Determinants and consequences of elephant spatial use in Southern Africa's arid savannas

by

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I dedicate this work to my father, Johan de Beer.

Although he doesn't share this life with us anymore,

he remains alive in my heart…..always.

Determinants and consequences of elephant spatial use in Southern Africa's arid savannas

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ABSTRACT

Elephants live in heterogeneous landscapes where they search for resources that conceivably will optimise their survival. The uneven distribution of such resources may be linked to landscape heterogeneity. I therefore hypothesized that landscape heterogeneity determines home range location and size. I evaluated home range sizes of elephants living in Etosha National Park (n = 6), Khaudum Game Reserve (n = 6) and Ngamiland District 11 (n = 4) during two wet and two dry seasons. I used landscape maps to quantify landscape heterogeneity based on five metrics calculated using FRAGSTATS and compared heterogeneity levels in elephant home ranges and randomly located ranges within each of the study areas. I further related elephant home range size to these landscape metrics and considered the relationship between home range size and water point density. Landscape metrics differed significantly between study areas. Elephants in Etosha and NG11 selected for Largest patch index,

Landscape shape index, Contagion and Shannon diversity index, while those in Khaudum selected only for Largest patch index and Landscape shape index. Elephants therefore seem to locate their home ranges in areas of the landscape where higher levels of heterogeneity occur during wet and dry seasons. The results of this study further suggest that differences in home range size can best be explained by water point density. Heterogeneity is an inherent characteristic of landscapes and seems to reflect on the availability of resources that may subsequently influence the way elephants utilise space. My study supports the notion that management of elephants should be directed at ensuring the inclusion of heterogeneous landscapes in conservation areas and at reconsidering water management policies that may impair landscape selection. This may address local elephant impacts through local and regional movements driven by landscape selection.

ACKNOWLEDGEMENTS

DISCLAIMER

The outline of this dissertation follows the format requirements for the *African Journal of Ecology.* This study originated from previous work (de Beer *et al.* 2006) published in the *Journal of Arid Environments* that deals with the consequences of landscape utilisation by elephants. I declare that *Determinants and consequences of elephant spatial use in Southern Africa's arid savannas* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

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Yolandi-Mari de Beer   August 2007

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CHAPTER 1

INTRODUCTION

BACKGROUND & RATIONALE

Across southern Africa, the transfrontier, transboundary and megapark initiatives aim to address biodiversity conservation through the development of networks of conservation areas throughout the region (van Aarde & Jackson, 2007). The ecological delineation of such areas may be based on the metapopulation requirements for species that will promote biodiversity conservation without excluding people. The focus is to enhance habitat connectivity through landscape restoration and thereby to promote the long-term viability of ecosystem processes by ameliorating undesirable impacts, such as those that may be induced by elephants that cannot move freely across landscapes (van Aarde *et al*., 2006).

The landscape approach to conservation is fashionable (Hansson & Angelstam, 1992; Simberloff, 1998) and is catered for by the so-called habitat paradigm (see Armstrong, 2005). This approach does not focus on a single species but also does not necessarily ensure the conservation of all the species concerned (Sergio *et al*., 2003). The metapopulation metaphor, with its compelling theoretical foundation (see Hanski, 1998; 1999), however, holds much promise for the integration of species and ecosystem approaches to improve conservation strategies (van Aarde & Jackson, 2007).

Empirical support for the metapopulation theory, especially for large mammals (Elmhagen & Angerbjörn, 2001; Dixon *et al*., 2006) is accumulating in the literature (Sæther *et al*., 1999; Brito & Fernandez, 2002; González-Megías *et al*., 2005). In an effort to provide ecological support, the megapark initiative that is

outlined by van Aarde *et al.* (2006) uses the African savanna elephant (*Loxodonta africana*) as a surrogate entity for conservation planning across southern Africa.

Conservation planning at the landscape level can benefit from single species as surrogates (Simberloff, 1998). For instance, the ecological role of elephants in their diversifying effect on ecosystems is regarded as that of a keystone species (Western, 2003). Elephants are also considered as an umbrella species (Andelman & Fagan, 2000) because their large ranges include those of most other species (Caro & O'Doherty, 1998). As a charismatic species, elephants attract much public and donor attention, making their status as a flagship of conservation very useful (Caro & O'Doherty, 1998; Simberloff, 1998; but also see William *et al.*, 2000). However, although the conservation of elephants makes sense, the management of elephants remain a complex and controversial issue (see van Aarde *et al.*, 1999; Gillson & Lindsay, 2003; Whyte *et al.*, 2003; Owen-Smith *et al.*, 2006; van Aarde & Jackson, 2007).

Elephants confined to protected areas may influence local biodiversity as they often modify vegetation structure and composition within the area (see Laws, 1970; Owen-Smith, 1988; Herremans, 1995; Owen-Smith, 1996; Cumming *et al.*, 1997; O'Conner *et al.*, 2007, Guldemond & van Aarde, in review). Consequently, the management of elephant numbers are motivated by the apparent impact they may have for biodiversity (e.g. Whyte, 2004). Management options range from culling and contraception to translocation and range expansion. The application of culling and contraception is controversial and does not necessarily address impact (see Whyte *et al.*, 1998; van Aarde *et al.*, 1999; Pimm & van Aarde, 2001; Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006). Translocation also does not address impact issues (see van

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Aarde & Jackson, 2007), especially when establishing populations on relatively small properties.

Management may further drive elephant impact on biodiversity. For instance, management interferences such as the construction of fences around some protected areas as well as the artificial redistribution of water has implications for the use of habitat (e.g. Grainger *et al.*, 2005; de Beer *et al.*, 2006). Fencing may preclude range adjustments needed to ensure the continued survival of species populations in the wake of global climate change (Ogutu & Owen-Smith, 2003; Thomas *et al.*, 2006). Also by reserving a relatively small fraction of a landscape the reduction of species imposed by species-area relationships (reviewed by Rosenzweig, 2003) may only be delayed as certain species alter the living conditions for co-occurring species (Owen-Smith, 1996).

The artificial provisioning of water as a management tool may alter patterns of landscape use and modify habitat conditions. For example, water augmentation negatively affected roan antelope by favouring more common water-dependent species such as zebra (*Equus burchelli*) and blue wildebeest (*Connochaetes taurinus*) in South Africa's Kruger National Park (Owen-Smith, 1996; Harrington *et al.*, 1999). Furthermore, the short-term benefits of increased water supply for ungulates may be at the expense of their long-term viability through starvation-induced mortality during extended droughts (Walker *et al.*, 1981; Owen-Smith, 1996). This is especially relevant for intensely managed conservation areas across southern Africa, where dry and hot conditions over several months of the year force water-dependent species to use artificial water points (Gaylard *et al.*, 2003).

For elephants, fencing and water provisioning may prevent shifts in the use of the landscape (Leggett, 2006; Smit *et al.*, 2007) and this may cause prolonged

pressure on occupied habitats. As the vegetation gets depleted elephants may enlarge the piosphere area through a spillover effect (Brits *et al*., 2002), which may further impede the survival of other species. Fencing and water provisioning also provides all the resources for elephant populations to increase without any natural reductions (i.e. drought-induced mortality – Walker *et al*., 1981; Dudley *et al*., 2001) which may control their numbers (Owen-Smith *et al*., 2006; van Aarde & Jackson, 2007).

The megapark research initiative therefore emphasises the metapopulation metaphor as a platform for the development of a conservation management alternative for elephants (van Aarde *et al*., 2006). The megapark concept aims to simulate some of the outcomes of metapopulation dynamics by allowing dispersal between presently distinct elephant populations. It aims to restore linkages and parts of the former elephant distribution range, thereby capitalizing on the outcomes of landscape heterogeneity for demography. The research specifically focuses on the demography, spatial dynamics and dispersal of all elephant subpopulations across southern Africa[1].

Functional megaparks need to include gradients of ecological conditions and both occupied and vacant habitats for elephants (van Aarde & Jackson, 2007). To encapsulate the spatial dynamics of a metapopulation the megapark needs to be delineated by landscape features. The outlining of sets of megaparks for elephant populations should consider the consequences of habitats for demography. Differences in habitat quality can be reflected on individual fitness, which, at the population level, shows up in demographic responses such as age-specific fecundity and survival (Sibly & Hone, 2003).

The foundation of metapopulation dynamics is that habitat selection starts with the individual having the ability and opportunity to select habitat that will optimise its

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[1] For further details about the ongoing research on the megapark initiative at CERU see
www.up.ac.za/academic/zoology/ceru/Home.htm

fitness (Morris, 2003). Landscape variables may have consequences for the physiological well-being of an elephant through properties that can enhance thermoregulation (Kinahan *et al*., 2007). At a larger scale, habitat patches with high productivity may provide resources of high quality, which elephants may select (Western & Lindsay, 1984). The availability of resources and the way elephants use resources at different scales may therefore influence their spatial dynamics at the landscape level. Thus, to determine if elephants may expand or shift their ranges to previously unoccupied areas, it is important to identify the underlying environmental causes of their movements within their current distribution. Understanding the relationship between elephant spatial use and landscape heterogeneity and how the landscape template and water distribution affects movement patterns of elephants are therefore essential.

The main purpose of this study was to investigate whether landscape heterogeneity was a key determinant of elephant home range variables such as location and size. Within the metapopulation framework described in the introduction, this study serves as the first step towards identifying landscape characteristics that may be used in the delineation and subsequent management of megaparks.

The megapark initiative incorporates research on elephants in the area between 18º and 20º E & 15º and 23º S. The area includes elephants living in the Etosha National Park and Khaudum Game Reserve in northern Namibia as well as those in the Ngamiland District 11 along the Okavango Panhandle in north-western Botswana. These three areas represent a longitudinal gradient of rainfall and signify different management situations (see Chapter 2) within the arid savannas. I therefore included the three study areas to investigate whether the proposed relationship between home

range variables and landscape heterogeneity holds across different environmental and management regimes.

Metapopulations

Theoretically, a collection of local populations forms a natural metapopulation. It persists on a regional scale by maintaining a balance between local population extinctions and colonisations (Hanski & Thomas, 1994). Metapopulation theory considers the role that spatial heterogeneity may play in determining population dynamics whereby different individuals of the same population occupy habitat patches of different qualities (Dunning *et al*., 1992). It allows for the migration of individuals between local populations from favourable habitat patches (sources) to unfavourable patches (sinks) (Pulliam, 1988; Hanski, 1998; Thomas & Kunin, 1999).

As metapopulations responds to habitat modification (e.g. through fragmentation or climate change), their persistence depends on the availability, suitability and accessibility of occupied and vacant habitats (Hansson, 1991; Freckleton & Watkinson, 2003). When habitats are isolated, the processes underlying metapopulation dynamics cannot function. The functioning of these processes is therefore dependant on connectivity between subpopulations (Hansson, 1991; Dias, 1996; Hanski, 1999; Olff & Ritchie, 2002). Consequently, when dealing with metapopulations, the conservation of habitat and connectivity between habitats should be emphasised (Dias, 1996; Freckleton & Watkinson, 2003; Bowne *et al*., 2006).

