentrated, as expected during a period of lower resource abundance. Furthermore, increasing rainfall and group size led to an expansion in home range size and is possibly associated with greater resource abundance and increasing competition within larger herds. Contrary to my hypothesis, utilization intensity was higher close to water in the wet season, and herds chose

areas of intermediate vegetation productivity in both seasons. Variation in patch size, shape and proximity also significantly affected home range size, particularly in the dry season.

Breeding herds could be clearly differentiated based on the dry season size and locations of their respective cores, with some herds tending to be far less mobile than others. The extent of variability in the size and shape of the home range and the intensity of use within it differed according to the distribution of resources and the level of intra-herd competition. Home ranges may become more fragmented when resources are randomly distributed compared to when resources are clustered (Mitchell & Powell 2004). For WR herds this pattern can be clearly seen in the more evenly spread use of space during the wet season as inferred by the lower rugosity and leading to multiple cores and larger home ranges. The dry season utilization pattern was more aggregated leading to a smaller, continuous home range and clumped use intensity peaks as indicated by the higher rugosity. For RR herds the size of the home range and the intensity of spatial use were similar in both seasons.

Past studies have shown that some elephant clans appear to exclude other clans from particular areas, specifically in the dry season (Douglas-Hamilton 1972; Moss & Poole 1983; Thouless 1996). In this study, an inspection of the individual trends revealed that although numbers within all herds varied similarly in the wet and dry season, merging and splitting was most prominent within larger herds. Tighter ecological constraints may be felt more within larger clans and could lead to greater levels of disassociation within higher social units (Wittemyer *et al*. 2005) due mainly to an increase in intra-group competition (Altmann 1974; Jarman 1974). Seasonal effects within larger units have been previously documented and suggest that a paucity of resources may instigate competitive interactions, causing trade-offs in group size to occur (Western & Lindsay 1984; Wittemyer *et al*. 2005). In Hluhluwe-iMfolozi, the frequency of fission-fusion events within larger herds suggests that competitive pressures between individuals occur all through the year.

In contrast, smaller groups or family units may be small enough to avoid competition (Wittemyer *et al*. 2005) and splits may not then be necessary. Such groups might also be able to obtain the necessary resources within smaller home ranges when resources are abundant, while larger groups may need to travel further for the same gains (Olupot *et al*. 1994). In this study, the strong correlations between group size and home range size in both wet seasons might be linked to a period of resource abundance. Large aggregations of elephants have been known to occur in the wet season as a result of the abundance of food and water (Thouless 1996).

Divisions into smaller units could occur to alleviate the competitive pressures of foraging in a larger group, while merging may occur when a resource is locally abundant. The timing of fission-fusion events may also ultimately be linked to the persistent expansion or contraction of home ranges. Increasing the size of the home range, as observed for larger herds in Hluhluwe-iMfolozi in the wet season, may increase the chances of encountering more resources and be an alternate response to escalating competitive pressures between individuals.

For large mobile animals like elephants, dispersal between favoured areas may be the most effective strategy to regulate population density and resource availability (Jachmann 1988; Clobert *et al*. 2001) particularly in response to changing environmental conditions (Laws *et al*. 1975). Water and food resources especially are rarely evenly distributed, but rather occur in patches that are clustered or randomly scattered (Wiens 1989). Variation in seasonal rainfall patterns may modulate the availability of water over time and create temporary wetter or drier periods. In Hluhluwe-iMfolozi, an increase in rainfall leads to an increase in home range size within each wet season. Such range expansion with increasing rainfall has also been reported for other African elephant populations (Galanti *et al*. 2006) due mainly to an increase in the availability and quality of food and water resources.

A reduction of home range size with increasing rainfall has been observed by some authors (Jachmann 1983; Shannon *et al*. 2006) with smaller home ranges in areas of higher annual rainfall (Thouless 1996). In this study, increasing rainfall within each dry season did not cause a decrease in home range size but instead had no effect. This suggests that dry season rainfall is not a limiting factor of breeding herd home range size in Hluhluwe-iMfolozi and that other factors may be more influential at this time of year. Interestingly, a reduction in rainfall between consecutive dry seasons appears to be associated, albeit not significantly, with an increase in home range size. Although this could be a limitation of the small sample size, it is possible that a rainfall threshold may exist during the dry season (with a breakpoint between 70-100 mm) beyond which some herds respond by increasing the size of their home range. A more severe dry season in a wet savanna system may therefore result in localized patterns of spatial use similar to those observed in drier savannas (Young *et al*. 2009b) where elephants roam further during drier periods. The above patterns are contrary to previous work in wet savannas, which indicate that seasonal differences in home range size and spatial use are less pronounced compared to dry savannas (Loarie *et al*. 2009). I demonstrate that variation in rainfall can necessitate noticeably different movement responses by separate elephant groups, irrespective of whether they reside in wet or dry landscapes.

Animal distributions and spatial use has been linked to the quality (Wilmshurst *et al*. 1995; Zinner 2002) and quantity (Willems & Hill 2009) of food within the home range. Elephant are known to select areas of higher vegetation productivity (Young *et al*. 2009a) but in this study herds spent most of their time in areas of intermediate vegetation productivity, in both seasons. Intermediate NDVI values (0.5-0.6) were associated with riparian and thicket habitat in both seasons, while the highest NDVI values (0.7-0.8) were associated with scarp forest. The considerably higher use intensity of moderately green vegetation by elephants in the wet season in particular may therefore be linked to their spatial proximity to rivers during this time, and is further supported by the pattern of utilization presented in the distance to rivers analysis (> 60% of locations < 2km from rivers). Bottomlands support large quantities of highly palatable grasses and herbs that are especially favoured by elephants in the wet season (Osborn 2004; O'Connor *et al*. 2007). Vegetation productivity therefore appears to be a weak determinant of utilization intensity for elephant herds although they prefer areas with moderately green vegetation throughout the year. This result is in contrast with previous studies that have associated elephant spatial use with higher vegetation quality (Chamaille-Jammes *et al*. 2007; Wittemyer *et al*. 2007b; Young *et al*. 2009b).

Spatial use by water-dependent herbivores may be constrained by the distance that they can move away from water sources (Western 1975; Redfern *et al*. 2003; Smit *et al*. 2007). This may manifest itself as a piosphere effect (Lange 1969) and can be pronounced, especially when dealing with elephant (De Beer *et al*. 2006; Leggett 2006). In this study, the intensity of use for elephants was higher closer to rivers in both seasons and significantly higher within two kilometres of rivers in the wet season compared to the dry. Many other studies have shown a greater concentration of elephants or increased spatial use by elephants closer to rivers during the dry season (Galanti *et al*. 2006; Wittemyer *et al*. 2007a; Smit *et al*. 2007). None have shown a greater concentration in the wet season perhaps due to the fact that these studies have all been conducted in larger and drier areas. The wet season period is generally characterized by an increase in the availability and quality of food and water resources (Wittemyer *et al*. 2007a) and the preferential use of areas close to rivers might indicate selection for forage quality as well as shade (riparian and closed woodland habitat). An increase in the use of areas further from rivers in the dry season is probably a response to declining quality and availability of food necessitating wider foraging.

Aspects of spatial and structural heterogeneity such as vegetation patch size, shape and density are known to influence animal movement patterns in various ecosystems (Kie *et al*. 2002;

Nellemann *et al*. 2002). I concentrated specifically on how the size, shape and configuration of patches of the same and different vegetation types influenced elephant home range size. Decreasing home range size with increasing patch size may result in greater foraging efficiency and is consistent with Optimal Foraging Theory (MacArthur & Pianka 1966). Similar effects have been reported in a previous study on range use by elephants (Grainger *et al*. 2005). In contrast, other authors found no significant relationship between home range size and landscape heterogeneity but noted selection for specific areas of the landscape based on the same metrics (De Beer & van Aarde 2008).

My results suggest that especially in the dry season, elephants favour larger, irregularly shaped vegetation patches that are nearer together in space compared to widely separated, smaller patches of the same vegetation type. They may choose these patches to maximize foraging efficiency as these aspects may afford a greater surface area to search for food, while minimizing the cost of traveling between patches. Herbivores are known to prefer feeding in patches offering the best eating rates and may feed for extended periods of time in such patches to minimize energetic costs (Owen-Smith 2002). Such foraging patterns are also known to be especially prevalent in the dry season when herds attempt to maximize nutritional intake (Owen-Smith 1988) due to the scarcity of high quality food.

Recent studies have focused on predicting patterns of spatial use for entire elephant populations within protected areas and have produced management recommendations based on this (Chamaille-Jammes *et al*. 2007; Shrader *et al*. 2010). Some of these have found little or no spatial partitioning between elephant groups during the wet season, either as a result of greater resource availability or due to the size of the area (Wittemyer *et al*. 2007a). In addition, competition within elephant herds and knock-on effects on fission-fusion events and patterns of spatial use is poorly understood but may play a major role in smaller, fenced protected areas with high elephant densities. My results indicate variation in the intensity of spatial utilization between seasons and between herds within the same population, with evidence for widespread, even use in the wet season and more focused use in the dry season.

The clearly different patterns of utilization even in the wet season suggest that large populations within smaller, fenced areas may react to density-dependent factors. Rainfall and intra-group competition were the most likely factors driving the differential use of space, although distance to rivers and vegetation patch heterogeneity also explained seasonal patterns of use. Differential spatial use within elephant populations may accentuate the degree of impact on the ecosystem,

particularly so in small reserves where herds may utilize the same areas in consecutive years (Owen-Smith *et al*. 2006). My study emphasizes the importance of considering this when attempting to manage elephant impacts within fenced protected areas.

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**Table 2.1** Home range size over the two-year study, in each year and in each season and core size in each season for each herd in Hluhluwe-iMfolozi (core displayed in bold brackets). Herd 1 & 2 = RR herds; Herd 3, 4 & 5 = WR herds.

| Time Scale | Herd 1 | Herd 2 | Herd 3 | Herd 4 | Herd 5 |
|---|---|---|---|---|---|
| 2 Year | 463.1 | 383.6 | 673.9 | 447.7 | 488.7 |
| Year 1 | 370.8 | 321.1 | 417.7 | 268.9 | 309.5 |
| Year 2 | 352 | 348.2 | 606.1 | 499.3 | 511.9 |
| Wet 1 | (54.7)238.2 | (48.2)247.6 | (99.2)388.1 | (104.2)389.5 | (84.3)340.5 |
| Wet 2 | (89.6)333.2 | (75.6)272.3 | (118.2)482.1 | (115.6)459.1 | (105)384.4 |
| Dry 1 | (72.1)287.6 | (62.9)270 | (59.3)265.3 | (22.9)90.9 | (33)118.9 |
| Dry 2 | (57.9)251.3 | (71.6)305.9 | (43.5)222.6 | (49.7)199.2 | (65.7)276.9 |

**Table 2.2** A summary of landscape metrics employed to determine vegetation patch heterogeneity within elephant home ranges in Hluhluwe-iMfolozi

| Metric | Description | Interpretation |
|---|---|---|
| Largest patch index | A measure of the percentage of the total area covered by the largest patch | Decreases with increasing patch heterogeneity |
| Mean shape index | Measures the mean shape complexity of patches in a landscape | Increases with increasing patch heterogeneity (values <=1 are compact shapes; >1 are irregular shapes) |
| Mean nearest neighbour distance | Measures the mean straight line distance between patches of the same type | Increases with increasing patch heterogeneity (values approaching 0 indicate close spatial proximity) |
| Patch richness density | Measure of patch diversity based on number of patches per unit area | Increases with increasing patch heterogeneity |
| Shannon diversity | Measure of patch diversity based on number and size of different patches in the landscape | Increases with increasing patch heterogeneity |

[a] Based on descriptions by McGarical and Marks (1995) and Lang and Tiede (2003)
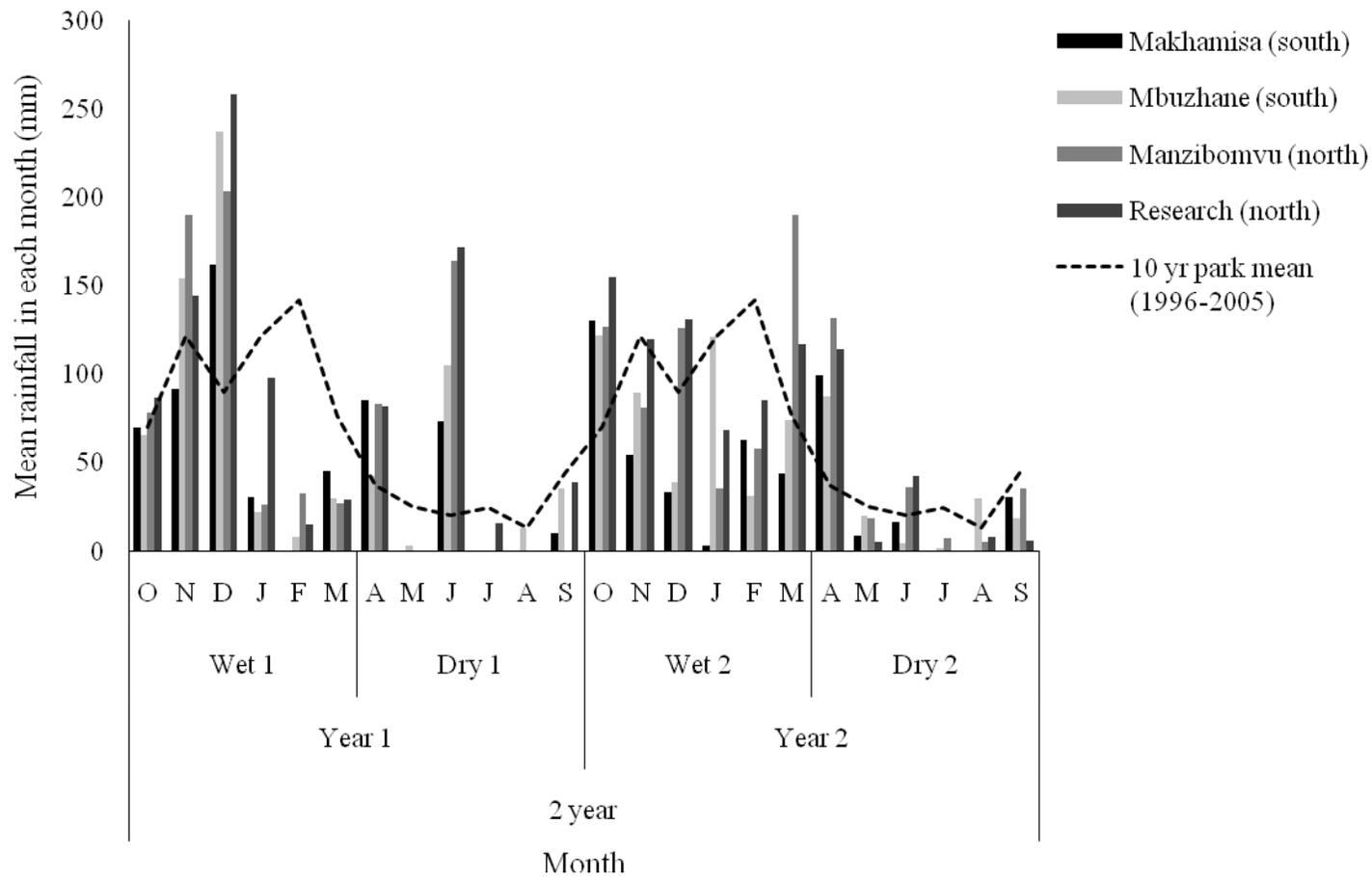
**Fig 2.1** Mean monthly rainfall at 2 south and 2 north stations in Hluhluwe-iMfolozi Park over the study period, in each year and in each season * Data is displayed from Oct 2006- Sep 2008 (Mean annual rainfall for HIP:  2006=846.4 mm; 2007=622.2 mm and 2008=555.8 mm based on the sum of total monthly rainfall at all 4 stations)
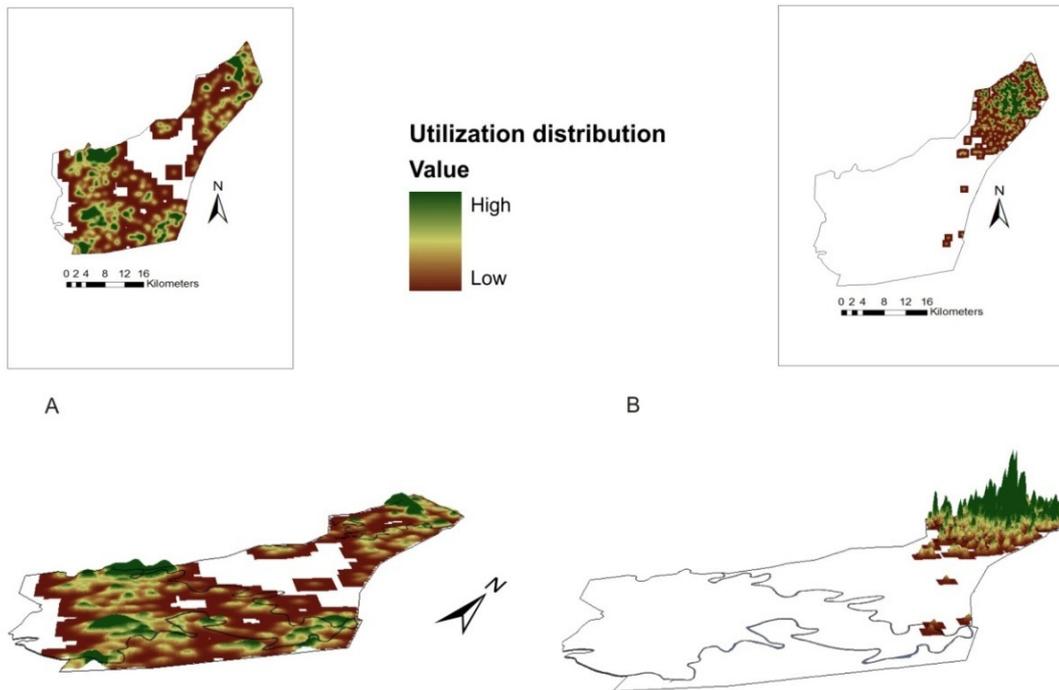
**Fig 2.2** Example of a wet season (A) and a dry season (B) utilization distribution for a wide-ranging (WR) herd as estimated by Least-squared cross validation kernel analysis (3-D representation showing peaks in the intensity of utilization in the core areas is displayed below each inset).
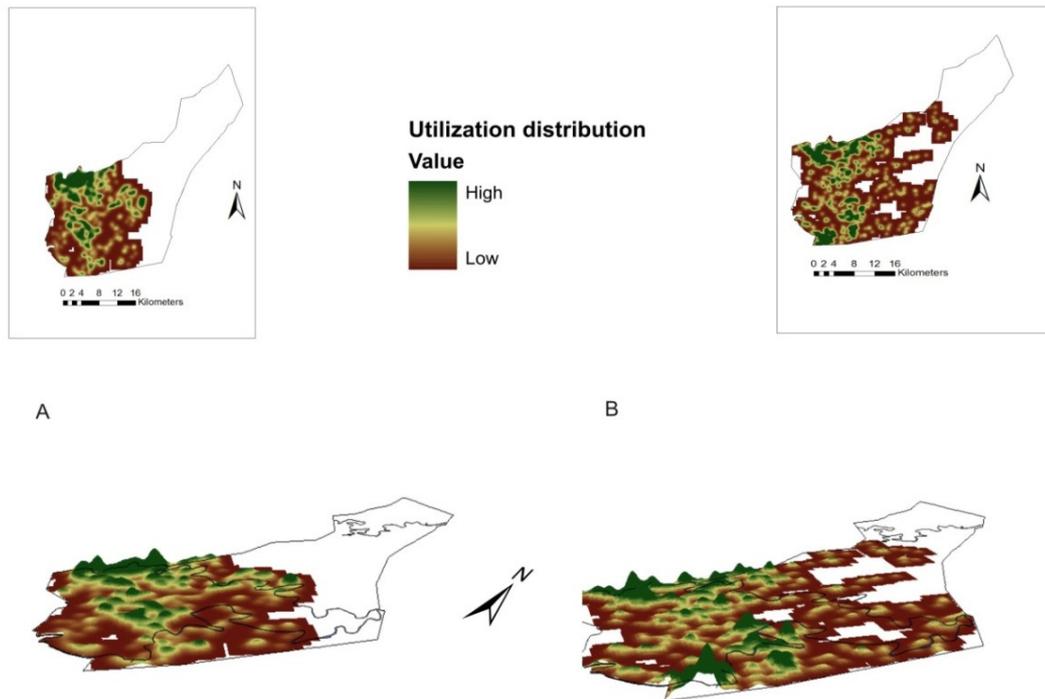
**Fig 2.3** Example of a wet season (A) and a dry season (B) utilization distribution for a range-restricted (RR) herd as estimated by Least-squared cross validation kernel analysis (3-D representation showing peaks in the intensity of utilization in the core areas is displayed below each inset).
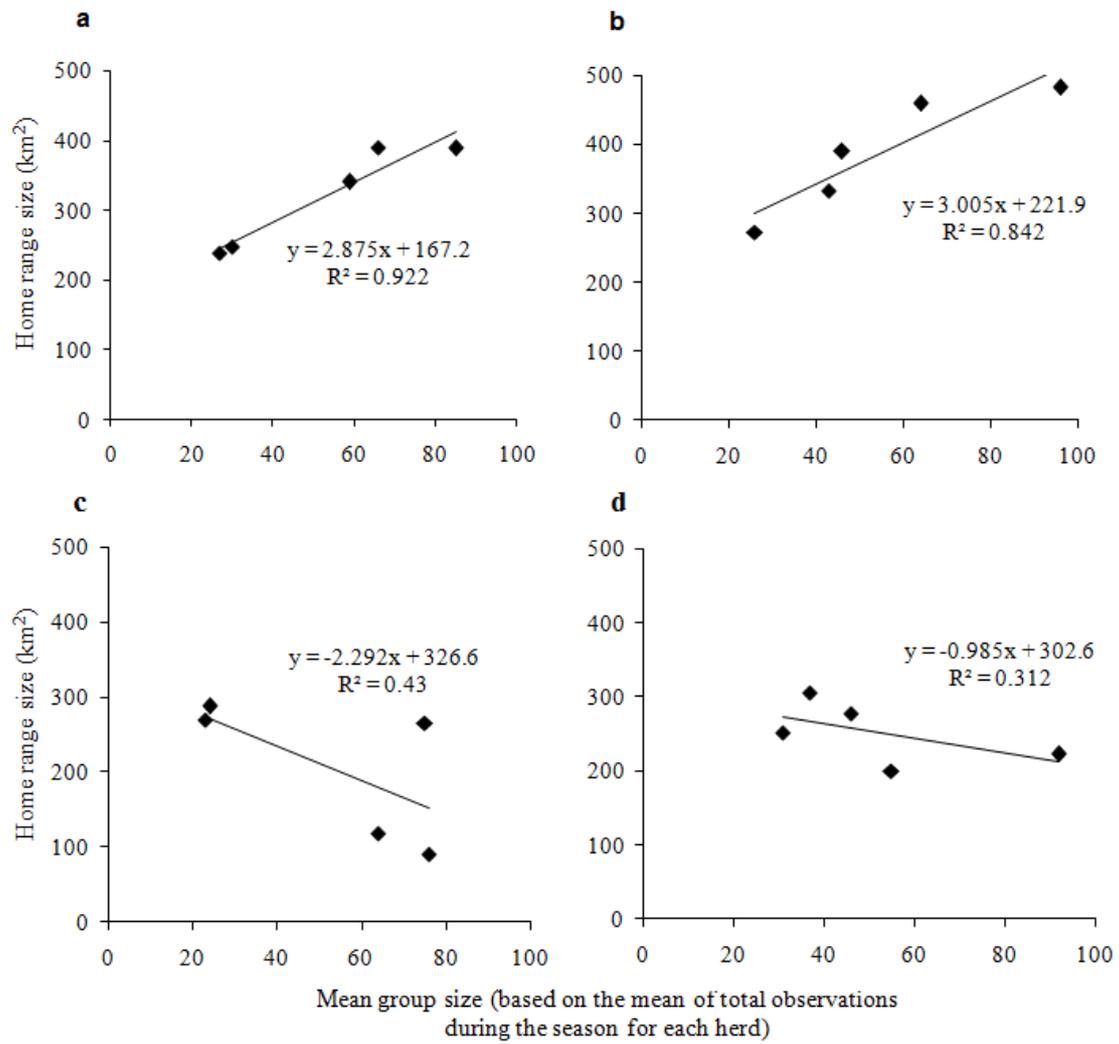
**Fig 2.4** Plots displaying mean group size against home range size for each herd in (a) Wet Season 1; (b) Wet Season 2; (c) Dry Season 1 and (d) Dry Season 2. Group sizes were calculated by averaging the totals from all counts ($> = 10$) during the 6-month wet period (Oct-Mar) and the 6-month dry period (Apr-Sep) in each study year.
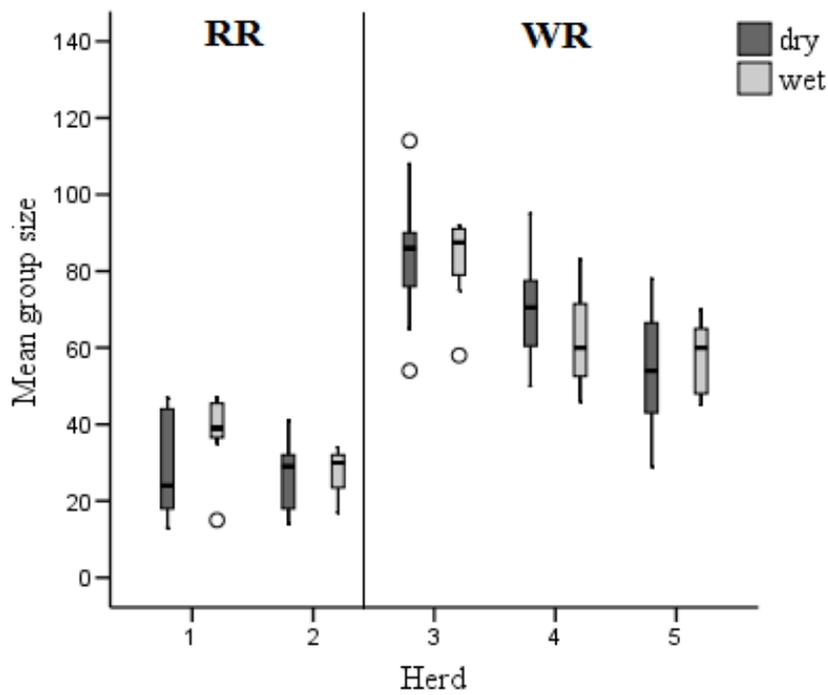
**Fig 2.5** Mean group size for each of five herds displayed for the wet and dry season. Plotted values represent the averaged total counts within the season for each of 2 wet and 2 dry seasons for each herd. The size of the herds over the study period in order of largest to smallest was: 3, 4, 5, 1 and 2.
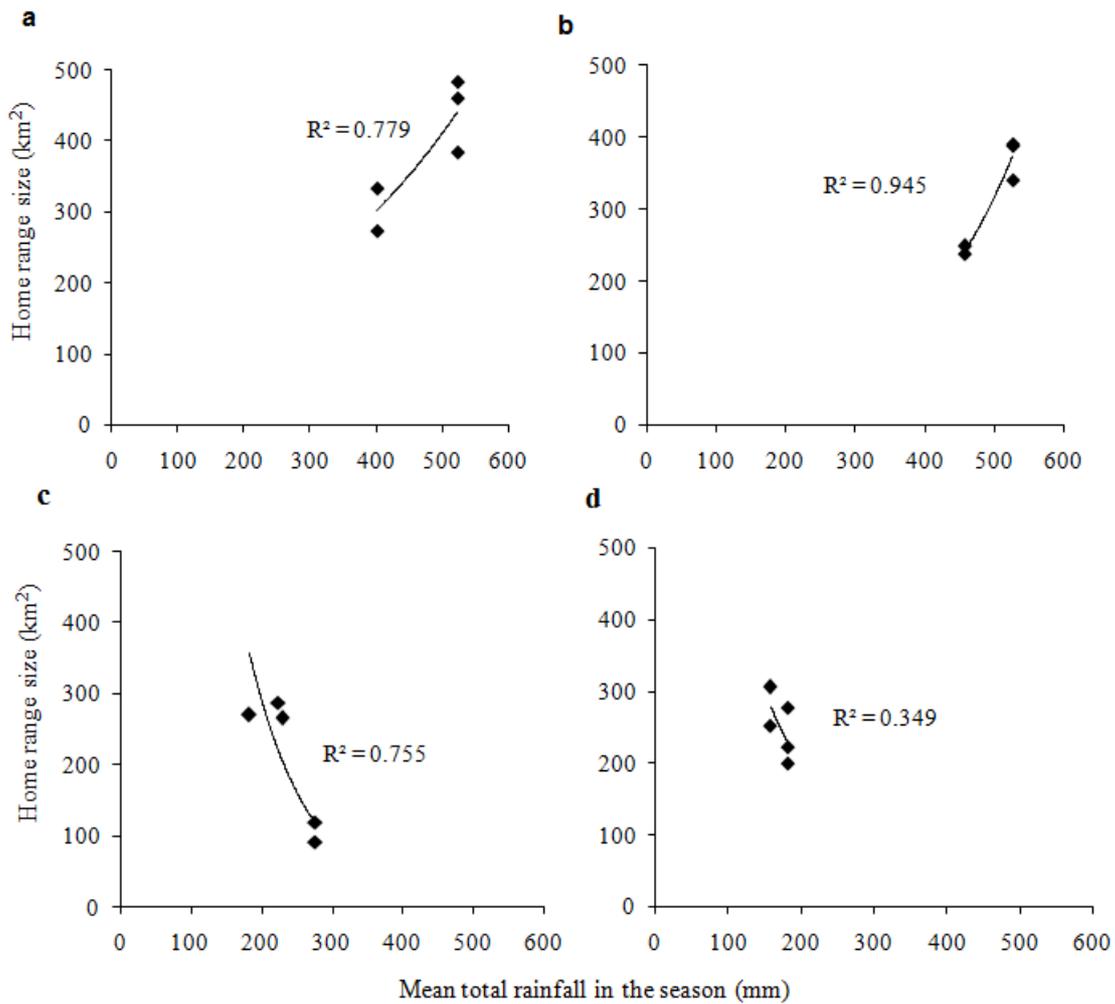
**Fig 2.6** Plots of home range size for five herds versus the mean total rainfall in each season for (a) Wet Season 1; (b) Wet Season 2; (c) Dry Season 1 & (d) Dry Season 2. Mean seasonal rainfall values were obtained by averaging the cumulative monthly rainfall at each station in the north (2), south (2) and park (4) from Oct-Mar for the wet season and Apr-Sep for the dry season. The values used reflect the location of each herd during that season (north, south or park).
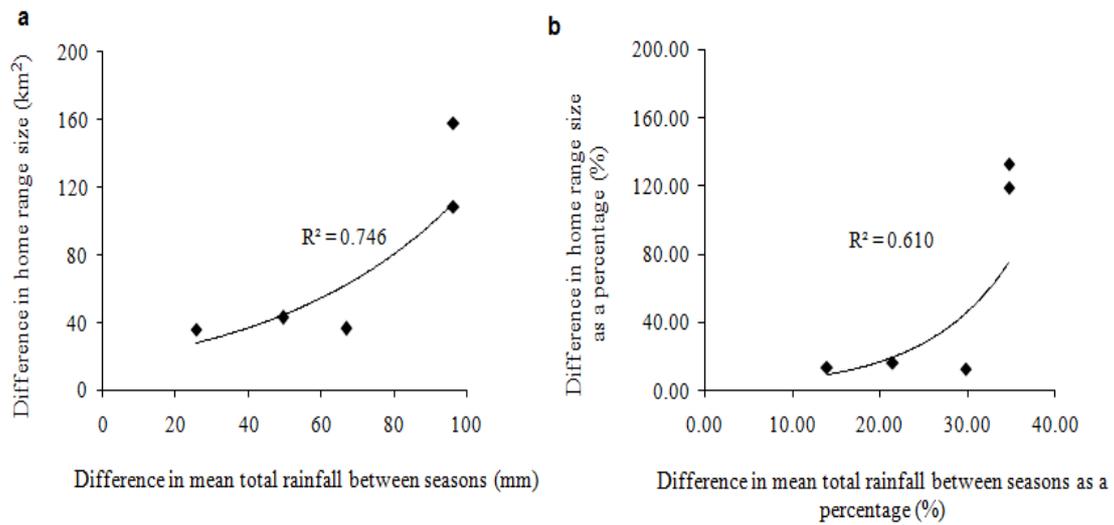
**Fig 2.7** Plots displaying a) the difference in home range size between two dry seasons versus the difference in mean total rainfall between each season and b) the difference in home range size between each dry season as a percentage of the size of the home range in the first dry season versus the difference in mean total rainfall between each dry season as a percentage of the mean total rainfall in the first dry season.
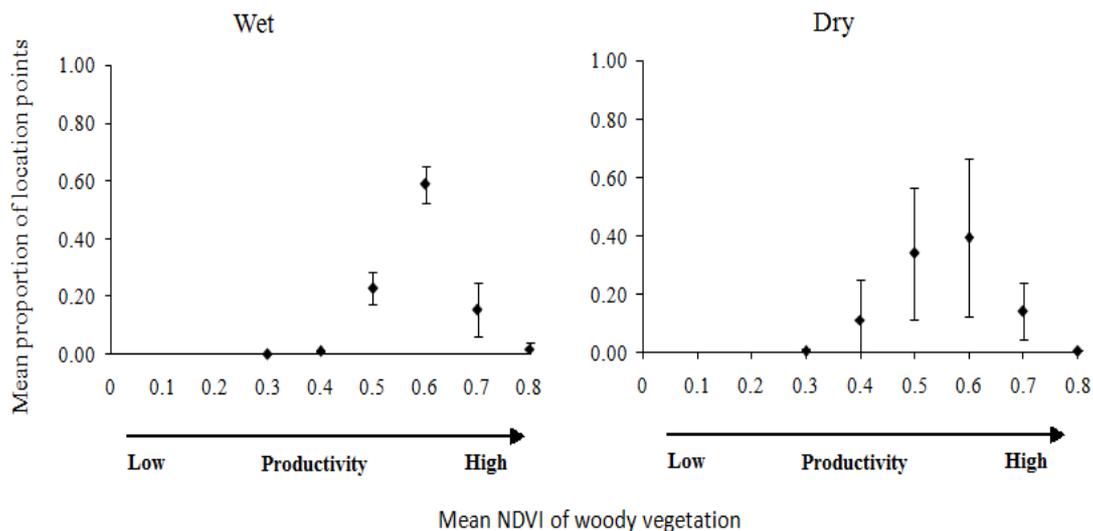
**Fig 2.8** Plot displaying elephant spatial use (based on the mean proportion of location fixes for all herds) in relation to vegetation productivity (represented by mean NDVI values) in the wet and dry season. Error bars depict standard deviation. Mean NDVI values were calculated by obtaining an average value for each grid-square across the park over a 3 month wet (Nov-Jan) and dry (May-Jul) season in each year.
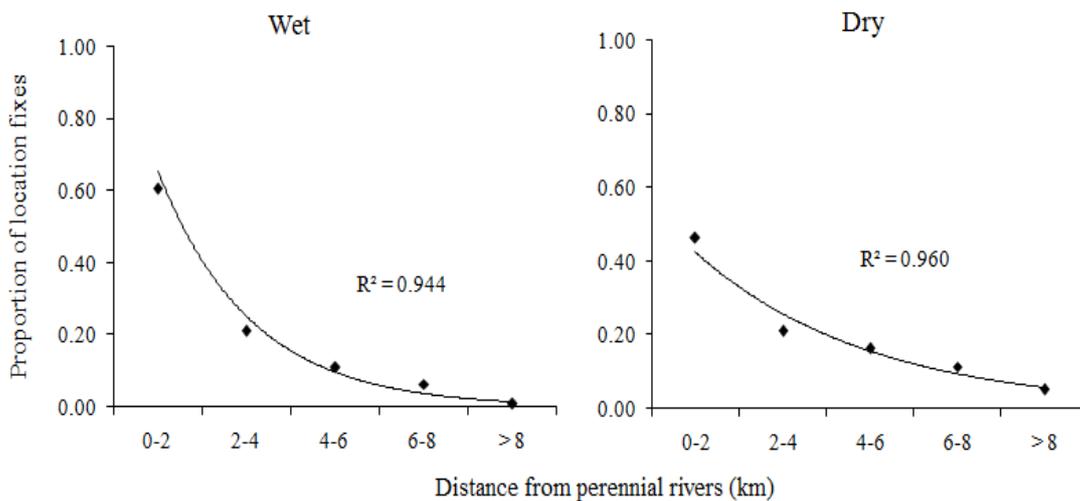