The landscape

The landscape is a heterogeneous mosaic of different land type patches (habitats or vegetation classes) in a defined area (Forman & Godron, 1986) that is usually scaled relative to the organism or process of interest (Wiens, 1989). Heterogeneity refers to the complexity and variability of the spatial pattern contained by the patches within the mosaic (Li & Reynolds, 1994). A patch is considered a homogenous area that differs from the surrounding landscape (Wiens, 1976). Heterogeneity in the landscape generally reflects on the spatial availability of resources, which may influence home range size (Johnson *et al.*, 1992). At the landscape scale, relatively high levels of heterogeneity due to an increased amount of edge habitat (Tufto *et al.*, 1996; Saïd & Servanty, 2005) or greater diversity of resources (Honnay *et al.*, 2003; Ortega *et al.*, 2004) may benefit elephants through stabilising the availability of resources. Increased heterogeneity therefore may imply increased availability of resources, which may result in an animal having a smaller range that will satisfy its resource requirements.

The composition and structure of the landscape mosaic is temporally and spatially dynamic (Wiens *et al.*, 1993). The landscape offers resources that vary in quantity and quality over time and space (Gough & Rushton, 2000). Resource distribution across landscapes has implications for the demographic variables such as mortality and natality (Sibly & Hone, 2003). For large herbivore populations, such as elephants, resource limitation may induce density-dependent mortality, especially during dry periods when environmental conditions result in a decline in resource availability and quality (Sæther, 1997; Sibly & Hone, 2003). In contrast, when resources are abundant and of good quality, it may allow for increased population growth rates through increased juvenile survival and decreased age at first

reproduction (Fritz & Loison, 2006; Illius, 2006). Thus, population growth seems to be regulated by the variability in resource quantity and quality, which are in turn affected by environmental conditions (Wang *et al*., 2006). Landscapes are the templates from which animals acquire resources and are the matrices through which animals move to locate new resources (MacDonald & Rushton, 2003). Resource distribution across landscapes therefore influences the way that animals utilise space (Johnson *et al*., 1992; Gough & Rushton, 2000).

Elephants as selective users of landscapes

Elephants are large-bodied mixed feeders that use low-quality plant matter (Owen-Smith, 1988). Although labelled as generalists, they do select for certain plant species and plant parts (Ben-Shahar, 1993; de Boer *et al.*, 2000; Barnes, 2001; Osborn, 2004). Their preferences for certain habitats have been ascribed to a range of variables, these including the availability of food (Dublin, 1996), selection for nutrient-rich habitats (Ruggiero & Fay, 1994; Verlinden & Gavor, 1998; Houston *et al*., 2001) and plants with higher palatability (Owen-Smith & Cooper, 1987; de Boer *et al*., 2000, O'Connor *et al*., 2007), avoidance of rugged terrain (Nelleman *et al*., 2002), body-size and sexual segregation (Stokke, 1999; Stokke & du Toit, 2002; Shannon *et al.*, 2006) and thermoregulation (Kinahan *et al.*, 2007). None of these has been singled out as more important than another to explain the uneven distribution of elephants across landscapes.

At the landscape scale, relatively high levels of heterogeneity due to an increased amount of edge habitat (Tufto *et al.*, 1996) may benefit elephants. Optimal foraging theory (Emlen, 1966; MacArthur & Pianka, 1966) suggests that elephants should select such habitat (Farnsworth & Illius, 1998; Morris, 2003). However, to

maximise their daily energy intake there should be a trade-off between selection for scarce, high quality resources and the utilisation of lower quality resources that are presumably more abundant (WallisDeVries *et al.*, 1999; Illius, 2006). During critical periods, such as the dry season, elephants may be reliant on 'key-resources' that are sought after regardless of the spatial distribution of other resources (Illius, 2006). It is therefore expected that elephants may differentiate between different quality resources. At larger spatial scales, resource selection is directed at plant communities, habitat types and seasonal ranges. Selection may therefore accumulate across scales so that patchiness at the landscape scale may be another determinant in space utilisation (WallisDe Vries *et al*., 1999). A quantification of landscape heterogeneity and the apparent selection for variables encapsulated in landscape heterogeneity metrics therefore may explain the uneven distribution of elephants across landscapes and their preferences for certain habitats.

The effects of landscape heterogeneity on the use of space by elephants have been investigated in the Kruger National Park (Grainger *et al.*, 2005). This study suggests that home range sizes are related to some measures of landscape heterogeneity. Water availability in Kruger, however, seems a strong determinant of home range size (Grainger *et al.*, 2005). Indeed, elephants in general tend to stay close to water during the dry season (see de Beer *et al.*, 2006) and to expand their ranges during the wet season (Osborn & Parker, 2003; Redfern *et al*., 2003; Gaylard *et al*., 2003; Leggett, 2006).

Selection for heterogeneity may be influenced by the artificial provisioning of water that may mask patterns in landscape use (Grainger *et al.*, 2005). Elephants may also respond differently to measures of heterogeneity across the region because of geographical variation in landscape heterogeneity.

AIM OF THE STUDY

The present study aims to determine whether variability in the location and size of elephant home ranges in Etosha National Park, Khaudum Game Reserve and Ngamiland District 11 can be explained by metrics of landscape heterogeneity.

WORKING HYPOTHESES

1. *Elephants locate their home ranges within areas of the landscape that are more heterogeneous than other areas.*

2. *Elephant home range size will decrease with increasing landscape heterogeneity.*

To evaluate the hypotheses I had to consider the following aspects related to landscape utilisation by elephants:-

The hypothetico-deductive approach to science is generally accepted as the most authoritative and favourable method to problem solving (Wu, 2006). I approached this study using this methodology, but kept in mind that this approach does provide some difficulties when dealing with landscape ecology (see Gutzwiller, 2002 for detail).

Landscapes are by their nature patchy. Indices of landscape heterogeneity are expected to vary across landscapes as abiotic variables such as climate and landform differ across space (Wiens *et al.*, 1993; Turner *et al.*, 2001). I therefore expected that landscape metric values would be different for the three study areas that are situated on different substrates and along a rainfall gradient that may range from around 200 to 700 mm. per year.

Landscape heterogeneity may also reflect on the availability of resources (Johnson *et al.*, 1992; Gough & Rushton, 2002). The uneven distribution of resources is expected to induce non-random patterns of spatial use and to induce landscape selection. Elephants are known to select for habitats that present optimal nutrition (Verlinden & Gavor, 1998; Houston *et al.*, 2001) and which provide for thermoregulatory needs (Kinahan *et al.*, 2007). Should heterogeneous landscapes provide better to the needs of elephants than those that are less heterogeneous I would expect elephants to select for aspects of landscape heterogeneity. Then landscape metrics measured for the elephant home ranges would imply higher heterogeneity than those for randomly located ranges.

Across southern Africa, elephants may concentrate their activities to areas near water during the dry season. During the wet season they may expand their ranges by roaming onto areas further a field (Western & Lindsay, 1984; Owen-Smith, 1996; Verlinden & Gavor, 1998; Wittemyer, 2001; Osborn & Parker, 2003; de Beer *et al.*, 2006; Leggett, 2006). I therefore expected that elephant home range sizes would be greater during the wet season than during the dry season.

Tufto *et al.* (1996) and Kie *et al.* (2002) suggest that the home range sizes of roe deer (*Capreolus capreolus*) and mule deer (*Odocoileus hemionus*), respectively, is inversely related to heterogeneity. I therefore expected that elephant home range size would be related to landscape metrics, especially during the wet season. The distribution of water underlies elephant movements (de Beer *et al.*, 2006; Jackson *et al.*, 2007) and I expected that water point density may further affect home range size of elephants. This may influence their apparent selection for resources and therefore, for landscape heterogeneity (Grainger *et al.*, 2005).

Summary of expectations

If landscape heterogeneity determined elephant home range location and size then I expect that:

1. Landscape heterogeneity within the home ranges of elephants will be higher than within similarly-sized, randomly located ranges.

2. Landscape heterogeneity within the wet season home ranges of elephants will be higher than within the dry season home ranges.

3. The size of elephant home ranges will differ between the wet and the dry seasons across the three study areas.

4. Elephant home range size will decrease with increasing landscape heterogeneity, especially during the wet season.

5. Elephant home range size will be related to water point density, especially during the dry season.

CHAPTER 2

STUDY REGION

The study region comprises three different areas, all situated between 15 and 23º East along the ~19^0 South longitude. From west to east, these study areas include the Etosha National Park, the Khaudum Game Reserve and the Ngamiland District 11 (Fig. 1).
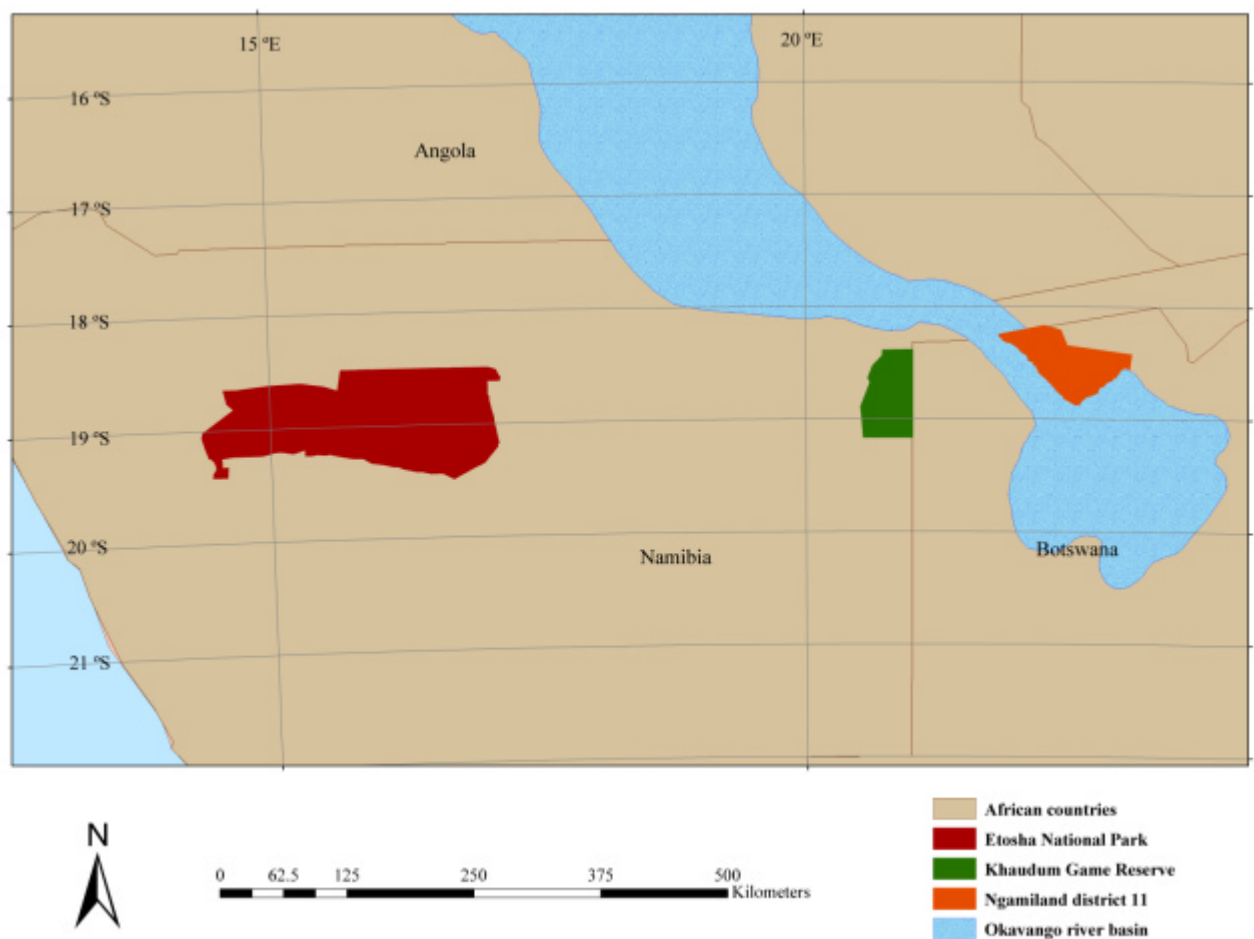
Figure 1. A map of the three study areas that occur along a regional west-east gradient along the 19º South longitude. The fences that surround Etosha National Park may restrict the movements of elephants living there, but this is not the case for elephants living in Khaudum Game Reserve and Ngamiland District 11. International boundaries that adjoin the latter areas could restrict elephant movements.