**Fig 2.9** Observed proportions of location fixes for all herds plotted to display spatial proximity to perennial rivers in the wet and dry season.
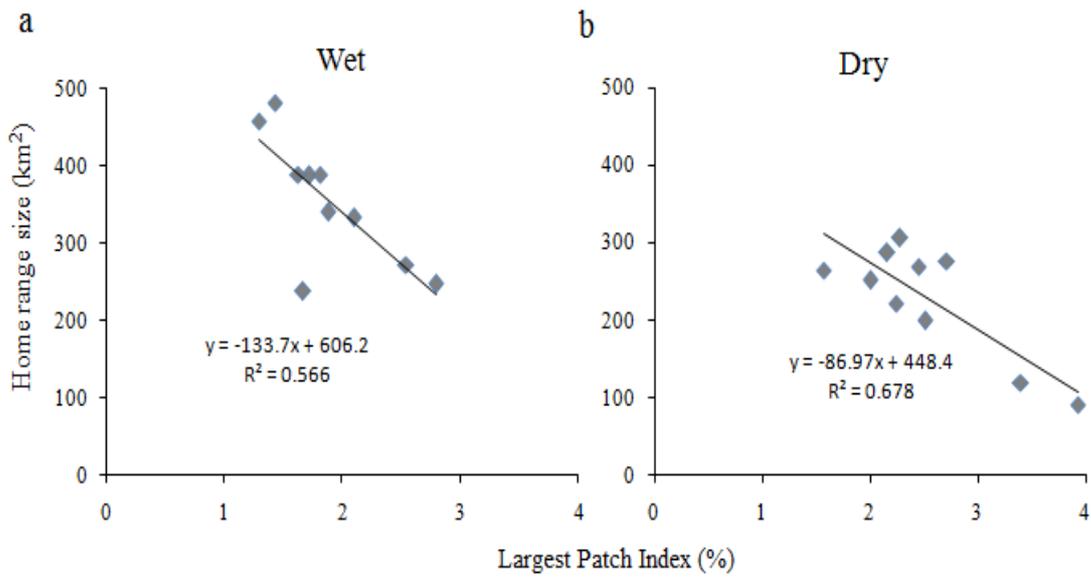
**Fig 2.10** Relationship between home range size and the largest vegetation patch index for each herd in the wet and dry season (based on data from 2 wet and 2 dry seasons).
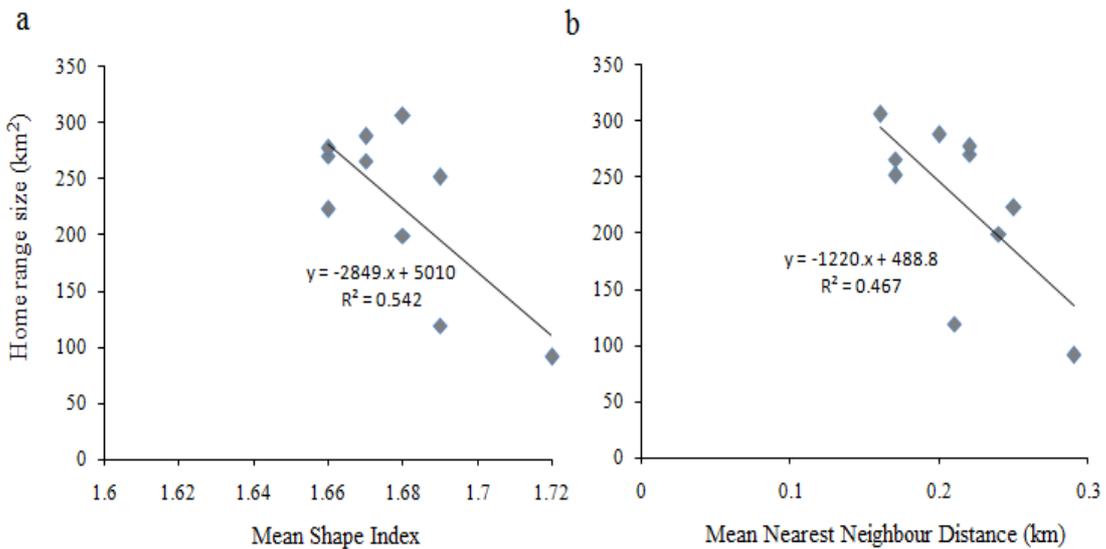


**Fig 2.11** Relationship between home range size and (a) the mean shape index of vegetation patches and (b) the mean distance between patches of the same vegetation type for each herd during the dry season (based on data from 2 dry seasons).

# Chapter 3

# Habitat preference by elephants determined from utilization intensity, path tortuosity and step length

## 3.1 Summary

The successful management of ecosystems requires that we understand patterns of habitat selection and movement by animals at different scales. Habitat selection and movement may become increasingly more flexible within spatially constrained environments or where habitats are highly fragmented. Using location data for five separate female herds, and spanning a two-year period, I explored differences in habitat preference by elephants in relation to seasonal vegetation productivity. I examined daily movement patterns within habitats in relation to the density of vegetation and determined the drivers of variation in movement over the course of a day. Elephant herds preferentially utilized greener habitat types over others in the dry season. Scarp forest and thicket habitat were intensively utilized in the dry season and scarp and riparian forest utilized in the wet season. Variation in daily movement responses was evident between herds and seasons. Elephants selected habitats with higher densities of certain favoured food species as reflected by path tortuosity, step length and diet selection. I argue that lower displacement rates in the early morning and evening are due to crepuscular foraging activity. Consistent with previous work on optimal foraging patterns, my results suggest that elephants prefer greener habitats in the dry season, concurrent with a diet focused on widespread woody species. This study indicates how animal movements can be used to evaluate the degree of utilization of specific habitats and highlights the need for managers of fenced protected areas to consider this when attempting to implement effective conservation practices.

## 3.2 Introduction

The successful management of biodiversity requires that we understand animal movements across different ecosystems and over a range of spatial and temporal scales. For example, insights on the factors determining movements are crucial towards our understanding of how processes such as climate change and habitat fragmentation influence distribution patterns (Nathan 2009). This is because ecosystems are generally patchy and tend to consist of heterogeneously distributed resources (Wiens 1989; Beyer *et al*. 2010). Spatial and temporal variation in the dispersion of resources across the landscape can dictate the movements of a species depending on their biological requirements at a given time (Mitchell & Powell 2004). Thus, movement patterns during times of resource scarcity can differ from those at times when

resources are widely distributed. Forage availability, habitat heterogeneity, surface water availability and the distribution of predators are among the variables that are known to influence animal movements (Matthews 2009; Smit *et al*. 2007; Kie *et al*. 2002; Willems & Hill 2009).

Natural and artificial barriers can also constrain animal movements at a large scale (McDonald & St. Clair 2004) by inhibiting the size of home ranges and dispersal routes. The biology of an animal combined with certain external factors can therefore drive repetitive or oriented movement behaviour (Wittemyer *et al*. 2008). This can be defined as repeated visits to the same area or directed movement towards a specific target. Animals may perceive and respond to these factors at different scales related to aspects of their behaviour (With *et al*. 1999; Nams 2005). The examination of larger temporal and spatial scales are useful in attempting to understand the broad spatial ecology of a species (Kie *et al*. 2002), while finer scales such as daily movement paths represent a short-term indicator of spatial use and affords a more precise evaluation of foraging strategy and food requirements (Garland 1983; Carbone *et al*. 2005).

Daily animal movement paths tend to consist of a series of relatively straight segments separated by turns (Dai *et al*. 2007). For many animals, daily path lengths are mostly short with a few longer distance displacements and turn angles are mostly small, with a few larger angles (Forester 2007). The complex nature of habitats and differing physiological requirements at different times of day or in different seasons can cause animal movement patterns to vary (Krebs & Davies 1997). This can result in animals travelling differently in different habitats over varying spatial and temporal scales (Nams 2005; Forester *et. al*. 2007). These differences can depend on the attractiveness of the habitat to the animal or the fulfilment of a particular physiological need. On a daily scale, movements may be slower or faster and more or less tortuous at particular times of day, in order to minimize energy losses by selecting for patches in the landscape where they will acquire the highest net gain (Krebs & Davies 1997; Morris *et al*. 2004).

Specific metrics can be employed to relate animal movement to the ecological context in which they occur and provide insight into behavioural decisions at the landscape scale, e.g. foraging versus water requirements (Getz & Saltz 2008; Nathan *et al*. 2008). The fractal dimension of a path segment (Mandelbrot 1983) and step length (the distance between two consecutive points) are two such metrics and they represent a simple way of examining animal movement patterns at finer scales (Doerr & Doerr 2004). Fractal dimension is a measure of path tortuosity and relates the total length of a path to the maximum possible area a path can fill based on step

length and turn angle (Loureiro *et al.* 2007). Fractals can reflect the intensity of the search for food by an animal (Nams 2005; Calenge *et al.* 2009). More tortuous paths within a habitat can indicate repetitive movement (Nams & Bourgeois 2004) and therefore the favourability of that habitat (Imre 2009). Similarly, step lengths measured at equal intervals are directly related to the speed of displacement of an animal (Morales *et al.* 2004). Rates of displacement and tortuosity can therefore represent movement modes e.g. travelling versus settlement (Owen-Smith *et al.* 2010). Recent studies have employed such measures to successfully describe animal movement patterns (Loureiro *et al.* 2007; Wittemyer *et al.* 2008; Van der Waal & Rogers 2009; Laporte *et al.* 2010).

Movement modes can be used to infer biological activities or the favourability of conditions within habitats (Owen-Smith *et al.* 2010). This can be deduced from the specific time of day when animals perform a particular activity and if the time between locations is sufficiently short (Fryxell *et al.* 2008). Animals tend to forage during the early morning and late evening and rest during the heat of midday and for much of the night (Owen-Smith 1988). Low displacements and high path tortuosity are indicative of restricted-area searching and can reflect intensive foraging behaviour (Johnson *et al.* 2002; Philips *et al.* 2004; Fryxell *et al.* 2008). Resting is indicated by immobility and therefore very low displacement rates (Owen-Smith *et al.* 2010). By relating the type of activity performed to actual resource requirements (e.g. food versus water) one can formulate an idea of how an animal might maximize foraging. Theories of optimal foraging predict that animals should forage selectively and more repetitively in resource-rich patches (Webb *et al.* 2009) particularly when there are greater energetic constraints, such as during the dry season (Stephens & Krebs 1986; Wittemyer *et al.* 2008).

Generally, individuals do not select habitats at random, but display a preference for certain types and occupy them more often than would occur with random movement (Rosenzweig 1981). This active selection is an adaptive behaviour that increases fitness (Weins 1989; Thomas & Taylor 2006). Habitat selection studies quantify the availability of habitats used by animals (Thomas & Taylor 1990; Manly *et al.* 2002) and usage is defined as selective if animals use a habitat more than predicted by random movement (Alldredge & Griswold 2006). Factors known to influence animal habitat selection include competition, prey availability, resource abundance, vegetation productivity and the density of cover (Apps 2001; Spong 2002; Fortin *et al.* 2003; Fritz *et al.* 1996; Slauson *et al.* 2007).

Habitat preferences determined by estimating frequencies of occurrence of animals in different habitats from random samples lack statistical precision (Jacobs 1974; Alldredge & Ratti 1986). A suitable alternative is to quantify use for each habitat type using kernel estimated utilization distributions obtained from telemetric data as a measure of the estimated probability of use (Kernohan *et al*. 2001; Millspaugh *et al*. 2006). By quantifying the intensity of use and relating this to habitats, one can derive a weighted probability of selection per habitat type. A given individual's utilization distribution, if calculated at the appropriate scale can be related to any resource in a spatially explicit manner (Marzluff *et al*. 2004) and reflects selection from the animal's point of view. The criteria for selection and use vary according to the geographic range of the species, home range of individuals, daily movement paths or actual forage selection (Johnson 1980) and studies examining more than one scale are not uncommon. Identifying the scale at which specific resources influence movement decisions is critical for the conservation of ecosystem heterogeneity and animal populations (Chalfoun & Martin 2007).

Differences in movements, habitat selection and foraging strategies have been observed in many species (Spong 2002; Boyce *et al*. 2003; Macdonald & St Clair 2004). Large herbivores are particularly well studied due to their ability to modify the structure and function of ecosystems and the potential impacts of this on biodiversity (Owen-Smith 1988; Fritz *et al*. 2002; Sankaran *et al*. 2008). This ability is linked to the metabolic demands associated with body size and digestive physiology (Bell 1971; Jarman 1974). Ungulate species belonging to smaller size classes such as klipspringer or suni are restricted by the quality of plants they can consume and therefore have very specific habitat requirements (Du Toit & Owen-Smith 1989; Skinner & Chimimba 2005). These species have become habitat specialists due to their lower energy demands and narrow dietary tolerance. As a consequence of mass-specific metabolic requirements and the passage rate of food, large herbivores generally have a wider dietary tolerance and are often habitat generalists (Du Toit & Owen-Smith 1989). Habitat selection among large herbivores often broadens over time due to their wider dietary tolerance (Owen-Smith 2002) and they are more restricted by the availability rather than the quality of food (Jarman 1974; Geist 1974). Consequently, highly mobile megaherbivores such as giraffe and elephant may use a disproportionately larger share of resources (Bond & Loffell 2001; Kerley *et al*. 2008) and have a greater impact on the habitats they occupy compared to species in smaller size classes.

African elephants are well-adapted to a wide range of habitats, from deserts (Viljoen & Bothma 1990) to forests (Tchamba 1995). They are classified as a water-dependent species (Western

1975) and may drink on a daily basis in arid regions (De Beer *et al*. 2006). Studies of elephant populations have revealed extensive seasonal and spatial variation in habitat selection and home range size (Viljoen 1989; Lindeque & Lindeque 1991; Babaasa 2000; Shannon *et al*. 2006). Crucially, elephant populations are increasing over most of southern Africa (Blanc *et al*. 2007) and their capacity as "ecological engineers" (Jones *et al*. 1994) is a major concern in fenced protected areas. They can significantly transform habitats by changing vegetation structure and composition (Cumming *et al*. 1997; Skarpe *et al*. 2004), assisting tree recruitment through seed dispersal (Kerley & Landman 2006) and promoting landscape level fragmentation (Hoft & Hoft 1995). Restrictions to movement can confine elephants to certain habitats and exacerbate adverse effects on faunal and floral assemblages (Wiseman *et al*. 2004; Botes *et al*. 2006; Mackey *et al*. 2006).

Differential use of habitats by elephants has been documented frequently (Short 1983; Tchamba 1993; De Boer *et al*. 2000) and often appears to coincide with seasonal changes in food availability and vegetation productivity (Babassa 2000; Codron *et al*. 2006; Young *et al*. 2009a). It has also been attributed to the distribution of water and forage and the presence of artificial barriers (Loarie *et al*. 2009; Young *et al*. 2009a; Vanak *et al*. 2010) and the abundance of favoured food species across the landscape (Tchamba & Seme 1993; De Boer *et al*. 2000; Steyn & Stalmans 2001; Gadd 2002). Large herbivore diets often consist of a wide range of forage species (Owen-Smith & Novellie 1982) and elephants may be expected to spend large amounts of time searching for these items. Few studies however, have attempted to explicitly relate daily movements to the abundance of preferred species within habitats. The specific influence of species-level utilization on foraging patterns and habitat selection therefore remains uncertain.

Non-random movements by elephant may be associated with optimizing foraging strategies at times when food and water resources are limited or widely separated in the environment (Dai *et al*. 2007; Wittemyer *et al*. 2008). Movements during the wet season at a time of resource abundance may then be expected to differ from those during the dry season when resource patches are more aggregated (Mitchell & Powell 2004). Some researchers have examined elephant habitat selection at larger spatial and temporal scales (Galanti *et al*. 2006; Shannon *et al*. 2006) and at least one has investigated activity budgets over the course of a day (Shannon *et al*. 2008). However, the determinants of habitat selection by elephants are not well understood and few studies have examined the factors influencing daily movements within habitats. Furthermore, no studies on elephant that we know of have attempted to link daily movement

responses with foraging behaviour. An understanding of the factors influencing daily elephant movements and habitat selection is essential to make informed decisions for the management of biodiversity in fenced protected areas.

My overall aim was therefore to determine if elephant herds displayed a notable preference for specific habitat types in terms of rates of occupancy, and to determine if these preferences were reflected by variation in movement characteristics (step length and tortuosity). I expected to explain these preferences in terms of vegetation productivity (greenness), density of preferred species, seasonality, time of day, distance to water and the proportion of habitat types in the home range. I predicted paths to be more tortuous and displacements lower in the dry season (due to resource aggregation) and to be more linear and displacements greater in the wet season (due to resource abundance). I predicted low displacements in the early morning and evening, known foraging times. I also expected elephants to be less mobile during the hottest time of day and predicted displacement rates to reflect this. I expected path tortuosity to increase and displacement rates to decrease within favoured habitat patches and when the density of preferred species was higher. Lastly, I predicted that elephants would choose to remain closer to perennial water sources in the dry season and predicted displacement rates to decrease at this time. I discuss the implications of differential habitat use for the conservation of sensitive habitats and biodiversity in fenced protected areas.

**3.3 Methods**

*3.3.1 Study Site*

Hluhluwe-iMfolozi Park covers an area of roughly 900 km$^2$ (90 000 ha) in northern Kwa-Zulu Natal between 28°00 - 28°26 S and 31°43 - 32°09 E. Altitude ranges from 40 to 590 m above sea level. Rainfall is highest in the far north (950 mm/pa) and lowest in the far south (600 mm/pa) based on a 25-year long-term mean (EKZNW, unpublished data). Three main rivers flow through the park, the Hluhluwe River in the north and the Black and White iMfolozi Rivers in the south. There are no artificial water sources in the park. Shales and sandstones from the Ecca and Dwyka groups and belonging to the Volkrust, Vryheid and Pietermaritzburg formations characterize the geology of most of the park, while some dolerite, basalt and alluvium is also present in the south (King 1970; Downing 1980). Swartland and Shortland are the main soil types in the north, while shallow Mispah and Glenrosa forms dominate much of the south (Mucina & Rutherford 2006).

*3.3.2 Vegetation*

As a result of variation in rainfall, geology, soil types, topography and burning, the vegetation is highly heterogeneous (Whateley & Porter 1983). Three broad veld units occur in Hluhluwe-iMfolozi Park: Scarp Forest, Northern Zululand Sourveld and Zululand Lowveld (Mucina & Rutherford 2006). Scarp forest patches occur at higher altitudes in the far north of the park on wetter south-facing slopes. Much of the north is comprised of Northern Zululand Sourveld while the remainder of the park falls within the Zululand Lowveld veld unit. Sixteen woody plant communities are recognized by Whateley & Porter (1983). I merged similar types from Whateley and Porter's 1983 community classification to produce six structural habitat types (Fig. 3.1). These were: 1) Closed woodland, dominated by *Spirostachys africana, Acacia grandicornuta* and *Berchemia zeyheri*; 2) Open woodland, dominated in the south by *Acacia tortilis* and *Acacia nigrescens* with *Acacia burkei* and *Sclerocarya birrea* communities occurring throughout the park and *Combretum* woodland on hill slopes; 3) Wooded grassland, dominated by *Dichrostachys cinerea, Acacia karroo, Acacia gerrardii, Acacia nilotica* or *Acacia caffra* in different areas; 4) Riparian forest, dominated by *Acacia robusta, Phoenix reclinata, Ficus sycamorus*, and *Schotia brachypetala*; 5) Scarp forest dominated by *Englerophytum natalense, Euclea racemosa, Celtis africana, Harpephyllum caffrum, Albizia suluensis* and *Commiphora harveyi* and 6) Thicket dominated by *Euclea divinorum, Euclea racemosa, D. cinerea, S. africana, Brachylaena ilicifolia* and *A. karroo*.

### 3.3.3 Herbivore guild

About 500 elephant are found in the park in 2010 together with most fauna typical of southern African savanna systems. These include large herbivore species indigenous to the area such as white (2312) and black rhino (198), buffalo (4789), zebra (2749), blue wildebeest (3002), impala (14 074), hippopotamus (20) and kudu (717) as well as introduced herbivore species such as giraffe (874) and nyala (4082). Estimates from the annual game count in 2010 are given in brackets.

### 3.3.4 Description of collared herd spatial use and data collection

GPS collars were fitted to the matriarchs of five different herds during October 2006. Two of these females (Herds 1 and 2) were collared in the south of the park and the other three (Herds 3, 4 and 5), in the north. Matriarchs tend to dictate movement and spatial use (Moss 1988) and collaring the matriarch in a group should ensure that any location data obtained is representative of that group (Wittemyer *et al*. 2007). I was able to differentiate two distinct patterns of spatial use among collared herds and also determined the mean group size plus standard deviation (in brackets). Herd 1 (34 ±12.6 SD) and Herd 2 (27 ±8.5 SD) maintained small home ranges in the south of the park in both seasons. Home ranges were seasonally variable in size and were utilized more intensely in the dry season. In contrast, home ranges for Herd 3 (86 ±18.7 SD), Herd 4 (67 ±12.9 SD) and Herd 5 (55 ±13.5 SD) spanned most of the park in the wet season but were concentrated in the north in the dry season. Wet season home ranges consisted of large core areas of high intensity use while dry season home ranges consisted of small core areas of higher intensity use.

For the purposes of this study, Herds 1 and 2 were called range-restricted (RR) herds and Herds 3, 4 and 5 wide-ranging (WR) herds. Position data were obtained every 30 minutes and the accuracy was within 10 metres. For the purpose of determining seasonal differences, the wet season was defined as October 1 to March 31 and the dry season from April 1 to September 30, based on rainfall records. Selecting an equal period of time ensures that kernel estimates were not biased by the number of fixes. I calculated the home range and utilization distributions (Worton 1989) using five locations per day at more or less even intervals. This reduces spatial autocorrelation in the data set without removing it completely. Complete removal of spatial autocorrelation from data has been shown to incur a loss of crucial information and compromise the accuracy and validity of actual space use (De Solla *et al*. 1999; Cushman *et al*. 2005).

## 3.4 Analysis

### 3.4.1 Habitat preferences in different seasons

I used a utilization distribution-weighted intensity of use over the home range of each group (Worton 1989) to determine preference for different habitat types in separate wet and dry seasons. I used the least-squared cross-validation (LSCV) fixed kernel density estimator within the Home Range Tools Version 1.1 add-on package to ArcGIS 9.3 (Rodgers *et al*. 2007) to determine home range (95%) and core (50%) isopleths and the utilization distributions for each of the five collared elephant herds. The LSCV home range estimator converts Cartesian point locations into a three-dimensional probability density surface termed as the utilization distribution (Willems & Hill 2009). The height of the utilization distribution at a given point indicates the relative probability of use of space within the home range and is determined by the concentration of location points (Marzluff *et al*. 2004) at a particular spot. I used ArcGIS 9.3 and Hawths Spatial Analysis Tools (Beyer *et al*. 2004) to overlay the utilization distributions on a map of the six structural habitat types. I defined the spatial extent of utilization as the 95% isopleth boundary (hereafter referred to as home range) as habitat preferences are more accurate when considered over the full area of the home range (Aberg *et al*. 2000; Burnham & Anderson 2002).

I used the utilization distribution output to calculate use intensity values for separate habitat types within the home range of each herd and employed a compositional analysis (Aebischer *et al*. 1993) to determine selection or avoidance of different habitat types for each of the five elephants in the two wet and two dry seasons separately. Compositional analysis allows for consideration of differential habitat use by individuals (Aebischer *et al*. 1993; Erickson *et al*. 2001) and is appropriate whether availability is estimated or known (Alldredge & Griswold 2006). I used the COMPANAL Microsoft Excel-Plug-in for Windows (Smith 2004) to conduct the analysis. The Chi squared statistic with alpha = 0.05 was used for significance tests. Zero use and availability values were substituted with 0.01 (Aebischer *et al*. 1993) to avoid division by zero errors. Scarp and riparian forest habitats were merged into one habitat called forest for this initial analysis as COMPANAL can only accommodate a number of habitats less than or equal to the number of samples (collared herds). Forest was split into the two functionally distinct types (riparian and scarp) for all subsequent analyses.

*3.4.2 Daily movements in different habitats in different seasons (Path tortuosity and step length)*

I examined a series of movement path segments for each collared female in each season. This was done in order to obtain a representative and non-biased sample of paths of the same time length for statistical comparison. Path segments were chosen from within a 24-h time block beginning at midnight and ending at 23:30 pm, and consisting of points every 30 minutes. This period was chosen to allow for a long enough time period (years) of data collection without extra animal stress involved with re-collaring but was also to avoid oversampling effects. Sequential movement lengths of an elephant herd have in the past been shown to be autocorrelated at intervals of less than 20 minutes (Dai *et al*. 2007) and 30 minute intervals was therefore deemed safe to avoid the effects of temporal autocorrelation. I calculated the fractal dimension (D) (Mandelbrot 1983) of a path segment as a measure of the tortuosity of that path using the equation: D = log (n) / (log (n) + log (d/L)), where n is the number of line segments that make up the path, d is the straight line distance between the start and end points of the path, and L is the total distance travelled (Loureiro *et al*. 2007; Matthews 2009).

I addressed criticisms on the use of fractal dimensions (Turchin 1996) by sampling only path segments of equal time lengths (same number of location fixes) in different habitats. Path segments were overlayed with a structural habitat type GIS layer for the park. I extracted step length and tortuosity values for each path within each habitat type in the wet and dry season separately using Hawth's Spatial Analysis Tools in ArcGIS. I calculated mean path tortuosity and mean step length for each habitat in each season to determine whether herds moved differently in different habitats and between wet and dry seasons. Step length and tortuosity data were not normally distributed and we used $\log^{10}$ transformations to meet the assumptions of a parametric analysis. Comparisons of path tortuosity and step length among individuals and between habitats and seasons were conducted using separate 2-way ANOVA statistical tests with LSD or Bonferroni correction for multiple comparisons ($p<0.05$).

*3.4.3 The influence of time of day, habitat type and distance to water on displacement rates*

I used the Akaike Information Criterion (Akaike 1974) in the Generalized Linear Model framework of SPSS Version 18.0 to determine temporal, seasonal and herd effects on variation in step length and investigated the influence of time of day, habitat type and distance to water on displacement rates in different seasons. To test a priori hypotheses on links between elephant movements and behaviour and the diurnal variations in these behaviours, I considered variation

in step length as the response variable. I examined daily movement paths during three distinct periods of day (each covering a 4-hour period) established by other studies as representing distinct activities: (i) morning (2-6am) as a foraging period, (ii) midday (10am-2pm) as a resting period and (iii) late evening (8pm-12pm) as a foraging/sleeping period (Owen-Smith 1988; Owen-Smith *et al.* 2010). I sampled approximately 35 path segments (of equal time length) at each time of day over a wet and dry season for each herd and calculated the mean half-hourly step length during each time of day. The proportions of different habitats along the same paths were examined to assess whether the presence and coverage of specific habitat types influenced displacement rate. Lastly, I calculated the distance from each path segment to the nearest perennial water sources and examined the relationship between step length and distance to water over the course of the day. The Spatial Analyst line intersect function in ArcGIS uses the midpoint of a line segment to generate a distance value from the source. The response variable (mean step length) was not normally distributed and we used the log function to log-transform the data and meet the assumptions of a parametric analysis. Habitat proportions were also arcsine transformed to meet the assumptions of a parametric analysis.

I developed a global model that included the following: season (wet and dry), time of day (morning, midday and evening) and herd (wide-ranging and range-restricted) as main effect parameters; habitat proportions (the proportion of each habitat type along a path) and distance to water (the shortest linear distance from the midpoint of the path to a river) as covariates, and interaction effects between these factors and covariates. For subsequent models, I excluded non-significant parameters in a stepwise fashion and analyzed the remaining factors. On the basis of corrected Akaike Information Criteria ($AIC_c$) selection criteria I compared different models in order to determine the best predictors of elephant movement patterns. I ranked models according to $\Delta AIC_c$ values and model weights ($w_i$) and accounted for model uncertainty by standardizing parameter coefficients and standard errors in models with $AIC_c < 2$ (Burnham & Anderson 2002). All statistical analyses were conducted in SPSS Versions 15.0 and 18.0 and ArcGIS 9.3.

### 3.4.4 Seasonal vegetation greenness within habitats

To question whether habitat use was associated with the "greenness" of woody vegetation in each habitat I obtained SPOT NDVI data for the period January 2006 - January 2009 from the VGT4AFRICA project. Data were scaled at 250 m resolution with NDVI values calculated using 16-day composite images. Mean NDVI values were obtained for each habitat in two wet and two dry seasons by calculating the mean of the summed values of each grid cell extracted

for each habitat in the park over the three wettest months (Nov/Dec/Jan) and the three driest months (May/Jun/Jul) in each season respectively. Mean NDVI and standard deviation for each habitat type in wet and dry seasons are plotted. I employed a two-way ANOVA with vegetation productivity (NDVI) as the dependent variable and habitat and season as factors and performed Tukey post-hoc tests to assess seasonal variation in vegetation greenness between habitat types. Interaction effects between season and habitat type were tested.

### 3.4.5 Diet selection and the influence of vegetation density on movement patterns

The main woody species comprising the bulk of the diet of breeding herds were determined by examining individual feeding records over the two-year study period. A total sample of 236 records was obtained via direct observations by myself of breeding herds over the course of the two years. Data collection was done along roads and therefore habitats restricted to inaccessible areas of the park (e.g. scarp forest patches along high ridges) were not as well sampled compared to more widespread habitats. More samples were also collected from the larger, more visible herds that roamed across the park rather than the infrequently encountered smaller groups in the south. A total of 154 samples were obtained during the dry season and 82 in the wet season and the proportional contribution of each species to the diet calculated for each season. The discrepancy in sample size is due to the fact that a large proportion of the diet ($>=$ 50%) in the wet season consisted of grass and herbaceous vegetation.

In order to determine vegetation density within each habitat, I examined woody vegetation utilization records from a long-term dataset gathered in three separate surveys (1999, 2003, 2007) and assessing elephant impact on vegetation (EKZNW, unpublished data). Woody vegetation was sampled along the length of a 50 m line transect and in different height classes based on the area of the transect (100 $m^2$ for 0.5-1 m height class; 250 $m^2$ for 1-2 m height class; 500 $m^2$ for 2-4 m height class; 1000 $m^2$ for > 4 m height class). I extracted only the species abundance data as we were interested in vegetation density and not utilization. I focused on trees of 1 m to 4 m in height as I expected this to be the main height class targeted by breeding herds. By multiplying the total transect area ($m^2$) sampled by the number of transects within each habitat I determined the total area sampled in square metres for each habitat type. I then calculated the density of all tree species per square metre for each habitat type and multiplied this by 10,000 to give the density of trees per hectare.

To assess the link with daily movement patterns, densities per hectare of some of the most favoured species (Table. 3.4) were extracted for each habitat type and plotted against mean path

tortuosity and mean step length within each habitat type. The tortuosity and step length values used for each habitat were determined in the movement path analysis (Fig. 3.2 & 3.3). This was done for each species individually and for the total density of favoured species for each habitat separately. I plotted only species that represented 4 % or more of the diet in both seasons (Table. 3.4). Mean path tortuosity (wet and dry season combined) and mean step length (wet and dry season separately) versus tree density are compared for each habitat.

## 3.5 Results

### 3.5.1 Habitat preferences in different seasons

The compositional analysis ranked forest (riparian and scarp combined) as the most preferred habitat in all seasons (Table. 3.1), significantly so in Wet 2 ($p$=0.03), Dry 1 ($p$=0.04) and Dry 2 ($p$=0.03). Wooded grassland was the next most preferred habitat in the wet season while thicket was avoided in preference for other habitat types during this time (Table. 3.1). By contrast, thicket selection increased considerably in the dry season and particularly in Dry Season 1 ($p$=0.04) whereas closed woodland was avoided in preference for other habitats at this time (Table. 3.1).

### 3.5.2 Daily movements in different habitats in different seasons

#### 3.5.2.1 Path tortuosity

Path tortuosity differed significantly between habitats (ANOVA $F$=2.598; $df$=5; $p$=0.024). Pair-wise comparisons after LSD correction revealed significant differences at $p<0.05$ between scarp forest and closed woodland ($p$=0.039), scarp forest and open woodland ($p$=0.012) and scarp forest and thicket ($p$=0.018), with scarp forest tortuosities being higher in all cases. Significant differences were also detected between riparian forest and open woodland ($p$=0.013) and riparian forest and thicket ($p$=0.041), with higher tortuosities in riparian forest. Overall, mean tortuosities were highest in scarp (1.70 ± 1.54 SD) and riparian forest (1.58 ± 1.48 SD), followed by thicket (1.49 ± 1.42 SD), wooded grassland (1.47 ± 0.91 SD), closed woodland (1.45 ± 0.89 SD), and open woodland (1.39 ± 0.75 SD) habitats (Fig. 3.2). Interaction effects were found to be non-significant and were excluded from the analysis. Tortuosity did not differ between herds (ANOVA $F$=2.019; $p$=0.155) or between seasons (ANOVA $F$=0.759; $p$=0.384).

#### 3.5.2.2 Step length

Mean half-hourly step length differed significantly between seasons (ANOVA $F$=221.18; $df$=2; $p<0.0001$), between habitats (ANOVA $F$=61.98; $df$=5; $p<0.0001$) and among herds (ANOVA

*F*=12.05; *df*=2; *p*<0.05). Overall, step lengths were considerably larger during the wet season (138.7 m ± 268.5 SD) compared to the dry season (96.0 m ± 142.8 SD), indicating quicker movements during this period (Fig. 3.3). Pairwise comparisons after Bonferroni correction revealed that step length was significantly larger in open woodland (147.9 m ± 294.4 SD; *p*<0.0001) and significantly smaller in scarp forest (56.2 m ± 81.7 SD; *p*<0.0001) but were similar in all other habitats: closed woodland (120.1 m ± 209.1 SD), wooded grassland (116.5 m ± 202 SD), riparian (112.6 m ± 170.4 SD) and thicket (111.1 m ± 211.8 SD).

A significant interaction effect was apparent between habitat and season (ANOVA *F*=10.30; *df*=5; *p*<0.0001). Mean step lengths were noticeably larger in the wet season compared to the dry for closed woodland (*Wet*=132.9 m ± 234.7 SD; *Dry*=95.8 m ± 146.1 SD); open woodland (*Wet*=172.3 m ± 351.3 SD; *Dry*=111.2 m ± 170.1 SD); riparian forest (*Wet*=123.3 m ± 201.8 SD; *Dry*=103.0 m ± 135.8 SD); thicket (*Wet*=125.2 m ± 261.6 SD; *Dry*=96.7 m ± 143.0 SD) and wooded grassland (*Wet*=133.5 m ± 237.1 SD; *Dry*=92.6 m ± 134.3 SD) habitats suggesting greater displacement through these habitats during the wet season and less displacement in the dry (Fig. 3.3). In contrast, step lengths in scarp forest habitat were comparable in both seasons (*Wet*=51.0 m ± 64.8 SD; *Dry*=57.7 m ± 86.0 SD) suggesting similar patterns of movement in both seasons (Fig. 3.4).