ETOSHA NATIONAL PARK

Etosha National Park[2] is a fenced off conservation area that stretches over an area of 22 270 km^2 in north-central Namibia (19ºS 16ºE). Etosha was first proclaimed as a Game Reserve in 1907 when it covered an area of 80 000 km^2. It then extended from the Kunene and Hoarusib River mouths eastwards to Namutoni (Berry, 1997). The Game Reserve was renamed the Etosha Game Park in 1958 when the area of the park had been reduced to 55 000 km^2. In 1976, the reserve was awarded national park status to become the Etosha National Park (Osborne & Versfeld, 2003). In 1970, the park was reduced to its current size (Berry, 1997).

Initially, boundary fences were constructed between 1955 and 1960 (Berry, 1997). In 1961, the establishment of a game-proof fence along the eastern and southern borders followed the outbreak of a foot-and-mouth epidemic. By 1973, the entire park was enclosed by fences (Berry, 1997). Tourism began in all earnest in 1955 and the three rest camps include Okaukuejo, Namutoni and Halali (Osborne & Versfeld, 2003).

Three distinct climatic seasons can be distinguished for the Etosha region: a cold, dry season from May to August, a hot, dry season from September until the rain starts, and a hot, wet season that starts with the onset of rains (usually in November) until April (Lindeque, 1988). Rainfall is highly erratic and in some years might start as early as September or as late as December. However, more than 95% of the annual rain falls between November and April (Data provided by the Etosha Ecological Institute, Namibia[3]). A rainfall gradient exists from east to west (Engert, 1997) where the mean (± SD) annual rainfall from 1971 to 2004 (n = 34 years) were 436 ± 127 mm at Namutoni in the east, 343 ± 113 mm at Okaukuejo in the central area of the park

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[2] From here on referred to as Etosha
[3] Etosha Ecological Institute, P.O. Box 6, Okaukuejo via Outjo, Namibia

and 287 ± 97 mm at Otjovasandu in the west. Since 1980, the annual rainfall has been mostly below the long-term average (see Fig. 2). Minimum and maximum daily temperatures vary between 6 ºC and 25 ºC and between 18 ºC and 35 ºC in winter (June - August) and summer (December - February), respectively (De Villiers & Kok, 1988).
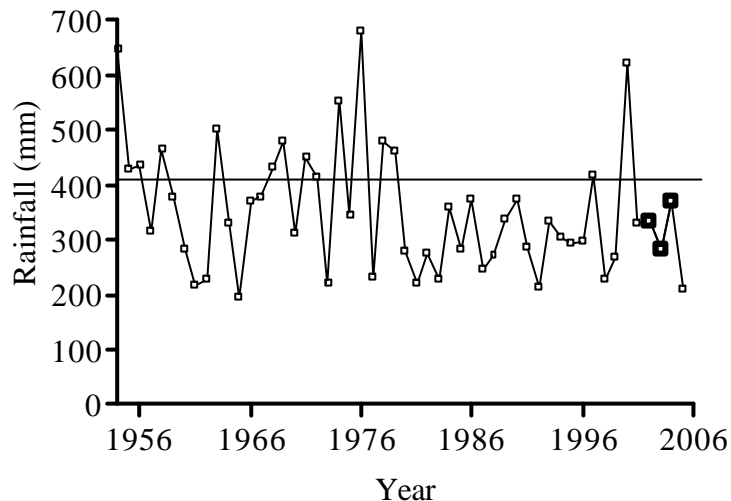
Figure 2. The annual rainfall recorded at Okaukuejo since 1940 varied greatly from year to year, but since 1980, values for most years were below the mean (indicated by horizontal line). The rainfall data were provided by the Etosha Ecological Institute, Namibia. Rainfall in the years during which elephant location data were collected (represented by bold symbols) were all below the long-term average.

Across Etosha 63 natural and artificial water points provide water for animals through the year (see Plate 1). Of these, 35 are boreholes and 28 are natural springs or artesian fountains of which five are maintained (Data provided by the Etosha Ecological Institute, Namibia). The quality of water of the waterpoints varies seasonally from good to saline (Auer, 1997).

The park is largely flat, except for the south-eastern and western edges that are rimmed by dolomite hills (Lindeque, 1988). Soils are mainly composed of calcareous sand and calcrete gravel (Lindeque, 1988; Beugler-Bell & Buch, 1997). Many low-lying turf clay pans are scattered across the park with the Etosha pan covering almost

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4 760 km^2 (Buch, 1997). These pans hold water mostly during the wet season and the beginning of the dry season after which this natural source of water becomes depleted.

Etosha is located in the transition area between the South West Arid, Namib Desert and Southern Savanna Woodland biotic zones. Consequently, it supports animals and plants that are typical of all three zones (Lindeque, 1988). Mopane woodlands and shrublands dominate the park (Lindeque, 1988). The woody vegetation in the south-central and eastern parts of the Park lies on calcrete and dolomite deposits (Lindeque, 1988). Mopane shrublands in the western parts of Etosha occur on loams and saline sandy soils. In the west, Kalahari woodlands are characterised by shrub-and-tree savanna, growing on deep sands and sandy loams. In the north-east, Kalahari woodlands grow on deep Kalahari sands. Scattered clay pans support some large trees and shrubs (Lindeque, 1988; Beugler-Bell & Buch, 1997).

Several large mammals live in Etosha. The most common species within the herbivore guild are the African elephant, Burchell's zebra, Hartmann's zebra (*Equus zebra hartmannae*), blue wildebeest, black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcephalus buselaphus*), black-faced impala (*Aepyceros melampus petersi*), kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), eland (*Taurotragus oryx*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), Damara dik-dik (*Madoqua kirkii*) and warthog (*Phacochoerus aethiopicus*). Large-bodied carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*) and black-backed jackal (*Canis mesomelas*) (Berry, 1997; Comley & Meyer, 1997).

De Villiers & Kok (1984; 1988), Viljoen (1989), Viljoen & Botma (1990), Lindeque (1988), Lindeque & Lindeque (1991), Leggett *et al.* (2003; 2004) and Leggett (2006) describes elephant distribution and movement in and around Etosha, but provide little more than speculation on the factors that explain variability in home range size. Some 2 000 elephants live in Etosha (van Aarde *et al.*, 2002), although breakouts do occur occasionally as a result of fences not being adequately maintained (Werner Kilian, pers. comm.[4]). The number of elephants remained relatively stable over the past few years (van Aarde *et al.*, 2002) possibly due to anthrax that induces a relatively high mortality rate (Lindeque, 1988).

KHAUDUM GAME RESERVE

The Khaudum Game Reserve[5] is situated in north-eastern Namibia (19ºS 20ºE) along part of the international border between Namibia and Botswana. This border forms the only boundary fence along the eastern side of the reserve (Fig. 1) and consequently animals are free to move across the other borders of the reserve. The reserve extends over 3 841 km^2 and is part of the Kavango region of Namibia (Mendelsohn & el Obeid, 2003).

The game reserve is bordered by communal land to the west and north, the Nyae-Nyae (Weaver & Skyer, 2005) and Gaum Conservancies (Dries Alberts, pers. comm.[6]) to the south and a large area of private farms that delineate a hunting concession to the west (Mendelsohn & el Obeid, 2003). Few people live in the areas bordering the reserve. In addition to the Nyae-Nyae and Gaum Conservancies, Namibian authorities are in the process of proclaiming other conservancies to the north and west of the Khaudum Game Reserve. The total area intended to be set aside

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[4] Werner Kilian, EEI, P.O. Box 6, Okaukuejo via Outjo, Namibia. eei.staff@mweb.co.na
[5] From here on referred to as Khaudum
[6] Dries Alberts, Ministry of Environment and Tourism, Tsumkwe. mettsumkwe@iway.na

for conservation in this region may add up to about 22 000 km^2 (Dries Alberts, pers. comm.). According to conservation officials, the conservancy development will entail the construction of additional water sources and the relocation of large mammals into these conservancies. These activities are directed at promoting tourism that may benefit the local economy.

Proclaimed in 1989, Khaudum is the only conservation area in Namibia that protects the northern Kalahari sandveld biome (Mendelsohn & el Obeid, 2003). The Namibian government is therefore considering the re-proclamation of Khaudum as a national park because of its importance to conservation (Dries Alberts, pers. comm.).

The wet (rainy) season in Khaudum begins in November and continues until April. More than 95% of the mean (± SD) annual rainfall of 487 ± 221 mm (n = 11 years) is received during the wet season (Fig. 3 - Data provided by the Ministry of Environment and Tourism, Tsumkwe, Namibia). Temperatures are typically hot in the summer and cold in the winter with daily variations of up to 20 ºC being usual for the region (De Sousa Correira & Bredenkamp, 1987).

Khaudum consists of a few temporary wetland systems that experience high evaporation rates and variability in water quality (Hines, 1993). In Khaudum, surface water accumulates in depressions and pans during the rainy season but water is also available from a few natural saline seepages and springs (Hines, 1993) that are typically opened by elephants in the dry riverbeds (omiramba[7]). During the dry season, the natural water supply disappears and elephants then apparently depend on water from 13 artificial sources maintained from boreholes (see Plate 2). The water provided in the reserve is generally of good quality with only two water points being unfit for game consumption (Wanke & Wanke 2007).

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[7] Dry riverbeds or drainage lines are locally referred to as omuramba (singular) or omiramba (plural).
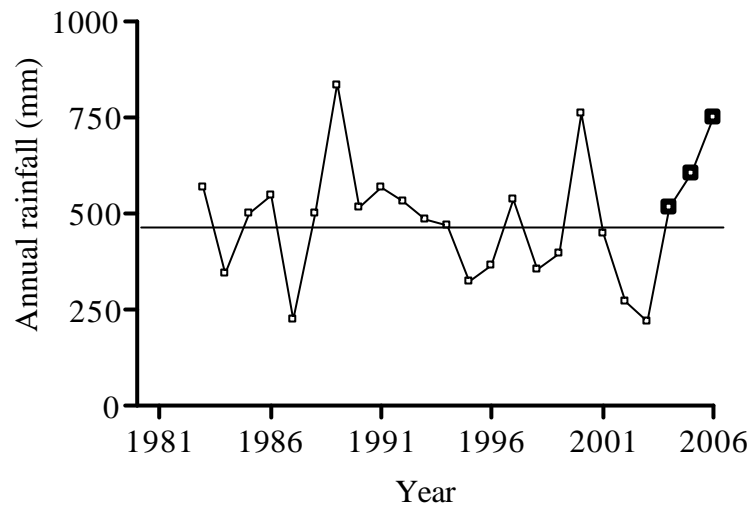
Figure 3. The annual rainfall recorded at Sikerretti in the southern-most part of Khaudum Game Reserve from 1985 to 2006 varied greatly from year to year. The horizontal line indicates the mean. The rainfall data were provided by Dries Alberts (MET, Tsumkwe). Rainfall in the years during which elephant location data were collected (represented by bold symbols) were all above the long-term average.