A significant interaction effect was also notable between habitat and herd (ANOVA *F*=6.338; *df*=4; *p*<0.0001). Mean step lengths for RR herds were larger than those for WR herds in open woodland (RR=167.8 m ± 362.4 SD; WR=125.6 m ± 188.5 SD), thicket (RR=125.4 m ± 297.4 SD; WR=103.2 m ± 143.8 SD) and wooded grassland (RR=125.3 m ± 235.3 SD; WR=106.9 m ± 157.4 SD), suggesting greater displacement within these habitats (Fig. 3.4). By contrast, mean step lengths were relatively equal for both herds within closed woodland (RR=120.3 m ± 228.8 SD; WR=119.7 m ± 176.3 SD) and riparian forest (RR=113.8 m ± 195.6 SD; WR=111.5 m ± 146.8 SD) habitats, suggesting similar displacement patterns (Fig. 3.4).

*3.5.3 The influence of time of day, habitat type and distance to water on displacement rates*

The global Generalized Linear Model was the strongest model (AIC$_c$=10088.75) explaining variation in mean step length (Table.3.2). The AIC model weight (*w$_i$*) showed that the inclusion of all main parameters and covariates accounted for 99% of the observed variance in mean step length (Table. 3.2). Model parameter estimates and confidence intervals revealed that the specific time of day and the proportion of habitat along a daily path were the best explanatory

parameters (Table. 3.3). Contrary to my expectation, mean step length (displacement rate) was notably higher between 10 am and 2 pm or midday ($\beta$=10.2; $p$<0.0001), indicating quicker movements and a greater net displacement during this time (Fig. 3.5). Step lengths were shorter in the early morning and late evening, indicating that elephant movement patterns were more similar during dawn and dusk (Fig. 3.5). Late evening mean step lengths were lower in both seasons ($\beta$=5.4; $p$<0.05) compared to those in the early morning and midday period and indicative of smaller displacements (Fig. 3.5).

Mean step length was inversely related to the proportion of particular habitats encountered along movement paths ($p$<0.0001) suggesting a decrease in displacement rates with increasing habitat availability (Table. 3.3). However, this effect did not differ between habitat types (see $\beta$-values in Table. 3.3). A similar inverse relationship was also evident for the interaction between time of day and the proportion of specific habitats (Table. 3.3). This effect was most notable in the morning within all habitats except open woodland but also at midday for scarp forest, thicket and wooded grassland habitats ($p$<0.0001). This indicates a significant decrease in displacement rates when greater proportions (> 0.68) of certain habitats were available (Fig.3.6). Herd, season and distance to water had no effect on step length (Table. 3.3) while the interaction effects of season-distance to water and time of day-distance to water were weak (Table. 3.3).

### 3.5.4 Seasonal vegetation greenness within habitats
Vegetation productivity differed significantly between habitat types (ANOVA $F$=18.259; $df$=5; $p$<0.0001) and between seasons (ANOVA $F$=57.526; $df$=1; $p$<0.0001). Dry season mean NDVI values and Tukey multiple comparisons revealed that scarp forest (6.52 ± 0.50 SD) and thicket (5.92 ± 0.59 SD) were the greenest habitats ($p$<0.05), while closed (4.75 ± 0.63 SD) and open woodland (4.82 ± 0.60 SD) were the least green (Fig. 3.7). In the wet season, scarp forest (7.58 ± 0.31 SD) and thicket (6.80 ± 0.61 SD) habitats were still considerably greener ($p$<0.05), with riparian forest being the next greenest (6.10 ± 0.55 SD). All other habitats were similar (5.85-5.98 NDVI) in terms of productivity (Fig. 3.7). Season-habitat interaction effects were not significant (ANOVA $F$=0.085; $df$=5; $p$=0.994).

### 3.5.5 Food preferences and the influence of vegetation density on movement patterns
Individual feeding records revealed that widely distributed species across the park were the ones most utilized by female herds, with seasonal preferences evident in many instances (Table. 3.4). Twelve species comprised 70 % of the woody plant feeding records for herds over the wet

season and 11 species comprised 71 % of records over the dry season. *A. karroo* comprised the highest proportion of the diet in both seasons and was heavily favoured in the dry season in comparison to all other species (Table. 3.4). *D. cineria*, *C. africana*, *A. robusta*, *E. racemosa, E. divinorum* and *S. brachypetala* also comprised large proportions of the diet (> 5%) but were consumed in similar proportions in both seasons. *Z. mucronata, A. grandicornuta* and *P. reclinata* represented large proportions of the diet (> 5%) in the wet season only.

Results from the vegetation utilization data revealed that there was no relationship between patterns of movement and the density of woody vegetation (1-4 m in height) within habitats. However, I did find clear relationships for some of the favoured food species. Significant correlations were evident between mean path tortuosity for each habitat and the density of *A. robusta* (n=6; Pearson *r*= 0.908; *p*<0.05) and *C. africana* (n=5; Pearson *r*= 0.963; *p*<0.05) in each habitat, indicating that path tortuosity increased in habitats where greater numbers of these species occurred. Non-significant trends were apparent for *A. karroo* (n=4; Pearson *r*= 0.797; *p*=0.203), *D. cinerea* (n=4; Pearson *r*= 0.891; *p*=0.109), *E. racemosa* (n=6; Pearson *r*= 0.743; *p*=0.090), *S. brachypetala* (n=6; Pearson *r*= 0.774; *p*=0.071) and *E. divinorum* (n=4; Pearson *r*= 0.768; *p*=0.232). A significant inverse correlation was evident between mean step length in each habitat and the density of *C. africana* in both the wet (n=5; Pearson *r*= -0.983; p<0.05) and the dry (n=5; Pearson *r*= -0.898; *p*<0.05) season and suggests that displacement rates were lower in habitats with more *C. africana*. Correlations between mean step length and tree density for all other species were not significant: *A. robusta* (n=6; Pearson *r*= -0.745; *p*=0.089), *E. racemosa* (n=6; Pearson *r*= -0.682; *p*=0.135) and *S. brachypetala* (n=6; Pearson *r*= -0.622; *p*=0.187) during the wet season and *A. karroo* (n=5; Pearson *r*= -0.753; *p*=0.142) in the dry season.

## 3.6 Discussion

Recent studies on elephant spatial use have identified factors such as rainfall, forage, surface water distribution, human activity and fences as key determinants of movement (Dai *et al.* 2007; Smit *et al.* 2007; Wittemyer *et al.* 2008; Loarie *et al.* 2009; Graham *et al.* 2009; Shrader *et al.* 2010; Vanak *et al.* 2010). However, the influence of vegetation productivity on habitat selection and how habitat type and the abundance of food resources compared to non-food items influences movement patterns has only been addressed in a few studies (Babaasa 2000; Young *et al.* 2009a).

Elephants are known to exhibit distinct habitat preferences despite their large body size (Shannon *et al.* 2006) and movement responses by large herbivores have been linked with the

search for high-quality food (Dai *et al*. 2007; Fryxell *et al*. 2008). My results indicated that elephants favoured greener habitats primarily in the dry season and that scarp forest and thicket were the most productive and the most utilized habitats at this time. Species commonly found in the above habitats (*S. brachypetala, C.africana, E. divinorum, E. racemosa* and *Z. mucronata*) were among the most favoured items in the diet of elephant herds. Higher tortuosities and smaller step lengths within these habitats suggest that displacement rates were lower and movements more convoluted. Particularly in the dry season, this may indicate an increase in foraging intensity. Similar patterns have been observed in other studies on elephant movement (Wittemyer *et al*. 2008; Van der Waal & Rodgers 2009). Widely distributed species associated with thicket and wooded grassland habitat such as *A. karroo* and *D. cinerea* comprised a high proportion of the diet of herds in both seasons, with *A. karroo* especially targeted in the dry season. Higher path tortuosities and lower displacement rates in habitats that supported high densities of these species suggest that elephant herds may spend more time foraging in these habitats to include such favoured species into their diet. In the case of *A. karroo*, this may reflect a narrowing in food selection around a commonly occurring species in the park. Contrary to Boundja & Midgley (2009), this may indicate that abundant woody species in Hluhluwe-Imfolozi Park are more utilized by breeding herds than rarer species.

In the wet season, herds also utilized riparian forest habitat although this is only partially explained by the greenness of woody vegetation. Feeding records indicated that trees with distinctly riparian affiliations (*A. robusta, E. racemosa* and *S. brachypetala*) were among the most utilized woody species and result show that path tortuosity increased and displacement rates decreased when these species were more prevalent. Additionally, bottomlands on alluvial plains support large quantities of highly palatable grasses and herbaceous plants (Scoones 1995) that are favoured by elephants in the wet season (Osborn 2004; O'Connor *et al*. 2007). Elephant may therefore spend large amounts of time occupying riparian habitats but not necessarily utilizing woody vegetation. The lack of relationship between movement responses and the total woody plant density within a habitat suggests that female herds may not select habitat for overall vegetation density. However, the presence of a relationship between movement responses and the densities of particular species indicates that the preference for favoured species at certain times of year can be influential in determining habitat choice (Babaasa 2000).

The specific time of day and the proportion of habitat along daily paths accounted for 99% of the total variation in displacement rates. Thus, daily elephant herd movements varied mainly according to the time of day and the availability of particular habitats along the way. Contrary to

my expectation and to other studies (Shannon *et al*. 2008; Loarie *et al*. 2009), I found that elephants were considerably more mobile at midday compared to the early morning and late evening. In some areas, elephants may move to water sources to drink at this time of day (Douglas-Hamilton 1973) but I did not find evidence for any relationship between time of day and distance to water in our analyses. A possible reason is that water is easily accessible in Hluhluwe-iMfolozi as no point in the park is further than eight kilometres from a river (Boundja & Midgley 2009). It is therefore likely that elephants can afford to drink at any time of day, rather than being restricted to a specific period. In contrast to this pattern, lower displacement rates can reflect foraging behaviour (Johnson *et al*. 2002; Morales *et al*. 2004) and in this study, suggest that elephants concentrate their foraging in dusk and dawn (Guy 1976; Shannon *et al*. 2008). Notably lower displacement rates were also evident when greater proportions of scarp forest, thicket and wooded grassland habitat occurred along a path. This implies that foraging becomes more intensive when these habitats are encountered and indicates that habitat availability may influence movement patterns.

Daily movements may be strongly linked with energetic requirements (Carbone *et al*. 2005) and for female herds, appears to be related to optimal foraging behaviour. In this study, foraging may be a crepuscular behaviour, indicated by lower displacement rates. I also found evidence for variation in daily movement responses between different herds in certain habitats. Displacement rates were significantly greater for RR herds than for WR herds in open woodland, wooded grassland and thicket habitats but were similar in closed woodland and riparian forest habitat. A possible explanation is that smaller herds may linger in thicker habitats as these areas may afford a greater sense of protection and move quickly through more open habitats where they may feel more exposed. Alternatively, disparities in habitat selection and movements within a population could be an indication of differing resource constraints at specific localities that elicit different responses within different groups (Wittemyer *et al*. 2007a).

In summary, elephant herds showed a preference for forest and thicket habitat in the dry season. This choice was influenced by the greenness of vegetation and the density of certain favoured food species within these habitats. Conversely, selection and movement responses were more similar among habitats in the wet season. Consistent with Optimal Foraging Theory (Macarthur & Pianka 1966), elephants appear to be selecting areas of high vegetation productivity (Woolley *et al*. 2009; Young *et al*. 2009a) while simultaneously focusing on commonly occurring woody species during a resource limited period. Habitat selection and movements by elephants often coincides with their nutritional requirements (Provenza *et al*. 2003) and any alteration can

reflect a behavioural response to environmental heterogeneity (Johnson *et al.* 2002) or to meet fitness demands at a time of resource scarcity (Shannon *et al.* 2006). The size of key resource patches also has the potential to affect movements (Fryxell *et al.* 2005) and my results suggest that movement characteristics are strongly associated with the proportions of specific habitat types available. This concurs with previous studies on selective habitat use and woody plant utilization by elephants in small fenced reserves (Lombard *et al.* 2001; Steyn & Stalmans 2001).

Observations of movements by naturally dispersing animals in heterogeneous landscapes can demonstrate the conservation value of habitats and associated corridors (Beier & Noss 1998). Many species require multiple habitats to obtain different resources (Law & Dickman 1998) and elephants may select some habitat types as key forage zones (scarp forest, thicket, riparian and wooded grassland) whereas others may be utilized only for travelling (open woodland) or their proximity to water (riparian). Well-wooded habitats in particular may be selected for foraging or shelter (Lucherini *et al.* 1995; Fisher 2000). Habitat selection and movement patterns may thus alternate between fixed or opportunistic, allowing elephants to make use of permanently or temporarily available resources (Leuthold 1977) and enabling a highly flexible system of utilization of space. My results demonstrate that breeding herds may intentionally alter their patterns of selectivity and movement between seasons and over the course of a day. At a seasonal level they may do so in order to utilize the most productive parts of a heterogeneous landscape. At a daily scale, they may seek to meet optimal foraging demands and be driven by the availability and abundance of favoured habitat and food species.

Across the southern African sub-region, escalating elephant numbers may threaten faunal and floral diversity (Whyte *et al.* 2003). Increased foraging pressure has been linked to the degradation of vegetation structure to the detriment of other species (Laws 1970) and to the adverse alteration of both the structure and composition of vegetation (Wiseman *et al.* 2004; De Beer *et al.* 2006; Kerley *et al.* 2006). Smaller protected areas like Hluhluwe-iMfolozi Park, with rapidly increasing populations and diverse vegetation communities are especially vulnerable to habitat level transformation (Western & Maitumo 2004; Owen-Smith *et al.* 2006). Fragmented habitats in particular may be under threat, especially if they are repeatedly occupied over consecutive seasons. Both riparian and scarp forest habitats are highly disjointed across Hluhluwe-iMfolozi Park and patches are becoming increasingly isolated across the country (Mucina & Rutherford 2006). From a biodiversity perspective, scarp forest is the most important forest type in the country (Boon 2010) and riverine forest is particularly sensitive to change (O'Connor *et al.* 2007). I show that female herds prefer forest habitat in both seasons

but that utilization intensity is greater in the dry season. The continuous occupancy of sensitive habitats by elephants all year round may exacerbate impacts on vegetation and more rigorous studies are required to test this.

In larger protected areas and open systems, allowing elephant numbers to fluctuate locally and naturally through dispersal may reduce the adverse impact on vegetation and other forms of biodiversity (Van Aarde & Jackson 2007). Increased dispersal relieves pressure on sensitive areas and gives faunal and floral assemblages time to recover. This option however, is not available to managers of large, spatially constrained elephant populations in small protected areas like Hluhluwe-iMfolozi Park. Other options for managing the density and movements of such elephant populations need to be considered, among which contraception and the creation of botanical reserves have had some success (Delsink *et al*. 2007; Lombard *et al*. 2001). Future research could focus on actual vegetation utilization within sensitive habitats and question why elephants in some areas are more mobile at midday. Studies such as this one are crucial towards overall conservation planning in that they can be used to evaluate threats to specific habitats, and thus emphasize the need for the preservation of ecosystem heterogeneity. This is especially critical when dealing with megaherbivores like elephant that can exert a wide range of influence on the environment.