The soils in the reserve are predominantly arenosols, but patches of more fertile calcisols occur along the omiramba (Mendelsohn & el Obeid, 2003). Clear differences exist between the vegetation on the sand dunes where *Burkea africana* and *Baikiaea plurijuga* woodlands with *Guibourtia coleosperma* occur and the vegetation on the more clayey soils in the inter-dune valleys where the shrubby mixed vegetation are dominated by *Terminalia sericea*, *Acacia* species and *Combretum* species (Weaver & Skyer, 2005). Woodlands in the omiramba and certain clayey areas are characterised by patches of *Acacia* species in grasslands.

Some 3 100 elephants lived in Khaudum in 2004 (Data provided by the Ministry of Environment and Tourism, Namibia, 2004). The reserve also supports mammalian herbivores such as steenbok, gemsbok, blue wildebeest, buffalo (*Syncerus caffer*), tsessebe (*Damaliscus lunatus*), red hartebeest, eland, reedbuck (*Redunca*

arundinum), giraffe, roan antelope (*Hippotragus equinus*), kudu, common duiker and warthog. Large carnivores include lion, spotted hyaena, leopard and wild dog (*Lycaon pictus*). Khaudum is of particular conservation importance given that it provides habitat to rare species such as wild dog and roan antelope.

Since the provisioning of water, the elephant population have increased rapidly from a guestimated 80 in 1976 to the present population in excess of 3 000 (Weaver & Skyer, 2005). Most of these elephants apparently dispersed from elsewhere into the reserve and Weaver & Skyer (2005) claim that such movements are continuing. Colloquial wisdom suggests that some of these elephants even move as far away as southern Angola, western Botswana and the Caprivi.

NGAMILAND DISTRICT 11

The Ngamiland District 11[8] is situated along the Okavango Panhandle in north-western Botswana (19ºS 23ºE). NG11 stretches over 4 704 km^2 and is situated within a controlled hunting concession that extends over an area of 112 691 km^2 (Data were extracted from www.sharingwater.net). The international border fence between Namibia and Botswana in the north and the Okavango River to the south and west form the boundaries of NG11. Although NG11 is not fenced in the adjoining areas, NG12 and NG13, the latter areas are bordered by the so-called buffalo fences that isolate the region's elephants from those areas occurring further to the east along the major rivers.

Some 13 000 people live in several villages along the Okavango Panhandle and use the land for subsistence agriculture (Central Statistics Office Botswana, 2002). These small-scale agricultural activities include the growing of crops (mainly

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[8] From here on referred to as NG11

maize, groundnut, millet and watermelon) and the keeping of livestock, such as goats, donkeys, horses, chickens and cattle (Mendelsohn & el Obeid, 2004).

The area receives 472 ± 154 mm (mean ± SD, n = 23 years) of rain annually and more than 95% thereof fall from November to April (Fig. 4 – Data provided by the Meteorological Services, Botswana 2004). Rainfall in Botswana is unpredictable and droughts commonly occur. No artificial water points exist within the area and during the dry season humans, livestock and wild animals are largely dependent on the Okavango River for water (McCarthy, 2006).

The soils are predominantly deep Kalahari sands, but arenosols (wind-blown sands) occur along the panhandle (Mendelsohn & el Obeid, 2004). *Burkea africana* and *Baikiaea plurijuga* woodlands dominate the area, but stands of mopane (*Colophospermum mopane*) woodland are also prominent along the panhandle (Mendelsohn & el Obeid, 2004). Other vegetation includes shrubbed grasslands and woodlands with *Acacia* species, where *Baphia massaiensis* and *Terminalia sericea* are typical. The NG11 supports a relatively low wildlife biomass, but mammals that occur here include common duiker, impala (*Aepyceros melampus melampus*), tsessebe, reedbuck, red lechwe (*Kobus leche*), sitatunga (*Tragelaphus spekei*), hippopotamus (*Hippopotamus amphibious*), buffalo, kudu, giraffe, eland, gemsbok, blue wildebeest, steenbok, lion, spotted hyaena and leopard (Mendelsohn & el Obeid, 2004).

In NG11, an estimated 3 579 elephants occurred during the 2003 dry season and 1 060 during the 2004 wet season (Jackson *et al*., 2007). Elephant movements in the region seem to be limited by the international and buffalo fences. In spite of this, they disperse widely during the wet season but remain relatively close to the river during the dry season (Jackson *et al*., 2007).
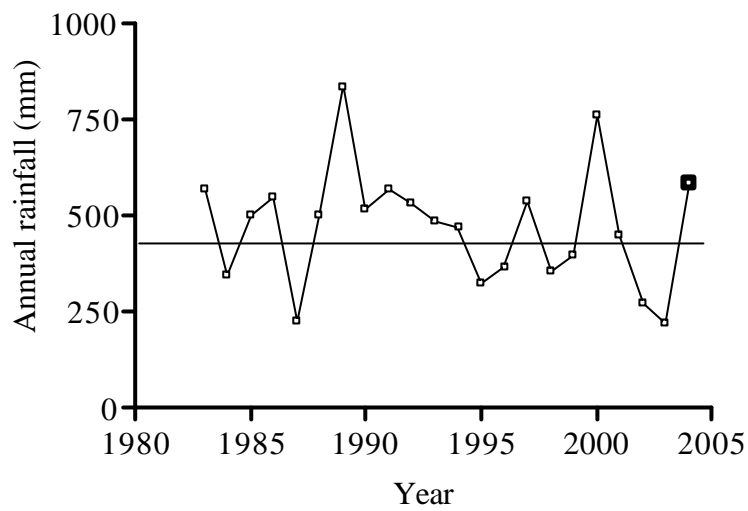
Figure 4. The annual rainfall recorded at Shakawe in Ngamiland District 11 from 1983 to 2004. The horizontal line indicates the mean. The data on rainfall was provided by the Meteorological Services, Botswana. Rainfall in the one year of available data during which elephant location data were collected (represented by bold symbols) was above the long-term average.

CHAPTER 3

MATERIALS & METHODS

ELEPHANT HOME RANGE ANALYSIS

The size of elephant home ranges were estimated from location data obtained from satellite GPS (Global Positioning System) units fitted to collars (model AWT SM2000E, Africa Wildlife Tracking[9]). The collars were placed around the necks of adult cows that live in different breeding herds in Etosha (n = 6), Khaudum (n = 6) and NG11 (n = 4). CERU used standardised procedures sanctioned by the ethics committee of the University of Pretoria that agreed with the standards maintained by the Namibian Ministry of Environment & Tourism and the Botswana Department of Wildlife & National Parks. These GPS units provided an accuracy of 9.0 ± 3.0 metres (mean ± SD; n = 6 – Martin Haupt[10], Africa Wildlife Tracking). These elephant cows were collared in different locations to represent the entire area of Etosha, Khaudum and NG11 and thereby to include all the different habitat types that the areas constitute.

More recent work by Ott (2007) suggests that the accuracy and precision of GPS locations are dependent on the topography and the vegetation cover of the area being located. For example, vegetation with dense cover such as forest patches may reduce the number of successful locations recorded by the GPS, resulting in a misrepresentation of elephant presence (Ott, 2007). Moreover, locations logged on flat terrain are more accurate than locations recorded in mountainous terrain. For my study, GPS error induced by closed canopy vegetation and by the topography of

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[9] Africa Wildlife Tracking. 18 North Street, Rietondale, Pretoria, 0084, South Africa, sophie@awt.co.za

[10] Martin Haupt, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, mahaupt@zoology.up.ac.za

mountainous areas should not be a major concern in any of my analyses. GPS error was further reduced by using 95% kernel density estimates instead of the locations as individual points (Dussault *et al.*, 1999).

The relatively small number of elephants per study area was inevitable considering the cost of collaring and retrieving data on a daily basis over two years in order to obtain more than one set of data for the wet and the dry season. Years during which the data were collected also differed between study areas (see Chapter 4, Table 5 for specific time periods) as the data were collected as part of a long-term research initiative on spatial and demographic aspects of elephants across southern Africa. These discrepancies are considered in the conclusions that were drawn from the results of all analyses.

Elephant home range sizes were calculated with the Animal Movement extension (Hooge and Eichenlaub, 1997) of ArcView GIS 3.3 (ESRI, Inc. 2002) using the 95% fixed kernel home range estimator with least square cross validation (LSCV) smoothing. I used the kernel density estimate as it provides a more accurate (least-biased) estimate than other methods (Worton, 1989; Seaman & Powell, 1996; Seaman *et al.*, 1999, Börger *et al.*, 2006). Following my analyses which were based on the 95% kernel density estimates, it has been suggested that kernel estimates between 50% and 90% may be more accurate (Börger *et al.*, 2006) and Hemson *et al.* 2005 further indicated that LSCV smoothing may be problematic. The information presented in these recent articles will be taken into account when preparing the thesis for publication. Seaman *et al.* (1999) further recommend that the sample size per animal should be =50, with a minimum of 30 locations being acceptable. The minimum sample size for an elephant in this study was 49 locations (see Chapter 4, Table 5, p.40). To reduce the potential effects of temporal autocorrelation on the

estimates of home range sizes, I used only one location per day over several months for each elephant (see Swihart and Slade, 1985).

Home ranges were calculated for two dry seasons (May to October[11]) and two wet seasons (November to April) for elephants living in each of the study areas. I used a one-way ANOVA (STATISTICA v.7.0, Statsoft, Inc.)[12] to evaluate differences in home range sizes for the various seasons and study areas. For Etosha, I used the Unequal sample *post-hoc* test and for Khaudum and NG11 the Tukey multiple comparison *post-hoc* test (Winer *et al*., 1991).

LANDSAT IMAGERY AND CLASSIFICATION OF LANDSCAPE MAPS

Landscape maps for Etosha and Khaudum, depicting the dominant structural classes of each area, were prepared by classifying satellite TM images using the ERDAS protocol (Leica Geosystems GIS & Mapping, Illinois). The map for Etosha was produced by Grant Harris[13] (see Harris *et al*., in review), while the map for Khaudum was produced by the Agricultural Research Council, Institute for Soil, Climate and Water, South Africa. CERU provided field data for the verification and ground-truthing of these two maps. The landscape map I used for NG11 was obtained from the Harry Oppenheimer Okavango Research Center at the University of Botswana[14].

Satellite TM images of the study areas were obtained from which unsupervised classifications were created. These images were for the wet season to enable classification and ground-truthing when the vegetation was still in leaf. Etosha was covered by two satellite images (22 April 2000; Landsat TM7, serial number: 179

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[11] Location data for the 2006 dry season in Khaudum were only from May to September.

[12] The home range size data were normally distributed except in some cases where the sample sizes were too small. Variances between the home range sizes across the seasons and study areas were similar.