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**Table 3.1** Pairwise preference of habitat types based on a compositional analysis of LSCV-determined utilization distributions for collared elephants in each home range for two wet and two dry seasons. Habitat types in the rows are listed in ascending order of rank of selection with 4 being the most selected and 0 the least. The selection for and against each type is indicated by + and - with +++ and --- denoting significant differences at $P < 0.05$. Wooded grassland was the denominator habitat for the analysis. THK=thicket; CW=closed woodland; OW=open woodland; WG=wooded grassland; FOR=forest (riparian and scarp)

| *Wet 1* | THK | CW | OW | FOR | WG | Rank |
|---|---|---|---|---|---|---|
| **THK** | | - | - | - | - | 0 |
| **CW** | + | | - | - | --- | 1 |
| **OW** | + | + | | - | - | 2 |
| **WG** | + | +++ | + | - | | 3 |
| **FOR** | + | + | + | | + | 4 |
| *Wet 2* | | | | | | |
| **THK** | | - | - | --- | - | 0 |
| **CW** | + | | - | --- | --- | 1 |
| **OW** | + | + | | --- | - | 2 |
| **WG** | + | +++ | + | --- | | 3 |
| **FOR** | +++ | +++ | +++ | | +++ | 4 |

**Table 3.1** *continued*

| *Dry 1* | THK | CW | OW | FOR | WG | Rank |
|---------|-----|-----|-----|-----|-----|------|
| **CW** | - | | --- | --- | --- | 0 |
| **WG** | **-** | +++ | - | --- | | 1 |
| **OW** | - | +++ | | --- | + | 2 |
| **THK** | | + | + | - | + | 3 |
| **FOR** | + | +++ | +++ | | +++ | 4 |
| *Dry 2* | | | | | | |
| **CW** | - | | --- | --- | --- | 0 |
| **OW** | - | +++ | | --- | - | 1 |
| **THK** | | + | + | --- | - | 2 |
| **WG** | + | +++ | + | --- | | 3 |
| **FOR** | +++ | +++ | +++ | | +++ | 4 |

**Table 3.2** AIC models tested to explain variance in mean step length for elephant herds in Hluhluwe-iMfolozi Park. Top model (in bold) had a $\Delta AIC_c <$ 2 based on a multiple linear regression analysis. Reported are the number of parameters ($K$); Akaike's Information Criterion adjusted for small sample size ($AIC_c$); the difference in corrected AIC values between models ($\Delta AIC_c$); and Akaike's model weight ($w_i$)

| Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| **Global = Time of Day + Habitat proportions + Interaction (Time of day*Habitat proportions) + Herd + Season + Dist to water + Interaction (Season*Herd), Interaction (Season*Dist to water) and Interaction (Time of day*Dist to water)** | **19** | **10088.75** | **0** | **0.99** |
| Distance to water removed | 16 | 10099.03 | 10.28 | 0.01 |
| Distance to water + Herd removed | 14 | 10108.12 | 19.37 | 0.00 |
| Distance to water + Herd + Season removed | 13 | 10108.63 | 19.88 | 0.00 |
| Herd removed | 16 | 10110.02 | 21.27 | 0.00 |
| Time of day*Habitat proportions + Herd + Season + Distance to water removed | 8 | 10148.6 | 59.82 | 0.00 |
| Time of day*Habitat proportions + Herd + Season removed | 9 | 10149.5 | 60.73 | 0.00 |
| Time of day*Habitat proportions + Herd + Distance to water removed | 9 | 10149.8 | 61.07 | 0.00 |

**Table 3.3** GLM model parameter estimates and key statistics of the top AIC-ranked model predicting variation in log-transformed step length as a function of habitat proportions, distance to water, season, herd and time of day for elephant herds in Hluhluwe-iMfolozi Park. CW=closed woodland; RIP=riparian; SCP=scarp; OW=open woodland; THK=thicket; WG=wooded grassland

| Predictor | B | SE(B) | β | Lower CL | Upper CL | Sig. |
|---|---|---|---|---|---|---|
| *Time of Day* | | | | | | |
| Midday | 2.32 | 0.40 | 10.2 | 4.638 | 22.42 | <0.0001[a] |
| Evening | 1.68 | 0.59 | 5.4 | 1.691 | 17.16 | 0.004 |
| *Habitat proportion* | | | | | | |
| Thicket | -0.95 | 0.20 | 0.4 | 0.271 | 0.585 | <0.0001[a] |
| Wooded grassland | -0.79 | 0.18 | 0.5 | 0.322 | 0.644 | <0.0001[a] |
| Scarp | -0.77 | 0.25 | 0.5 | 0.282 | 0.761 | <0.0001[a] |
| Riparian | -0.76 | 0.15 | 0.5 | 0.348 | 0.627 | <0.0001[a] |
| Closed woodland | -0.71 | 0.17 | 0.5 | 0.348 | 0.689 | <0.0001[a] |
| Open woodland | -0.68 | 0.14 | 0.5 | 0.390 | 0.661 | <0.0001[a] |
| Eve*CW | -1.80 | 0.58 | 0.2 | 0.053 | 0.517 | 0.002 |
| Mid*CW | -1.91 | 0.43 | 0.1 | 0.065 | 0.343 | <0.0001[a] |
| Eve*RIP | -1.88 | 0.55 | 0.2 | 0.042 | 0.454 | 0.001 |
| Mid*RIP | -1.49 | 0.37 | 0.2 | 0.110 | 0.462 | <0.0001[a] |
| Eve*SCP | -3.00 | 1.45 | 0.0 | 0.003 | 0.842 | 0.038 |
| Mid*SCP | -1.80 | 0.53 | 0.2 | 0.059 | 0.466 | <0.0001[a] |
| Eve*OW | -1.65 | 0.49 | 0.2 | 0.074 | 0.497 | 0.001 |
| Mid*OW | -1.46 | 0.36 | 0.2 | 0.115 | 0.469 | <0.0001[a] |
| Eve*THK | -2.08 | 0.68 | 0.1 | 0.030 | 0.471 | 0.002 |
| Mid*THK | -1.55 | 0.42 | 0.2 | 0.093 | 0.480 | <0.0001[a] |
| Eve*WG | -1.85 | 0.58 | 0.2 | 0.050 | 0.493 | 0.002 |
| Mid*WG | -1.79 | 0.41 | 0.2 | 0.075 | 0.370 | <0.0001[a] |
| *Season and herd* | | | | | | |
| Season*herds | 0.34 | 0.09 | 1.4 | 1.170 | 1.687 | <0.0001[a] |
| Season | -0.12 | 0.08 | 0.9 | 0.760 | 1.043 | 0.150 |
| HIP Herds | -0.07 | 0.07 | 0.9 | 0.818 | 1.058 | 0.275 |

**Table 3.3** *continued*

| Predictor | B | SE (B) | β | Lower CL | Upper CL | Sig. |
|---|---|---|---|---|---|---|
| *Euclidean distance to water* | | | | | | |
| Dist to water | 0 | 0 | 1.0 | 1.000 | 1.000 | 0.179 |
| Season*dist to water | 0 | 0 | 1.0 | 1.000 | 1.000 | 0.002 |
| Eve*dist to water | 0 | 0 | 1.0 | 1.000 | 1.000 | 0.004 |
| Mid*dist to water | 0 | 0 | 1.0 | 1.000 | 1.000 | 0.305 |

Global model: $\Delta$AICc < 2 based on a multiple regression analysis. Model particulars: B = unstandardized regression parameter; SE (B) = unconditional standard error; β = standardized regression parameter, Lower & Upper CL = standardized confidence limits; Sig = statistical significance. Time of day = morning was a denominator variable and had the same effect as Time of day=evening. [a] = significant effect at *p*<0.05.

**Table 3.4** Seasonal woody vegetation diet selection for elephant herds from direct observations of feeding over the two year study period. The proportion contributed by each species to the overall diet in each season is included. Only species comprising three percent or more of the diet in the season are shown.

| Species | Number of records | Proportion of diet |
|---|---|---|
| *Wet Season* | | |
| **Acacia karroo** | **8** | **0.10** |
| **Dichrostachys cineria** | **7** | **0.09** |
| *Phoenix reclinata* | 6 | 0.07 |
| **Euclea divinorum** | **5** | **0.06** |
| **Schotia brachypetala** | **5** | **0.06** |
| *Ziziphus mucronata* | 5 | 0.06 |
| *Acacia grandicornuta* | 4 | 0.05 |
| **Euclea racemosa** | **4** | **0.05** |
| **Celtis africana** | **4** | **0.05** |
| **Acacia robusta** | **4** | **0.05** |
| *Peltophorum africana* | 3 | 0.04 |
| *Sclerocarya birrea* | 3 | 0.04 |
| *Dry Season* | | |
| **Acacia karroo** | **32** | **0.21** |
| **Dichrostachys cineria** | **17** | **0.11** |
| **Acacia robusta** | **14** | **0.09** |
| **Celtis africana** | **10** | **0.06** |
| **Euclea divinorum** | **8** | **0.05** |
| **Schotia brachypetala** | **7** | **0.05** |
| **Euclea racemosa** | **5** | **0.04** |
| *Acacia nilotica* | 4 | 0.03 |
| *Maytenus heterophylla* | 4 | 0.03 |
| *Rhus pentheri* | 4 | 0.03 |
| *Ziziphus mucronata* | 4 | 0.03 |

Species highlighted in bold were selected for movement patterns analysis as they represented >= 4% of the diet in both seasons.
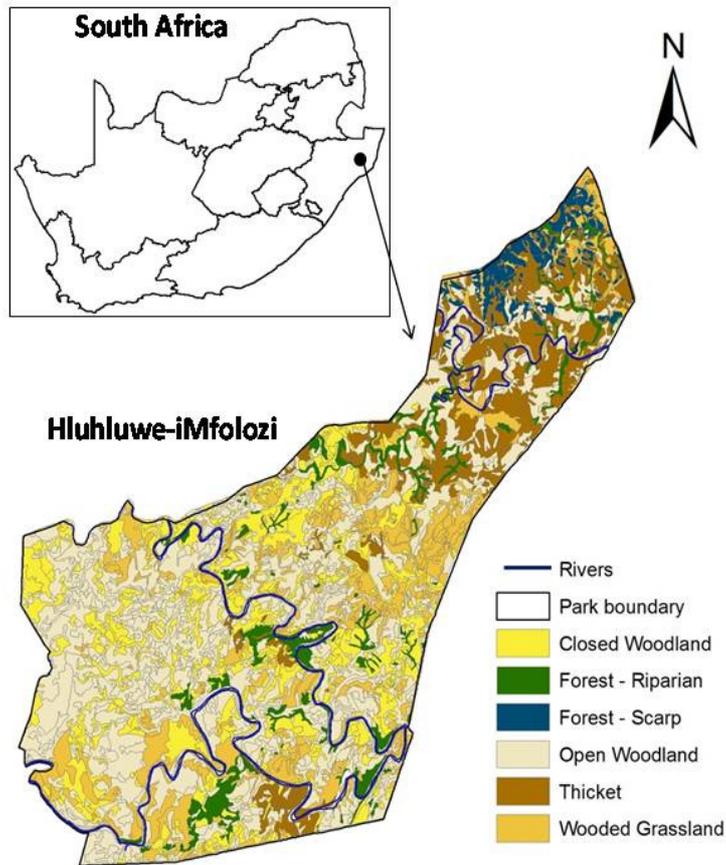
**Fig 3.1** Map displaying the location of Hluhluwe-iMfolozi Park within South Africa and the distribution of structural habitat types and perennial rivers within the park. Modified from Whateley-Porter 1983 Vegetation Layer for HIP
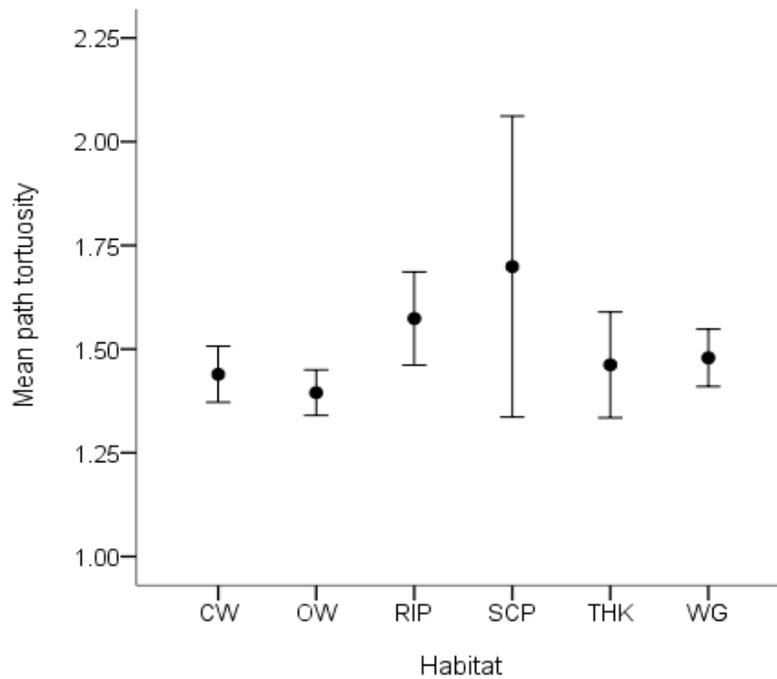
**Fig 3.2** Plot of mean path tortuosity per day within each habitat type for breeding herds (means and 95% confidence intervals displayed). Habitat abbreviations: closed woodland (CW); open woodland (OW); riparian (RIP); scarp forest (SCP); thicket (THK); wooded grassland (WG). Insufficient path samples were available to determine a mean path tortuosity for scarp forest in the wet season.
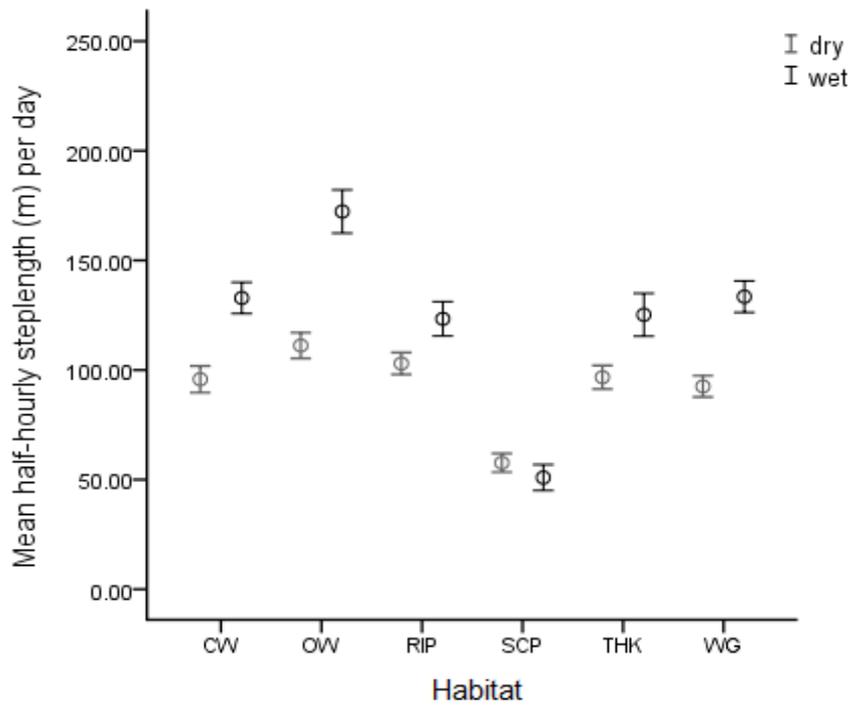
**Fig 3.3** Plots displaying the mean half-hourly step length per day within each habitat type in the wet and dry season for all herds (means and 95% confidence intervals displayed). Habitat abbreviations: CW=closed woodland; OW=open woodland; RIP=riparian; SCP=scarp; THK=thicket; WG=wooded grassland.
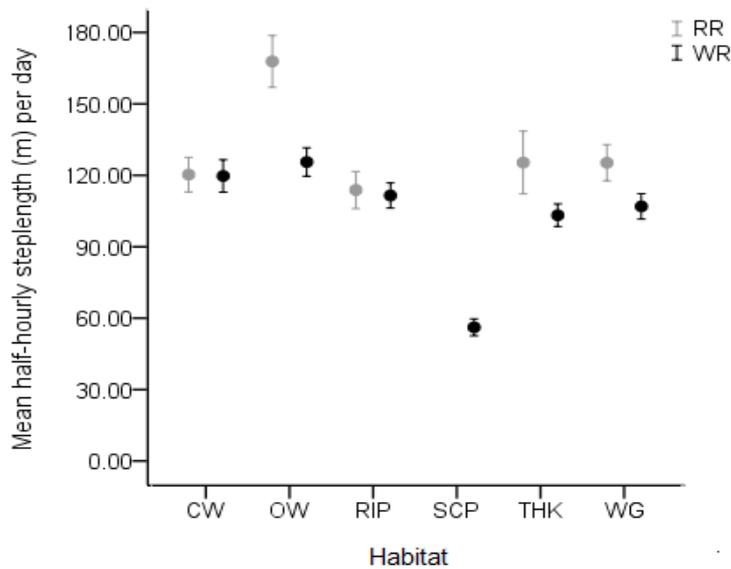
**Fig 3.4** Plot displaying the mean half-hourly step length per day within each habitat type for wide-ranging (WR) and range-restricted (RR) herds (means and 95% confidence intervals displayed). Habitat abbreviations: CW=closed woodland; OW=open woodland; RIP=riparian; SCP=scarp; THK=thicket; WG=wooded grassland. RR-herds did not utilize scarp forest and as such there are no recorded step lengths within this habitat for these herds.
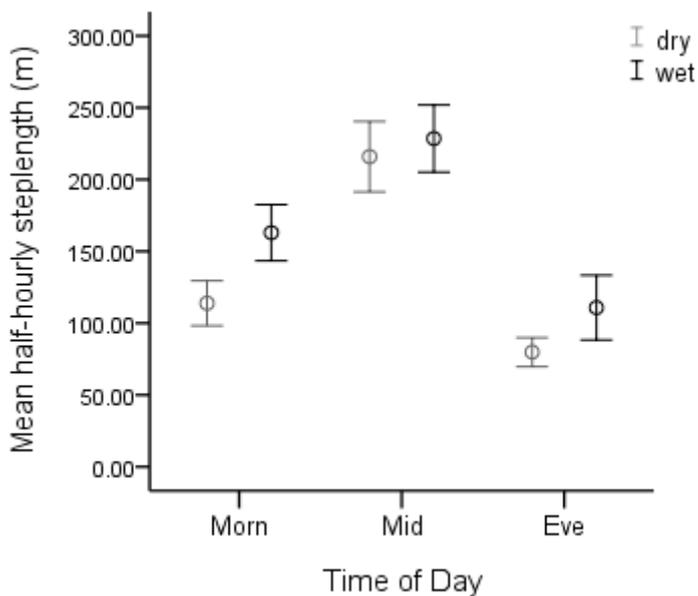