[13] USDA Fo rest Service - Chugach National Forest, 3301 C Street, Anchorage, AK 160; 99503, USA

[14] Conservation International, University of Botswana – Harry Oppenheimer Okavango Research Center. (2005) Elephant Habitat Mapping Project. Maun, Botswana.

- 73 & 19 April 2002; Landsat TM7, serial number: 180 - 73) (Harris *et al*., in review) while Khaudum was covered by one image (20 April 2004; Landsat TM5, serial number: 176 - 73). I visited the areas and recorded the locations of the various structural classes using a GPS. The structural classes depicted the dominant canopy species and growth structure (trees or shrubs) of the vegetation. Water was also considered a structural class. These data were used to develop signatures using the seed pixel technique with ERDAS Imagine software. These signatures enabled the supervised classification through maximum likelihood decision rules.

The supervised maps comprised a number of structural classes. Points randomly located on each of the maps provided a separate set of information for validation. The assessment of accuracy was based on the Kappa statistical procedure (Congalton, 1991).

All three of the maps were based on a raster grid of 30 × 30 m pixels as the minimum mapping unit. The maps were therefore considered to be fine-grained for the purpose of the study. Patch mosaic classifications that divide landscapes into homogeneous units may be biased and may lead to a loss of information (Murwira and Skidmore, 2005), especially in landscapes that are characterised by gradients of change rather than distinct patches, such as savannas (Pearson, 2002). However, information loss and changes in the landscape structure depend on the scale and grain (resolution) of the patch mosaic (Gustafson, 1998; Turner *et al*. 2001). The relatively high resolution of the maps I used therefore made it possible to retain the differences in the habitat characteristics and therefore landscape heterogeneity at the landscape scale, which may have been lost at lower resolutions (Boyce, 2006).

The Etosha map (Plate 1) with an overall accuracy of 76% (Harris *et al*., in review) originally consisted of 19 structural classes, which I reduced to 10 by

regrouping all classes that consisted of similar vegetation structure (Table 1). Two structural classes with *Acacia* species as the dominant vegetation were grouped as **Acacia dominant savanna**. I regrouped five structural classes that are dominated by *Colophospermum mopane* as **Mopane dominated woodland savanna**. Mopane mixed with *Catophractes alexandri* and/or *Acacia newbrownii* were also grouped together as **Mopane shrubs with *Catophractes & Acacia***. The **Broad-leafed savanna** in my structural classes comprises the original "Mixed tree savanna and *Lonchocarpus*[15] tree savanna". I also grouped "Grass", "Steppe" and "Peschuel shrub" together as **Grass & Steppe** as these have similar structural features.

The map for Khaudum (Plate 2) consisted of eight structural classes (Table 2). The accuracy assessment procedure yielded a value of 56%. For NG11, 10 structural classes (Table 3) were identified from the map (Plate 3) but the producers of the map did not provide an independent Kappa statistic.

The structural classes of the three study areas differ except for Mopane woodlands that occur in Etosha and NG11, *Baikiaea* woodlands and *Terminalia sericea* dominated woodlands that occur in Khaudum and NG11 and *Acacia* dominated woodlands that occur in all three study areas. Analyses were done separately for the three study areas because of the differences in the structural class component of the study areas.

The structural classes represent broad-scale patchiness in plant community types. Although it is implied that herbivores follow a selective foraging path within their directly visible environment (small-scale selection), WallisDe Vries et al. (1999) suggest that large scale heterogeneity in habitat types should elicit a directed search if the animal draws on previous experience to guide it. Broad-scale patchiness as

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[15] The genus *Lonchocarpus* recently changed to *Philenoptera*.

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defined by the structural classes in my study areas were therefore expected to be

meaningful to elephants.

Table 1. A description of the structural classes for the landscape map of Etosha National Park. The landscape map was produced by Harris *et al.* (in review) but the structural classes were reduced to those listed in the table.

Structural class	Description
Acacia dominant savanna	Vegetation dominated by shrubs and trees of various *Acacia* species on sandy soils.
Catophractes & *Acacia* savanna	Landscapes where *Catophractes alexandri* is interspersed with *Acacia newbrownii,* principally on loams and calcrete soils.
Catophractes alexandri savanna	Homogenous stands of *Catophractes alexandri* that mostly occur on calcrete soils but sometimes also on loams.
Dolomite rock savanna	A mixture of shrub and tree species that grow in red dolomite sands.
Broad-leafed savanna	Woodlands characterised by a variety of broad-leafed trees, including *Lonchocarpus nelsii* dominated patches, *Combretum* species *Commiphora* species, *Euclea* species, *Baikiaea plurijuga* and *Burkea africana.* The vegetation occurs on sandy soils.
Mopane shrub savanna with *Catophractes & Acacia*	Landscapes where *Colophospermum mopane* shrubs dominate and where *Catophractes alexandri* and/or *Acacia newbrownii* often co-occur.
Mopane dominated woodland savanna	Landscapes which are dominated by *Colophospermum mopane* shrubs and trees that occur on loams and saline sandy soils.
Pan	Sparsely vegetated low-lying saline silt areas where water may accumulate during rains.
Steppe & grass	Grasslands or grasslands that are interspersed with shrubs and/or invasive peschuel shrub that mostly occur at the edge of the Etosha pan on loams or loamy sands.
Water	Water accumulates in the field during the rainy season. Natural springs and artificial provisioning of water in the form of boreholes occur across the area. The availability of water changes from season to season and may influence its reflectance on the landscape map.
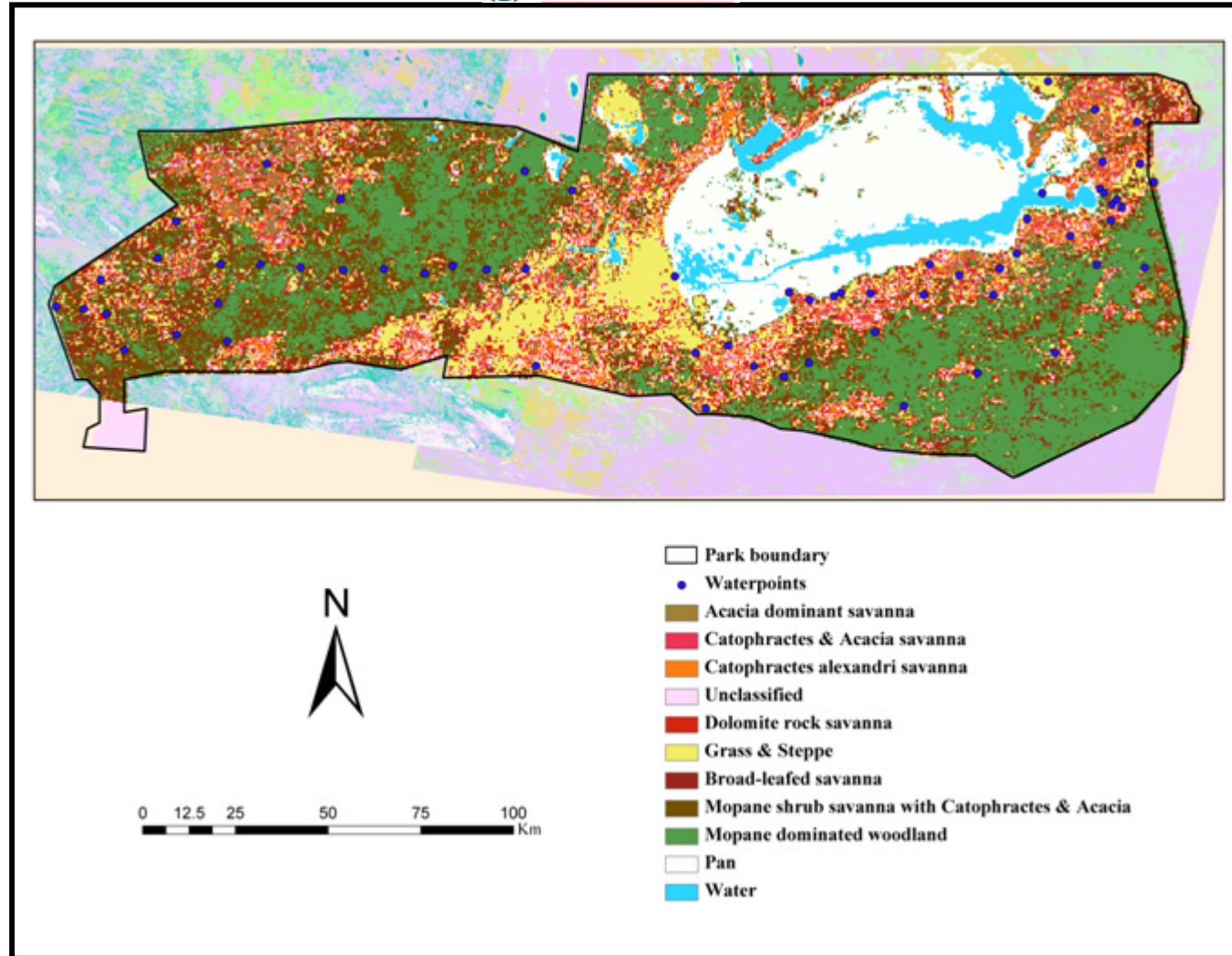
Plate 1. A landscape map of the Etosha National Park based on 10 structural classes (see Table 1) and the locations of waterpoints. The structure class 'unclassified' on the map refer to areas that were not covered by the satellite images and therefore not classified. The original landscape map was produced by Harris *et al*. (in review) using ERDAS software to classify a composite of Landsat TM 7 images. The present map is based on a reduction of structural classes.

Table 2. A description of the structural classes for the landscape map of the Khaudum Game Reserve. The descriptions are based on CERU's field observations and Wanke (2006).