**Fig 3.5** Plot of mean half-hourly step length calculated over a 4-hr timeframe during three times of day: Morning (2-6 am); Midday (10-12 am) and Evening (8-12pm) for herds in the wet and dry season (mean and 95% confidence intervals displayed).
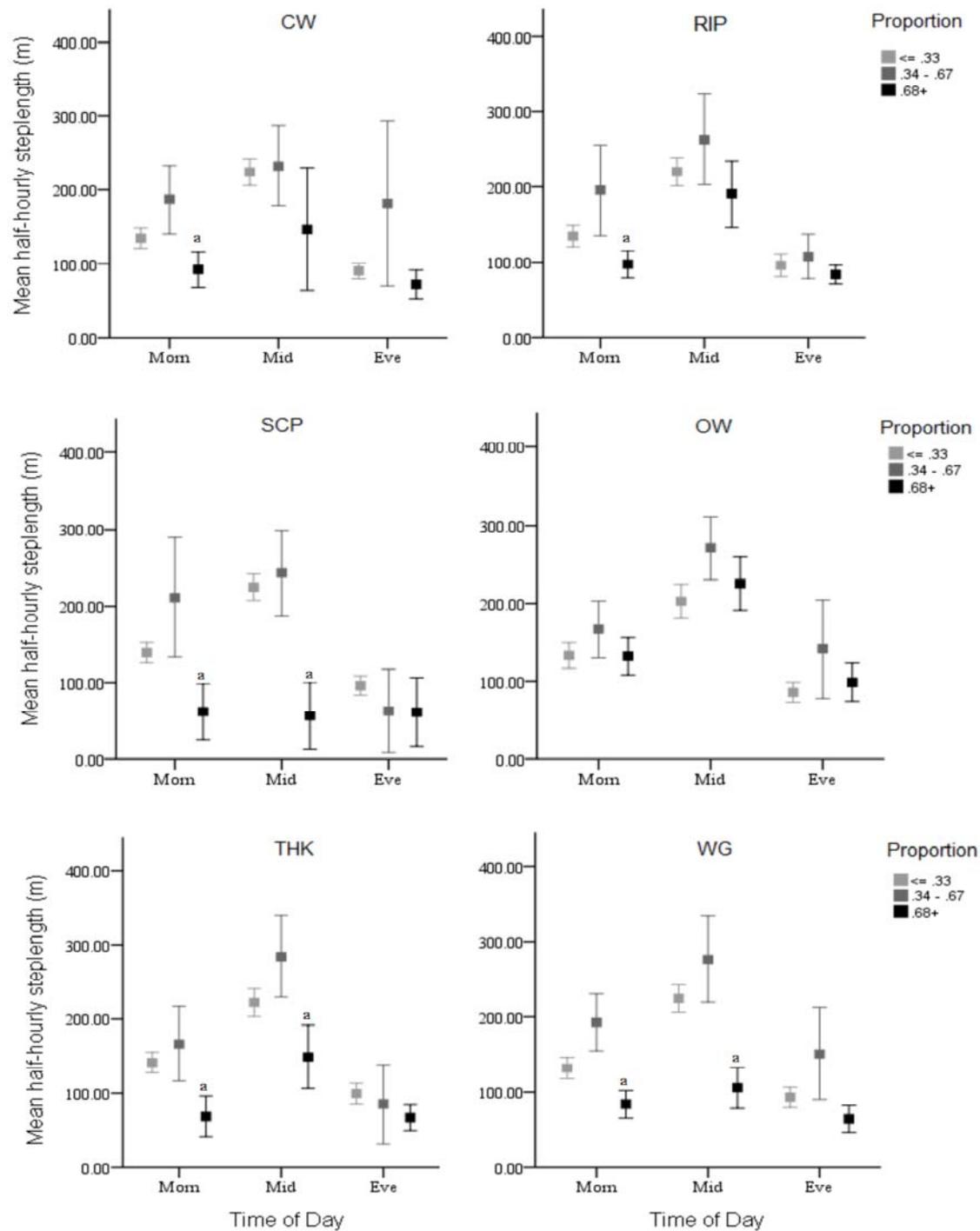
**Fig 3.6** Plots displaying mean half-hourly step length at three times of day as a function of the proportion of different habitat types selected at each time of day for all herds (means and 95% confidence intervals displayed). Times of day are: Morning (Morn), Midday (Mid) and Evening (Eve). Habitat plots are: Closed woodland (CW), riparian (RIP), scarp forest (SCP), open woodland (OW), thicket (THK) and wooded grassland (WG). a= significant effect at $p<0.05$.
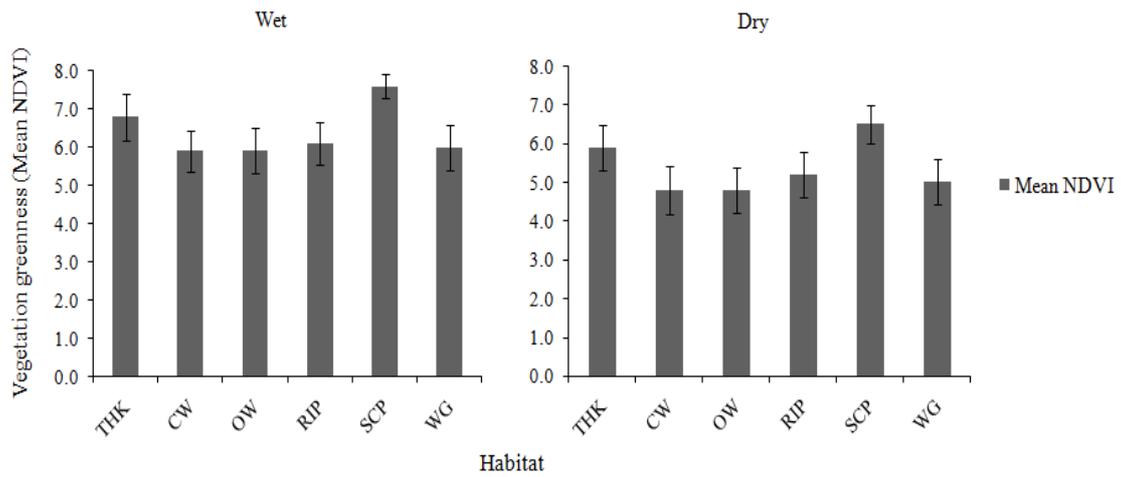
**Fig 3.7** Average seasonal NDVI values representing primary productivity ("greenness") per habitat type in Hluhluwe-iMfolozi Park in 2 wet and 2 dry seasons over the study period (Mean NDVI values were calculated for the 3 wettest months (Nov/Dec/Jan) and 3 driest months (May/Jun/Jul in each season)

# Chapter 4

# Conclusions and Recommendations

In order to effectively manage elephants in fenced protected areas it is vital that conservation authorities develop a sound knowledge of the factors causing variation in spatial use (van Aarde *et al*. 2006; Biggs *et al*. 2008). Included in this is the consideration of habitat preferences and movement patterns and how these are influenced by biotic and abiotic factors at multiple scales. Fenced systems remove the opportunity for extensive dispersal (Slotow *et al*. 2005; Vanak *et al*. 2010) and effectively reduce heterogeneity in spatial utilization (O'Connor *et al*. 2007). Rapidly increasing elephant densities within fenced reserves in South Africa (Blanc *et al*. 2007) has lead to widespread utilization of habitats and concerns regarding impacts on biodiversity are being voiced by managers and researchers alike (Cumming *et al*. 1997).

Using spatially explicit techniques I determined the main factors influencing the size of the home range and the intensity of use within the home range for separate female herds from a spatially constrained elephant population. I also determined seasonal habitat preferences for these herds and examined the drivers of variation in daily movement patterns within different habitats, in separate seasons and over the course of a day. I found extensive variation in home range size and utilization intensity between seasons and herds. Larger herds occupied bigger home ranges in the wet season and smaller home ranges in the dry. Utilization intensity within core areas was substantially higher during the dry season suggesting concentrated use. These patterns are best explained by intraspecific competition and by spatio-temporal differences in the distribution of rainfall, green vegetation and surface water throughout the year. Furthermore, I present evidence indicating that the seasonal preference for specific habitats is linked to the greenness of vegetation in these habitats. Lastly, I demonstrate that daily movement responses can be explained by the specific time of day, the availability of particular habitat and the density of favoured woody species within these habitats. More specifically, crepuscular movements appear to be related to foraging behaviour.

GPS telemetry potentially enables the behavioural responses of animals to be linked to environmental characteristics (Beyer *et al*. 2010). Resource selection studies often integrate radio-tracking data and GIS technology to provide information on the types of resources selected by animals (Manly *et al*. 2002). The use of kernel-based techniques in particular has helped improve our ability to analyze spatial relationships between animals and their resources (Seaman *et al*. 1999; Kie *et al*. 2002). Such studies allow conservation managers and scientists

to identify home ranges, conserve important habitats, and model species distributions (Frair *et al.* 2004; Millspaugh *et al.* 2006). Recent advancements in the field have allowed researchers to map habitat use as a continuum using the utilization distribution concept (Marzluff *et al.* 2004; Rittenhouse *et al.* 2008). By examining the manner in which animals use habitats, researchers can surmise a great deal about the way they perceive their environment (Beyer *et al.* 2010) and understand the complex demands that affect behavioural responses (Rosenzweig 1981). I used these techniques to demonstrate how principles of optimal foraging can be applied to elephant habitat preferences and movement patterns at different temporal scales.

Resource distribution and competition are among the major factors limiting elephant spatial use and their influence is acknowledged in the literature (Fritz *et al.* 2002; Wittemyer *et al.* 2007a; Chamaille-Jammes 2008). Rainfall for instance, determines the availability of both food (Scholes *et al.* 2003) and seasonal surface water (Chamaille-Jammes *et al.* 2007) and plays a major role in dictating elephant movements (Shrader *et al.* 2010). Surface water is a primary driver of elephant distribution across the landscape (Redfern *et al.* 2005) and the manipulation of water sources has become a powerful tool in elephant management (Smit *et al.* 2007). Resources that occur reliably in different parts of the landscape at particular times of the year promote seasonally disparate home ranges, or movements between widely separated ranges (Owen-Smith *et al.* 2010). My results revealed that some herds displayed major contraction in home range size during the dry season centered primarily on variation in rainfall distribution but also possibly linked to heightening competition between individuals over concentrated food and water resources. This often occurs in areas where resources are spatially predictable and particularly during the dry season when resources are scarcest (Chamaille-Jammes *et al.* 2007). Conversely, an expansion in home range size during the wet season appeared to be driven by a wider availability of resources (Loarie *et al.* 2009) and an associated increase in group size. Previous studies have noted prominent seasonal differences in spatial use in dry, arid savannas (Loarie *et al.* 2009; Young *et al.* 2009b) but few have observed this pattern in wetter areas.

Contrary to other studies (De Beer & van Aarde 2008; Leggett 2006; Redfern *et al.* 2005), I established that utilization intensity was more pronounced near rivers in the wet season compared to the dry. I suggest that in the wet season, this pattern may be due to an abundance of forage material in bottomlands near rivers. In the dry season the utilization of areas further from rivers may be a response to declining food availability near rivers causing an increase in competitive interactions and resulting in broader foraging patterns. This may ultimately lead to divisions into smaller and presumably more efficient foraging groups as a trade-off (Wittemyer

*et al*. 2005). Additionally, variability in habitat selection and movements within the population were mostly evident during the dry season. Larger herds clearly utilized some habitats more intensely than smaller herds at this time of year. Elephants are known to be susceptible to intraspecific competition (Wittemyer *et al*. 2005) and smaller groups may attempt to avoid it by utilizing habitats with fewer other elephants. Similar competition-induced trade-offs in terms of group size have been observed in other mammalian species (Wrangham *et al*. 1993; Dammhahn & Kappeler 2009).

The size and shape of vegetation patches within the home range, the type and greenness of habitat and the densities of specific woody species in a habitat also influenced habitat preferences, utilization intensity and daily movement patterns. Particularly during the dry season, elephants selected larger, more irregularly-shaped vegetation patches and preferentially utilized greener habitats (scarp forest and thicket). Elephants utilized habitats with higher densities of favoured food species (riparian forest, scarp forest, thicket and wooded grassland) in both seasons. Interestingly, elephants also utilized areas close to water more in the wet season, probably due to an abundance of palatable grass and herbaceous vegetation. High densities of favoured woody species also occurred in riparian habitat (e.g. *A. robusta, E. racemosa* and *S. brachypetala*).

Large herbivores are dependent on vegetation resources that are often seasonally variable in availability and nutritional value (Owen-Smith *et al*. 2010) and the preference for specific species at certain times of year can be influential in determining habitat selection (Babaasa 2000). Furthermore, foraging in a group and supporting offspring is energetically demanding (Wrangham *et al*. 1993; Wittemyer *et al*. 2007b) and female herds may seek to improve their nutritional acquisition by changing their behaviour during stressful periods such as the dry season (Stokke & du Toit 2000; Woolley *et al*. 2009). I propose that they may accomplish this by foraging more selectively and intensely and by modulating group size to alleviate competition. The above patterns suggest that elephant conform to optimal foraging principles during energetically constrained periods and agrees with previous studies on spatial use and habitat preference by elephants (Shannon *et al*. 2006; Chamaille-Jammes *et al*. 2007; Wittemyer *et al*. 2007b; Young *et al*. 2009b).

Resources critical to animals tend to be heterogeneously distributed across the landscape (Wiens 1989; Mitchell & Powell 2004). Optimal foraging theory predicts that animals should take advantage of this by foraging selectively in resource-rich patches (Webb *et al*. 2009) and

altering movements to stay longer in such patches (Zollner & Lima 1999). I propose that elephants may do this by reducing speed and increasing the sinuosity of their search paths in key forage patches. I also suggest that foraging activity occurs mainly during the early morning and evening, a pattern well known from previous literature on herbivores (Owen-Smith 1988). Activity patterns can be deduced from movement modes or from the specific time of day when particular activities predominate (Johnson *et al.* 2002). This level of spatial accuracy allows researchers to relate movement responses to foraging and the actual consumption of food through supporting field observations (Owen-Smith & Novellie 1982). However, there is a distinct paucity of such studies in the literature and in fact some of my results contradict findings from previous studies. I show that in Hluhluwe-iMfolozi, elephants utilized areas close to water more in the wet season whereas it is generally accepted that they this pattern typically occurs during the dry season (Wittemyer *et al.* 2007a; Smit *et al.* 2007; De Beer & van Aarde 2008). It has also been suggested that elephants move less during the hottest times of the day and that daily movements are dictated by their proximity to water sources (Loarie *et al.* 2009). This study finds no relationship between daily movements and proximity to water sources and in fact indicates that elephants can be highly mobile at midday.

Displacement rates and path tortuosity are often used to infer biological activities and the energetic benefits derived from particular habitat types (Fryxell *et al.* 2008; Owen-Smith *et al.* 2010). Consistent with broader patterns of spatial use, female herds in this study covered greater distances in the wet season, a time of resource abundance and restricted their movements in the dry season, a time of resource scarcity. In the dry season, movement paths were more tortuous in scarp forest and riparian habitats while displacement rates were smaller in scarp forest and thicket compared to other habitats. These habitats contained higher densities of favoured woody species (e.g. *A. karroo*, *D. cinerea, C. africana*). The diet of herbivores is typically made up of abundant forage species (Owen-Smith & Novellie 1982) and daily elephant movement responses may be linked to the search for these items. Consequently, they preferentially utilized greener habitats in the dry season and targeted widely distributed woody species, perhaps in response to diminishing forage quality. Similar movement patterns have been observed in a study on elk and can indicate area-restricted foraging at a time of resource scarcity (Fryxell *et al.* 2008).

I detected lower rates of displacement during the early morning and evening, suggesting crepuscular foraging activity. Restricted displacement is indicative of intensive foraging and a more selective use of habitats (Johnson *et al.* 2002) and is expected due to greater energetic

constraints in the dry season. Such patterns of utilization have been noted for many herbivore species including elephant (Fryxell *et al*. 2008; Van der Waal & Rodgers 2009; Webb *et al*. 2009; Young *et al*. 2009a; Vanak *et al*. 2010). Contrastingly, displacement rates were substantially higher at midday, a time during which elephant are normally expected to move as little as possible due to high temperatures (Loarie *et al*. 2009). A similar study on elk found that they responded strongly to time of day, and moved more during crepuscular hours to avoid predation by wolves (Forester *et al*. 2007). Elephants have no natural predators in South African reserves and my results suggest that they do not move in a manner that minimizes predation risk at any time of day.

## 4.1 Future research recommendations

Thus, my results suggest that by analyzing broad and fine-scale patterns of spatial use and habitat preference and linking this to potential optimal foraging behaviour, one can describe the drivers of variation in utilization intensity and daily movements for elephants in fenced protected areas. Intraspecific competition, rainfall and the greenness of vegetation were the major determinants at a seasonal scale, while time of day, the density of favoured woody species and habitat availability appear to be the main explanatory variables of daily movement responses. In examining habitat use I satisfy three aspects of multiple scale resource selection as laid out by Johnson (1980) namely, habitat selection within the home range, daily movement patterns and the utilization of actual food items. It remains to be seen however, whether these patterns of spatial use by elephant can be extrapolated into the future, within Hluhluwe-iMfolozi Park and in similarly sized protected areas. An immediate concern is the effect of the above drivers on population growth rates, a crucial aspect not covered by this study. Future studies should attempt to investigate the relative influence of each of the above components on population fecundity and mortality.

More crucially perhaps, is the gap in knowledge regarding measurable impacts of intensive elephant utilization on ecosystem functioning and overall biodiversity. A few studies have addressed this by examining the responses of specific taxa and they present conflicting results (Herremans 1995; Govender 2005; Pringle 2008). Further work is required on the potential ability of elephants to promote habitat fragmentation through their activities. Hoft & Hoft (1995) for example found that elephants impeded forest regeneration in Kenya through increased utilization of forest patches. Such disruptive patterns of utilization have implications for the management of elephants in the context of ecosystem conservation. Native species may be lost from habitat fragments because of disturbances to the vegetation, reduced immigration,

edge effects and invasion by exotic species (Gordon *et al.* 2004; Turner 1996). This is especially true for forest fragments, which may contain localized or threatened taxa and act as source pool for recolonizing species (Turner & Corlett 1996). These effects can be exacerbated in smaller properties if landscape-level fragmentation has already begun due to anthropogenic activities such as fencing and road-laying.

Exploring the movements of naturally dispersing animals in heterogeneous landscapes can demonstrate the conservation value of habitats (Law & Dickman 1998). Certain habitats may be foraging hotspots while others may serve a simple but critical function as movement corridors. In this study, elephants utilized heavily fragmented scarp forest patches extensively in the dry season and similarly fragmented riparian forest patches in both seasons. Although they mainly targeted common woody species, prolonged utilization of sensitive habitats by elephants may compromise biodiversity in ways we do not yet perceive (Cumming *et al.* 1997). Future observational studies of animal habitat use should attempt to detect movements between isolated patches via corridors (Beier & Noss 1998) and question how this affects habitat connectivity. Further points of research emanating from this study would be to compare daily movement patterns for different elephant populations and test the hypothesis that lower displacements reflect foraging or that greater mobility at midday reflects drinking.

## 4.2 Management recommendations

Management practices in the form of culling and translocation have been frequently applied in both open and closed systems but are controversial or flawed solutions (Van Aarde & Jackson 2007). On the other hand, metapopulation principles have been advocated for the management of wild herbivores (Gordon *et al.* 2004; Van Aarde & Jackson 2007) and involve the development of linkages between conservation areas to make more space available to species like elephant. This is especially relevant to an area like Hluhluwe-iMfolozi Park that is ideally placed to expand towards and eventually encompass isolated, smaller protected areas that are in close proximity.