Structural class	Description
Acacia woodland savanna	Landscapes where *Acacia* species dominate on shallow loamy sands, depressions, and drainage lines. Co-occurring species include *Grewia* species, *Boscia* species, *Combretum* species, *Dichrostachys cinerea*, *Peltophorum africanum* and *Catophractes alexandri*.
Baikiaea woodland savanna	Woodlands where *Baikiaea plurijuga* trees dominate on deep Kalahari sands (up to 8 m deep) with an understorey of shrubs and trees that include *Terminalia sericea*, *Baphia massaiensis*, *Ochna pulchra*, *Dichrostachys cinerea*, *Peltophorum africanum*, *Grewia* species & *Combretum* species.
Burkea woodland savanna	Woodlands where *Burkea africana* trees, which are often associated with the sporadic occurrence of *Schinziophyton rautanenii, Guibourtia coleosperma* and *Pterocarpus angolensis,* dominate on deep Kalahari sands (up to 8 m deep) with an understorey of shrubs and trees that include *Terminalia sericea*, *Ochna pulchra* and *Baphia massaiensis*.
Grassland	Homogenous patches of grass with the sporadic occurrence of individual shrubs and trees that occur along the dry river beds on dark clayey soils or other clay patches.
Terminalia prunioides woodland	Homogenous stands of dense woodlands that are dominated by *Terminalia prunioides* trees and mainly occur in the southern region of Khaudum on very shallow soils resting on bedrock ridges or calcretes.
Terminalia sericea woodland	Landscapes where *Terminalia sericea* shrubs and trees dominate on shallow Kalahari sands (up to 1.5 m deep) and co-occur with *Baphia massaiensis*, *Combretum* species & *Grewia* species.
Pan	Patches of bare ground and clayey pan areas that occur along the dry riverbeds and near dune valleys where it is often adjacent to *Acacia* woodland savanna and/or grassland.
Water	Water accumulates in pans during the wet season, but also occurs in the form of 13 artificial boreholes that are provided and maintained throughout the year. The availability of water changes from season to season and may influence its reflectance on the landscape map.
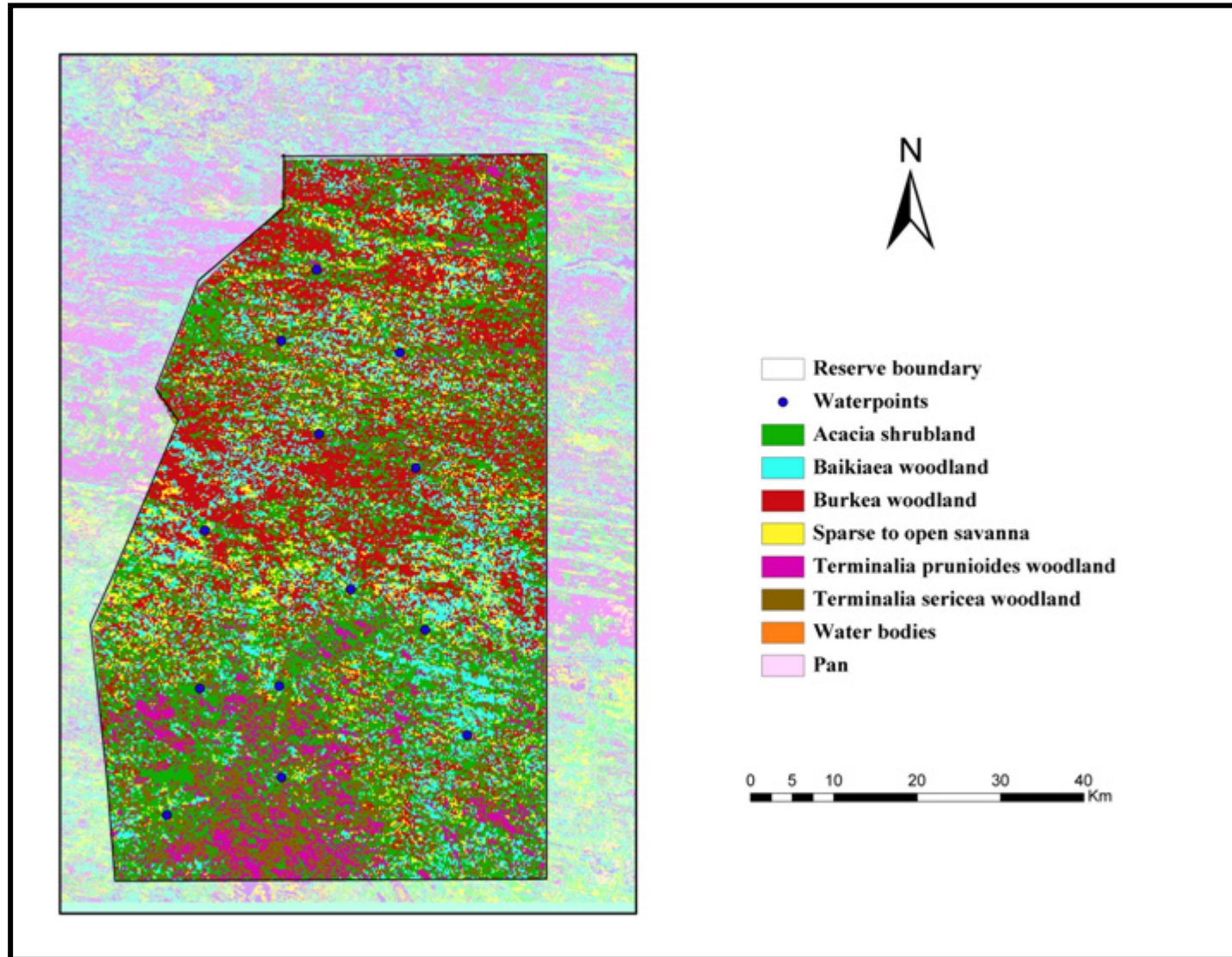
Plate 2. A landscape map of the Khaudum Game Reserve based on eight structural classes (see Table 2) and the locations of waterpoints. The landscape map was produced on contract by the Agricultural Research Council, South Africa using ERDAS software to classify a Landsat TM 7 images.

Table 3. A description of the structural classes distinguished for the landscape map of Ngamiland District 11. These descriptions are based on the information provided on the map obtained from the Harry Oppenheimer Okavango Research Center at the University of Botswana (2005) and Roodt (1998).

Structural class	Description
Terminalia and *Baphia* savanna	Dune valleys that are covered with a grass layer and dominated by *Terminalia* species and *Baphia massaiensis* shrubs and trees.
Mopane woodland	Woodlands that are dominated by *Colophospermum mopane* shrubs and trees and often associated with *Boscia mossambicensis* and *Grewia bicolor.*
Acacia dominated savanna	Landscapes where a variety of *Acacia* species dominate as trees and shrubs of differing heights.
Baikiaea woodland savanna	Open woodlands that area dominated by *Baikiaea plurijuga* trees and shrubs and which co-occur with a dominant grass layer.
Former floodplain	Plains that were previously flooded and which are covered with grass and shrubs that includes *Combretum* species.
Riparian zones	Riparian zone woodlands characterised by shrubs and trees of various species including *Myrica serrata.*
Dry floodplains and island interiors	Floodplains and island interiors that have become dry and which consist of bare ground and /or river vegetation that includes *Cyperus papyrus*, *Pechuel-loeschea leubnitziae* and *Carissa edulis.*
Swamp	Swamp vegetation that includes *Syzygium guineense*, *Garcinia livingstonei*, *Cyperus papyrus*, *Pechuel-loeschea leubnitziae* and *Phoenix reclinata* with *Capparis tomentosa*.
Burkea & *Baikiaea* savanna	Landscapes where *Burkea africana* and *Baikiaea plurijuga* trees and shrubs dominate.
Grasslands with sagebush	Grasslands where the shrub *Pechuel-loeschea leubnitziae* also occur.
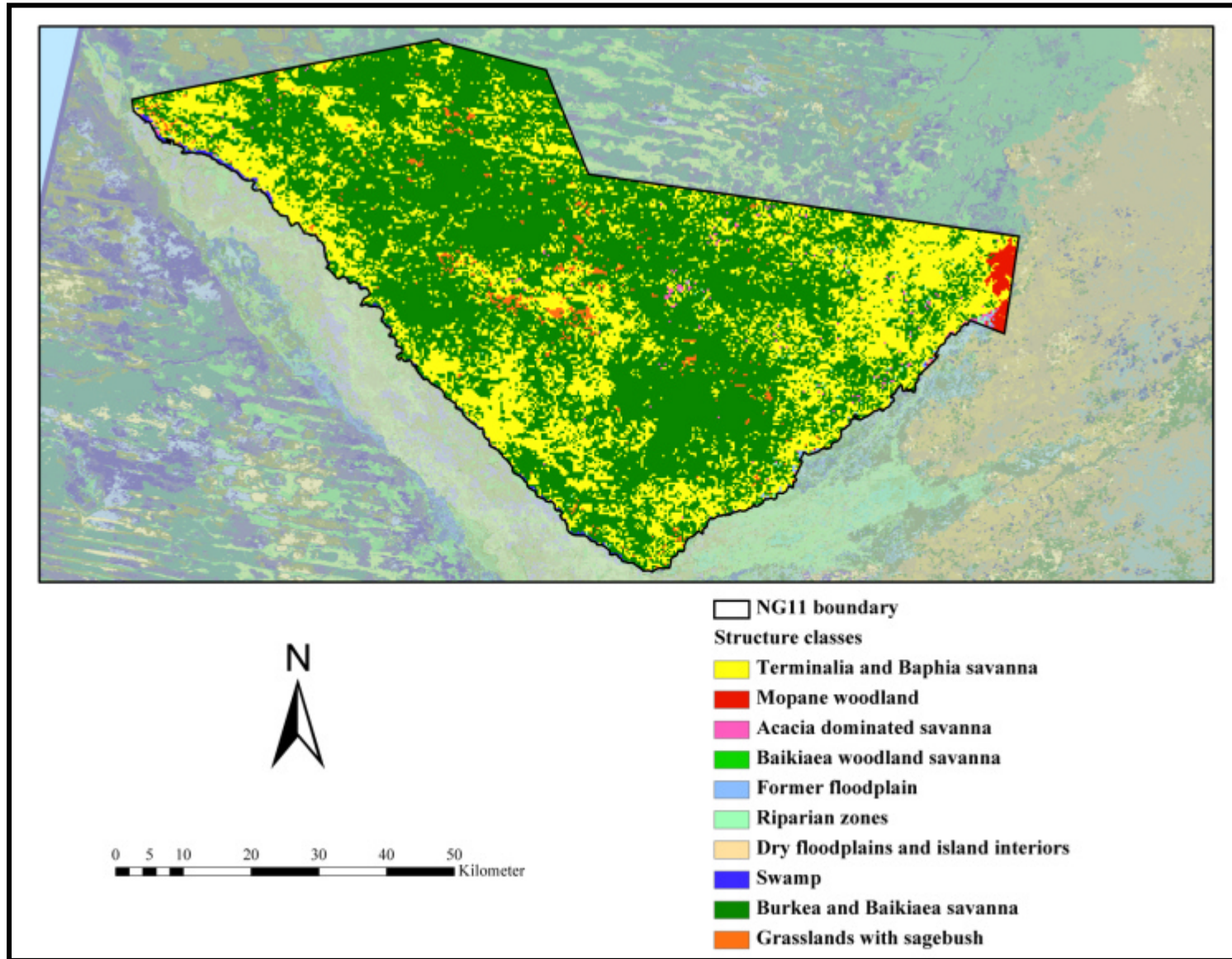
Plate 3. A landscape map of the Ngamiland District 11 along the Okavango Panhandle in northern Botswana that depicts ten structural classes (see Table 3). The map was obtained from the Harry Oppenheimer Okavango Research Centre at the University of Botswana.

LANDSCAPE HETEROGENEITY AS A DETERMINANT OF ELEPHANT SPATIAL USE

The use of FRAGSTATS to quantify landscape heterogeneity

Quantifying heterogeneity of the landscape requires measurements of different aspects of spatial patterns and structures (Li & Reynolds, 1994; Riitters *et al.*, 1995). Aspects such as the number, spatial arrangement and the shape of patches can be measured through a variety of different metrics (see McGarical & Marks, 1995) and software programmes (e.g. r.le programmes for GRASS GIS – Baker & Cai (1992), IAN – DeZonia & Mladenoff (2004) and RULE – Gardner (1999)).

FRAGSTATS v 3.3 (McGarical & Marks, 1995) is a spatial pattern analysis programme which quantifies landscape composition and configuration at different scales (patch, class and landscape) for categorical maps. Patch metrics quantifies aspects of each patch in the landscape mosaic. Class metrics measure the spatial distribution and pattern of each patch type within a landscape and can therefore be interpreted as fragmentation indices. Landscape metrics represent the spatial distribution and pattern of the entire landscape mosaic and consider all patch types simultaneously. Landscape metrics can therefore be interpreted more broadly as landscape heterogeneity indices (McGarical & Marks, 1995).

I used FRAGSTATS to quantify five landscape metrics (Table 4) as indices of heterogeneity to compare the landscape heterogeneity of the three study areas. The landscape metrics were selected following Riitters *et al.* (1995) and Li & Reynolds (1994). I considered metrics that were the least correlated and that were most representative of the different aspects of heterogeneity (See Turner *et al*., 2001) which includes the number of patches (Patch density), composition (Largest patch index), shape of patches (Landscape shape index) spatial configuration (Contagion) and diversity (Shannon diversity index). I only used area-corrected metrics as these

enabled comparison between the different areas and home ranges. I had no prior expectation about the meaningfulness of the metrics to elephants however, I assumed that it would depend on which aspects of heterogeneity might be meaningful to elephants.

The five landscape metrics were measured within the randomly located ranges (see next section) and the elephant home ranges. These were then used to determine selection by elephants for aspects of heterogeneity within the study areas. I used a single class metric, Percentage of land, to compare the composition of the structural classes within the study areas (representative of availability) to the composition within the elephant home ranges (representative of use).

A comparison of landscape metrics of randomly located ranges and elephant home ranges between the three study areas

Randomly located ranges were produced as independent random samples to represent the landscapes of each of the study areas. These ranges allowed me to quantify landscape metrics (see Table 4) for the study areas and allowed for their comparison with metrics that I calculated for the elephant home ranges.

Locations placed randomly in each of the study areas served as centroids for the positions of the randomly located ranges (ArcView GIS 3.3). Different locations were then generated at various size intervals around the centroids to create different sizes of randomly located ranges that were similar to those of elephant home ranges. Size intervals were at $500km^2$ circles within which the locations were randomly generated and the number of intervals depended on the minimum and maximum size of elephant home ranges. The locations were then used to estimate the areas of the ranges using the 95% fixed kernel density estimate. The shapes and sizes of the randomly located ranges were therefore reliant on the distribution of the randomly

generated locations within the circles at different size intervals. Initially, 10 repeats of each size interval were simulated to create enough variation in random range sizes between the upper and lower limits set by the elephant home range sizes. However, the logarithmic transformation of the data caused clumping towards the larger ranges and therefore I added more of the smaller ranges and deleted some of the larger ranges at random to enable a more even spread of the data. I thereby established a series of randomly located ranges of which the sizes ranged between the minimum and maximum values recorded for elephant home range sizes in each of the study areas[16].

I used FRAGSTATS to determine the five landscape metrics (see Table 4) for each of the randomly located ranges in the three study areas. I applied a one-way ANOVA with Tukey's multiple comparison *post-hoc* test (GraphPad Prism v.3; GraphPad Software, Inc.) for each of the five landscape metrics to determine if the landscape metrics calculated for the randomly located ranges differed between the three study areas.

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[16] The $\log_{10}$-transformed data (sizes and landscape metric values) obtained for the randomly located ranges were normally distributed and the variances were similar across the three study areas.

Table 4. A summary of the landscape metrics that were used to compare different measures of heterogeneity among the randomly located ranges within study areas and elephant home ranges. These are calculated with FRAGSTATS and based on the descriptions provided in McGarical & Marks (1995).

Landscape metrics	Metric description	Units	Range
Patch density	Measures the number of all patches per unit area and *increases with increasing heterogeneity.*	#/km^2	Patch density > 0, constrained by cell size. Maximum Patch density is attained when every cell is a separate patch.
Largest patch index	Measures the percentage of the total area comprised by the largest patch. The *metric decreases with increasing heterogeneity*.	%	0 < Largest patch index = 100. Largest patch index approaches 0 when the largest patch in the landscape is increasingly small. Largest patch index = 100 when the entire landscape consists of a single patch.
Landscape shape index	Measures the total edge or edge density while adjusting for the size of an area. The *metric increases with increasing heterogeneity*.	n/a	Landscape shape index = 1, without limit. Landscape shape index = 1 when the landscape consists of a single square patch; Landscape shape index increases as landscape shape becomes more irregular and as the length of edge within the landscape increases.
Contagion	Measures aggregation and interspersion of patches in an area and *decreases with increasing heterogeneity*.	%	0 < Contagion = 100. Contagion approaches 0 when the patch types are maximally disaggregated and interspersed. Contagion = 100 when all patch types are maximally aggregated; i.e., when the landscape consists of a single patch.
Shannon diversity index	Measures the proportional distribution of area among patch types and *increases with increasing heterogeneity*.	n/a	Shannon diversity index = 0, without limit. The index increases as the number of different patch types (i.e., patch richness) increases and/or the proportional distribution of area among patch types becomes more equal.

I also used FRAGSTATS to measure the five landscape metrics within each of the wet and dry season elephant home ranges. Given the small sample size of elephants and the relatively large sample size of randomly located ranges in each of the three study areas, statistical comparison of the means (or medians) of the metrics

measured for the elephant and the random ranges would bias the results. I therefore used a qualitative approach by comparing the distributions of the landscape metric values obtained for the elephant home ranges and those obtained for the randomly located ranges in the previous section (see p.34). Using scatterplots, I visually compared the means and the distributions of the landscape metric values for the randomly located ranges to the values for the wet and dry season elephant home ranges. I tabulated the results and summarised the differences and similarities of the results for each of the landscape metrics across the three study areas.

I used a one-way ANOVA to compare the landscape metrics measured for the wet and the dry season elephant home ranges of each study area. For Etosha, I used the Unequal sample *post-hoc* test and for Khaudum and NG11 the Tukey multiple comparison *post-hoc* test.

I calculated Percentage of land for the study areas to provide a measure of the availability of the structural classes within the study areas. I used a second-order (Johnson, 1980) compositional analysis (Aebischer *et al.*, 1993) to determine if elephants showed specific preferences for any of the structural classes relative to the availability of the structural classes.

I used curve-fitting facilities of Graphpad Prism v.3.0 to search for possible relationships between elephant home range size and the five landscape metrics (see Table 4, p.35) measured within elephant home ranges for each of the three study areas.

Water point density was expressed as the number of water points per 100 km^2 of elephant home ranges within Etosha and Khaudum. Here, water points are boreholes that provide water artificially, natural springs and natural springs that are artificially maintained. I used curve-fitting facilities of Graphpad Prism v.3.0 to search for possible relationships between home range size and water point density.

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CHAPTER 4

RESULTS

ELEPHANT HOME RANGE ANALYSES

A comparison of elephant home range sizes of the three study areas

The home range sizes for elephants in Etosha, Khaudum and NG11 are presented in Table 5. A one-way ANOVA suggested significant seasonal differences in the 95% kernel home range sizes of elephants in Etosha ($F_{3,17} = 6.563$, $p < 0.01$). The Unequal sample *post-hoc* testing showed that home range sizes were significantly smaller during the 2003 dry season than during both wet seasons ($p < 0.05$ & $p < 0.01$, respectively). However, this was not the case during the 2004 dry season ($p = 0.323$ & $p = 0.976$, respectively) and the difference between the home range sizes of the two wet seasons of Etosha was also not significant ($p = 0.833$).

In Khaudum, elephant home range sizes were similar during all seasons ($F_{3,20} = 2.833$, $p = 0.643$). The significant difference in home range sizes between seasons in NG11 ($F_{3,12} = 4.102$, $p < 0.05$) results from larger ranges during the 2004/05 wet season than during the 2004 dry season ($p < 0.05$). Home range sizes were similar for the two dry seasons ($p = 0.763$) and for the two wet seasons ($p = 0.975$). There was further no statistical difference in the home ranges sizes of the 2005 dry season and both wet seasons ($p = 0.0961$ & $p = 0.0726$, respectively) of NG11.

Elephant home range size did not change significantly with longitude during the wet (Fig. 5a) or the dry seasons (Fig. 5b).
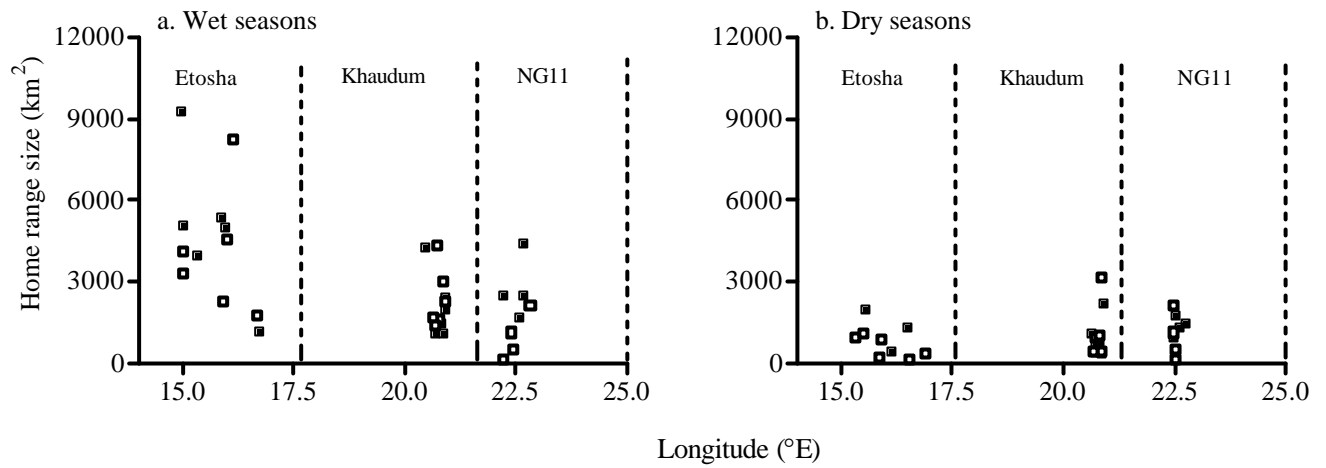
Figure 5. Elephant home range sizes during (a) the wet seasons and (b) the dry seasons as a function of the longitude at the centroids of the home ranges for Etosha National Park, Khaudum Game Reserve and Ngamiland District 11. Open and closed symbols indicate different years of home range sizes for the same elephants.

Table 5. The 95% kernel home range sizes for 16 elephants from three study areas. Mean home range sizes and standard errors of the means are presented for each of the areas and seasons, where wet seasons spanned from November to April and dry seasons from May to October. Values in brackets represent the number of satellite GPS locations for each of the elephants. Home range sizes for the 2002/03 and the 2003/04 wet seasons of Etosha National Park were significantly larger than those for the 2003 dry season. Home range sizes were also significantly larger during the 2004/05 wet season than the 2004 dry season of NG11.