Conservation and management objectives include the protection of natural vegetation and the faunal assemblages they support (Lombard *et al.* 2001). Scarp forest is listed as one of the most important forest types in the country (Mucina & Rutherford 2006; Boon 2010) due to the high levels of endemism and species richness it exhibits. Riverine forest is also a critical habitat for wildlife in many protected areas throughout the world (Stauffer & Best 1980) and it is particularly sensitive to change (O'Connor *et al.* 2007). Hluhluwe-iMfolozi Park contains

heavily fragmented examples of both these habitat types but also supports a rapidly growing elephant population. The carrying capacity of enclosed protected areas is limited and the mismanagement of herbivore populations can threaten the integrity of sensitive habitats and of overall species diversity (Fritz *et al*. 2002; Makhabu *et al*. 2006). The successful management of elephant populations therefore depends on the size and state of the system, the extent of impacts and on local climatic variation (Owen-Smith *et al*. 2006). Based on the outcomes of this study, it is crucial that managers of small protected areas like Hluhluwe-iMfolozi Park realise that elephant spatial use and impacts may vary considerably over time and between groups, and that this should be incorporated into monitoring frameworks and decision making at the reserve level.

Ultimately, competition within herds driven by resource limitation may play a crucial role in regulating elephant populations within fenced reserves. Interpretations of animal movement patterns revealed by GPS tracking are becoming increasingly more common in the literature although studies on large herbivores are dominated by species from northern temperature latitudes (Owen-Smith *et al*. 2010). This study represents a contribution to the examination of broad and fine-scale movement patterns of an African herbivore and provides insight on elephant behaviour in small, fenced conservation systems.

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**APPENDIX 1**: HOME RANGES OF ALL BREEDING HERDS IN DIFFERENT WET AND DRY SEASONS
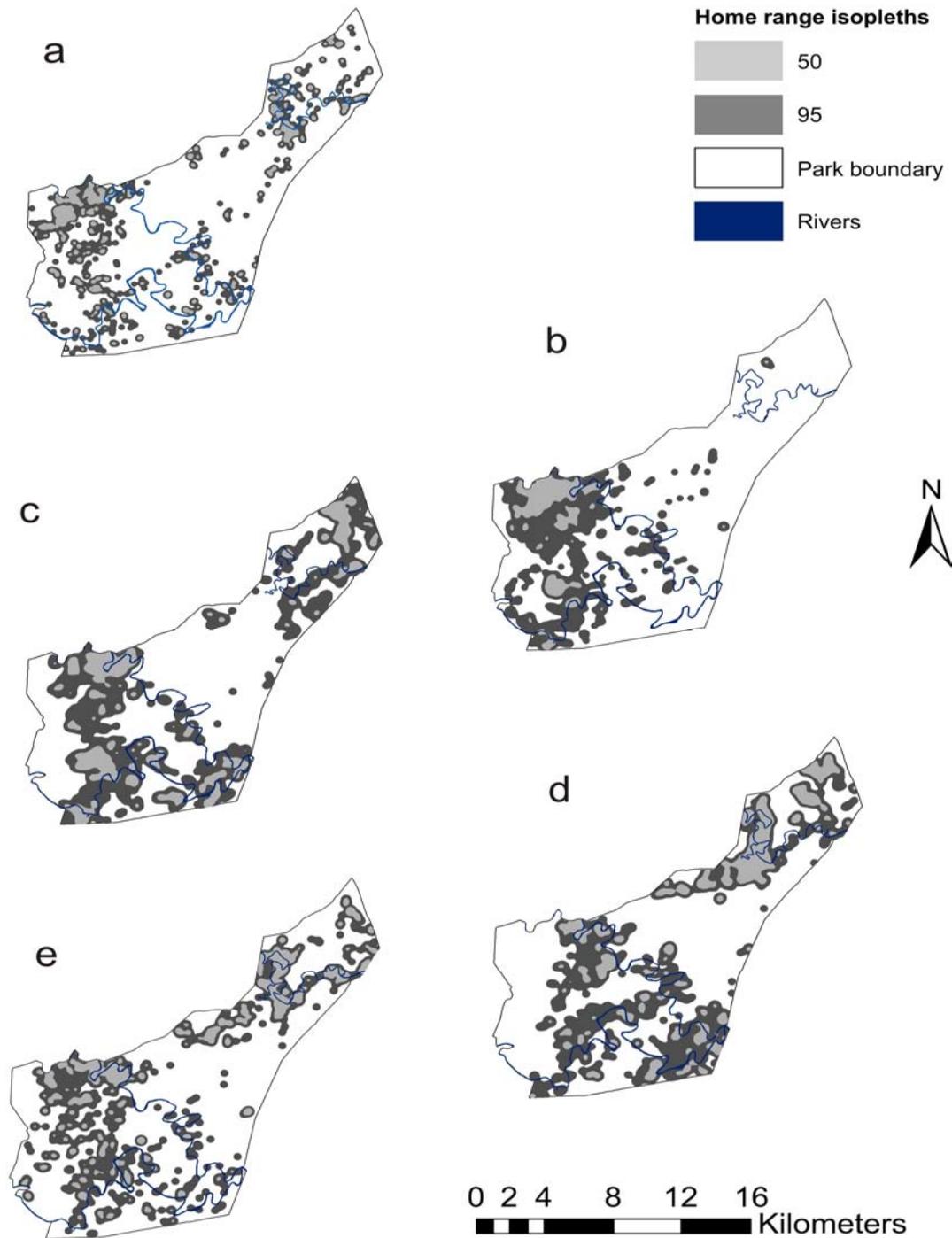


**Fig. 1**: Home ranges for each breeding herd in Hluhluwe-iMfolozi Park in Wet Season 1. Herds are identified by letters (Herd 1 (a); Herd 2 (b); Herd 3 (c); Herd 4 (d); Herd 5 (e)).
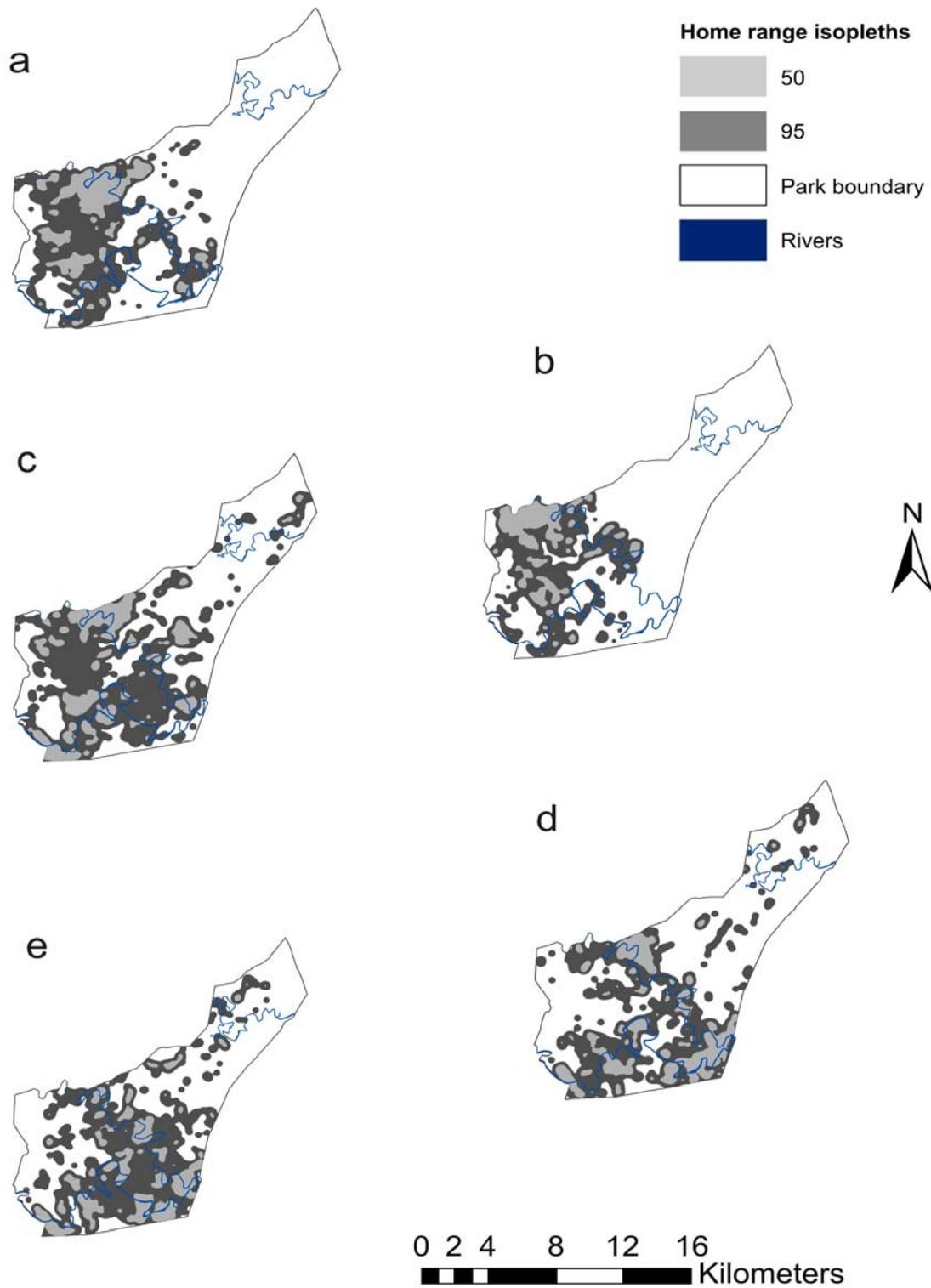
**Fig. 2**: Home ranges for each breeding herd in Hluhluwe-iMfolozi Park in Wet Season 2. Herds are identified by letters (Herd 1 (a); Herd 2 (b); Herd 3 (c); Herd 4 (d); Herd 5 (e)).
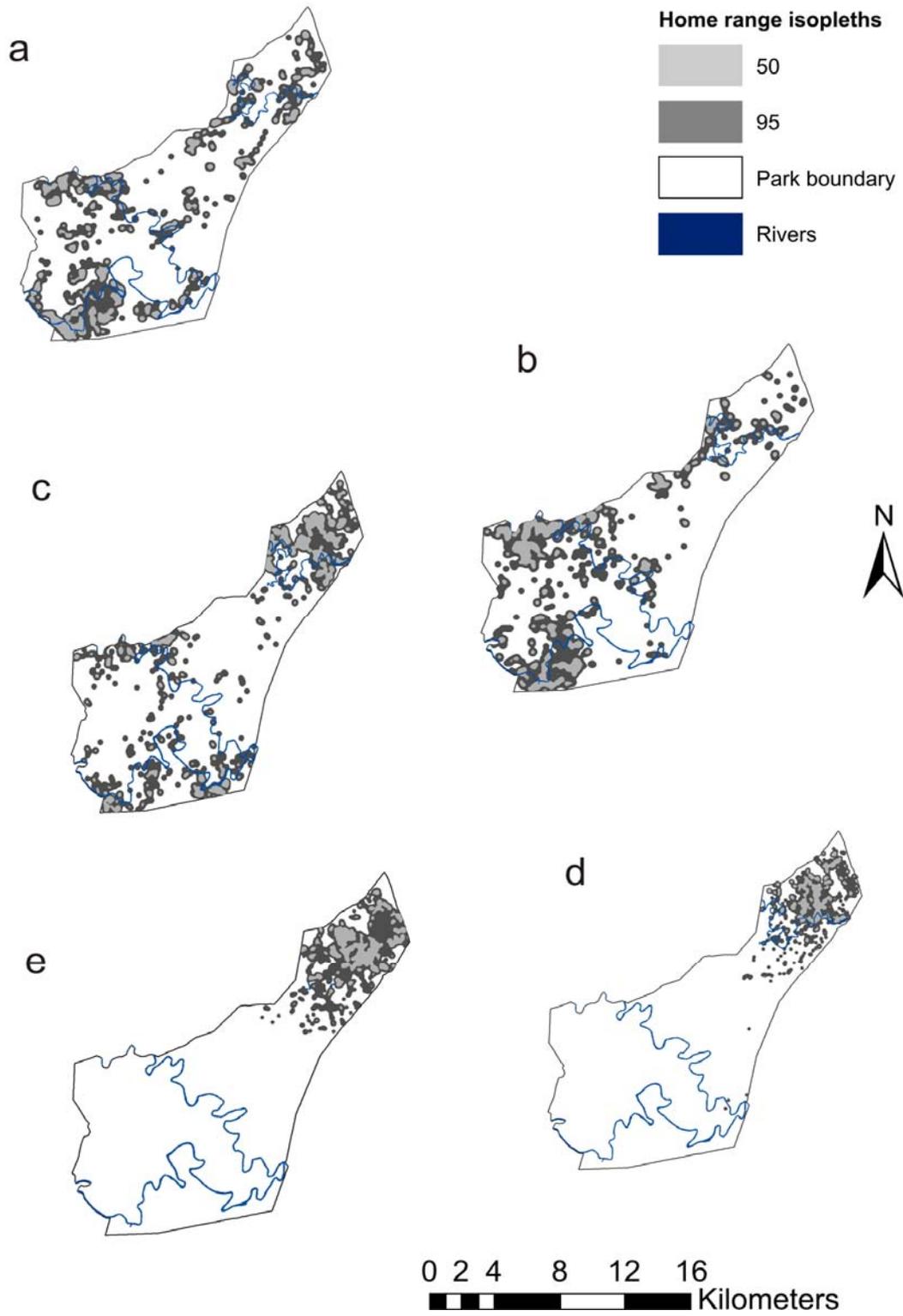
**Fig. 3**: Home ranges for each breeding herd in Hluhluwe-iMfolozi Park in Dry Season 1. Herds are identified by letters (Herd 1 (a); Herd 2 (b); Herd 3 (c); Herd 4 (d); Herd 5 (e)).

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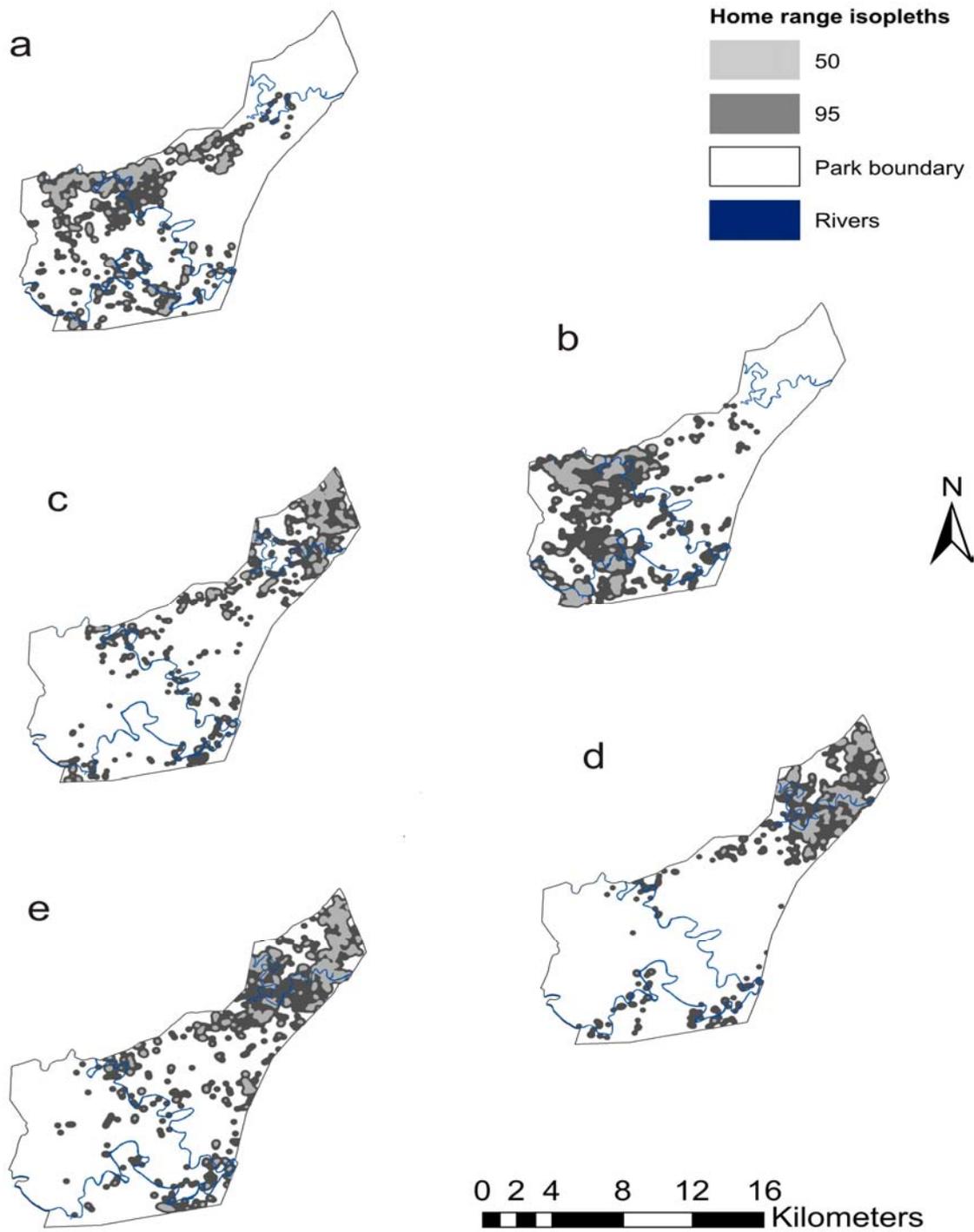


**Fig. 4**: Home ranges for each breeding herd in Hluhluwe-iMfolozi Park in Dry Season 2. Herds are identified by letters (Herd 1 (a); Herd 2 (b); Herd 3 (c); Herd 4 (d); Herd 5 (e)).