Study area	Elephant ID	Home range size (km^2) 95% fixed kernel			
		Wet season 2002/03	Dry season 2003	Wet season 2003/04	Dry season 2004
Etosha	1	8174 (137)	863 (175)	9216 (144)	no data
	2	3268 (138)	938 (176)	5018 (133)	no data
	3	2224 (132)	207 (155)	5308 (164)	443 (115)
	4	4531 (110)	369 (176)	4942 (49)	no data
	5	4055 (138)	1062 (178)	3941 (170)	1941 (104)
	6	1710 (133)	112 (178)	1145 (162)	1310 (114)
n		6	6	6	3
Mean		3994	592	4928	1231
S.E. of mean		942	168	1062	434
		Wet season 2004/05	Dry season 2005	Wet season 2005/06	Dry season 2006
Khaudum	1	1586 (138)	899 (106)	1068 (93)	345 (123)
	2	3011 (156)	972 (133)	2360 (178)	393 (128)
	3	1629 (149)	423 (133)	1072 (170)	628 (128)
	4	2252 (148)	3151 (97)	1973 (166)	816 (126)
	5	1347 (148)	382 (120)	1428 (165)	2202 (125)
	6	4334 (155)	426 (135)	4251 (175)	1081 (125)
n		6	6	6	6
Mean		2360	1042	2052	911
S.E. of mean		465	435	492	281
		Dry season 2004	Wet season 2004/05	Dry season 2005	Wet season 2005/06
NG11	1	1105 (137)	1345 (158)	934 (129)	2433 (170)
	2	2074 (107)	3873 (124)	1440 (127)	4357 (164)
	3	82 (103)	2533 (141)	1298 (113)	2475 (157)
	4	493 (106)	3115 (153)	1724 (131)	1623 (168)
n		4	4	4	4
Mean		939	2717	1349	2722
S.E. of mean		433	533	164	579

LANDSCAPE HETEROGENEITY AS A DETERMINANT OF ELEPHANT SPATIAL USE

A comparison of landscape metrics for randomly located ranges between the three study areas

Comparisons of the five landscape metrics of the randomly located ranges of the three study areas yielded significant differences. Patch density (Fig. 6a), Landscape shape index (Fig. 6c) and the Shannon diversity index (Fig. 6e) values were the highest for Khaudum and the lowest for NG11. Largest patch index (Fig. 6b) and Contagion (Fig. 6d) values were the lowest for Khaudum and the highest for NG11. All five landscape metric values for Etosha were between those for Khaudum and NG11.
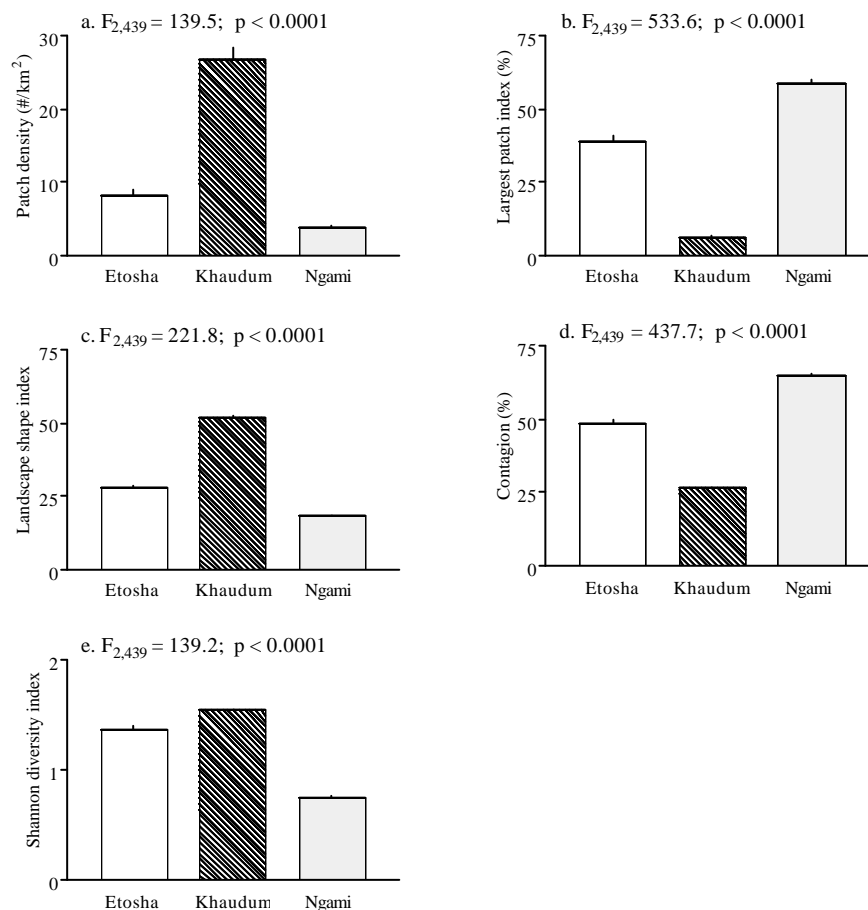
Figure 6. Illustration of the values (mean ± SE) for five landscape metrics measured within the randomly located ranges of Etosha National Park (n = 153), Khaudum Game Reserve (n = 147) and Ngamiland District 11 (n = 142). One-way ANOVA analyses indicated significant differences between the three study areas for each of the five landscape metrics. Tukey's multiple comparison *post-hoc* testing indicated significant differences (all p < 0.0001) between each of the three study areas for all the landscape metrics.

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A comparison of landscape metrics for elephant home ranges and randomly located ranges

A summary of the most prevalent qualitative trends for the comparisons between the elephant and the randomly located ranges for each of the landscape metrics is provided in Table 6. For Patch density (see Table 6 & Fig. 7a-c), values for the elephant home ranges were below the mean of the randomly located ranges during the wet seasons across all three study areas. In Etosha, there was an obvious seasonal difference in Patch density where elephant ranges had values lower than the mean of the randomly located ranges during both wet seasons (Fig. 7a). During the dry seasons, however, the variation between individuals was higher than during the wet seasons. In Khaudum, the 2004/05 wet season and the 2005 dry season showed more variation than the wet and dry seasons during the following year (Fig. 7b). In NG11, Patch density values were below the mean of the randomly located ranges, except for the 2004 dry season (Fig. 7c).

In all three study areas, Largest patch index (see Table 6) measured for the elephant home ranges were below the mean of the randomly located ranges across the wet and the dry seasons (Fig. 8a-c). The only exception was the 2005/06 wet season of NG11 where Largest patch index values were similar to that of the randomly located ranges. The apparent variation in the values for both wet seasons in Etosha was caused by the values for the home range of one individual (Fig. 8a).

The distribution of the values for Landscape shape index (see Table 6) indicated much individual variation (Fig. 9a-c). Landscape shape index for the elephant home ranges also varied within and between seasons across the study areas. In all three study areas, values of Landscape shape index tended to be higher than the mean of the randomly located ranges. The exceptions here were the 2005/06 wet

season of Khaudum and the following dry season, which tended towards the lower end of the distribution range of the values for the randomly located ranges (Fig. 9b).

During all seasons in Etosha (Fig. 10a) and the two dry seasons in NG11 (Fig. 10c), Contagion values (see Table 6) tended towards the lower end of the value distribution for the randomly located ranges. Mean Contagion values for elephant home ranges were similar to that of the randomly located ranges during all the seasons in Khaudum (Fig. 10b). Mean values during the 2004/05 wet season in NG11 were also similar to the mean values of the randomly located ranges (Fig 10c).

The Shannon diversity index values (see Table 6) for the elephant home ranges were above the mean of the randomly located ranges during the two wet seasons of Etosha (Fig. 11a) and the two dry seasons of NG11 (Fig. 11c). During the two dry seasons of Etosha (Fig. 11a) and all the seasons of Khaudum (Fig. 11b), the values of Shannon diversity index varied within the distribution range of the values for the randomly located ranges.

Table 6. Comparisons of the five landscape metrics measured for the elephant and the randomly located ranges for Etosha National Park, Khaudum Game Reserve and Ngamiland district 11 are presented in this table. The comparisons were based on the distributions of the values for the landscape metrics that are presented in Fig. 7 (Patch density), Fig. 8 (Largest patch index), Fig. 9 (Landscape shape index), Fig. 10 (Contagion) and Fig. 11 (Shannon diversity index). The differences and similarities across the three study areas are summarised in the last column. 'Random mean' refers to the mean value for the randomly located ranges.

Landscape metric	Study areas			Summary
	Etosha	Khaudum	NG11	
Patch density	• Values for elephant ranges same within seasons • Values for elephant ranges differed between seasons • Values for elephant ranges varied more during dry seasons • Values for elephant ranges below random mean during wet seasons	• Values for elephant ranges differed within seasons • Difference in values for elephant ranges within wet seasons same as dry seasons • Values for elephant ranges below random mean, except 2005 dry season • Two individuals caused variation during 2004/05 wet season and 2005 dry season	• Values for elephant ranges differed within seasons • Values for elephant ranges below random mean except 2004 dry season • One individual caused more variation during 2004 dry season	• Values for elephant ranges below random mean during all wet seasons of all three study areas • Seasonal difference in values for elephant ranges clear only in Etosha • Variation in values for elephant ranges caused by individuals
Largest patch index	• Values for elephant ranges same within seasons • Values for elephant ranges varied more during wet seasons, but caused by one individual • Values for all elephant ranges below random mean	• Values for elephant ranges same within seasons • Values for elephant ranges same between seasons • Values for elephant ranges below random mean	• Values for elephant ranges same within seasons • Values for elephant ranges differed between seasons • Values for elephant ranges below random mean except 2005/06 wet season	• Values for elephant ranges same within seasons • Values for elephant ranges below random mean during wet and dry seasons • Variation in values for elephant ranges caused by individuals

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Table 7. continued

Landscape shape index	• Values for elephant ranges same within wet seasons • Values for elephant ranges differed within dry seasons • Values for elephant ranges differed between seasons • Values for elephant ranges varied more during wet season, caused by individuals • Values for elephant ranges tend to be above random mean, but high variation between individuals	• Values for elephant ranges differed within seasons • Values for elephant ranges varied more during 2004/05 than 2005/06 • Values for elephant ranges during 2006 dry season below random mean • Values for elephant ranges during 2004/05 wet and 2005 dry seasons tend to be above random mean	• Values for elephant ranges differed within dry seasons • Values for elephant ranges differed between seasons • Values for elephant ranges above random mean except 2004 dry season	• Values for elephant ranges differed between seasons • Values for elephant ranges tended towards higher values than the random mean, but high individual variation
Contagion	• Values for elephant ranges same within seasons • Values for elephant ranges differed between seasons • Values for elephant ranges varied more during wet season, caused by one individual • Values for elephant ranges tend to be below random mean	• Values for elephant ranges differed within seasons • Values for elephant ranges differed between seasons • Values for elephant ranges similar to random	• Values for elephant ranges differed within dry seasons • Values for elephant ranges differed between seasons • Values for elephant ranges varied more during dry seasons • Values for elephant ranges similar to random during wet seasons • Values for elephant ranges below random mean during dry seasons	• Values for elephant ranges differed between seasons • Values for elephant ranges similar to random, except tend to be below random mean in Etosha (dry and wet seasons and NG11 (dry seasons)

Table 7. continued

Shannon diversity index			
	• Values for elephant ranges same within wet seasons • Values for elephant ranges differed within dry seasons • Values for elephant ranges tend to be above random mean, except 2003 dry season	• Values for elephant ranges differed within seasons • Values for elephant ranges similar to random	• Values for elephant ranges similar within seasons • Values for elephant ranges differed between seasons • Values for elephant ranges varied more during dry seasons • Values for elephant ranges above random mean during dry seasons	• Values for elephant ranges tend to be above random mean in Etosha and the dry seasons of NG11, but not Khaudum

Figure 7. The values for Patch density measured within randomly located ranges and within elephant home ranges during two wet and two dry seasons in a) Etosha National Park, b) Khaudum Game Reserve and c) Ngamiland District 11. The horizontal lines indicate the means.
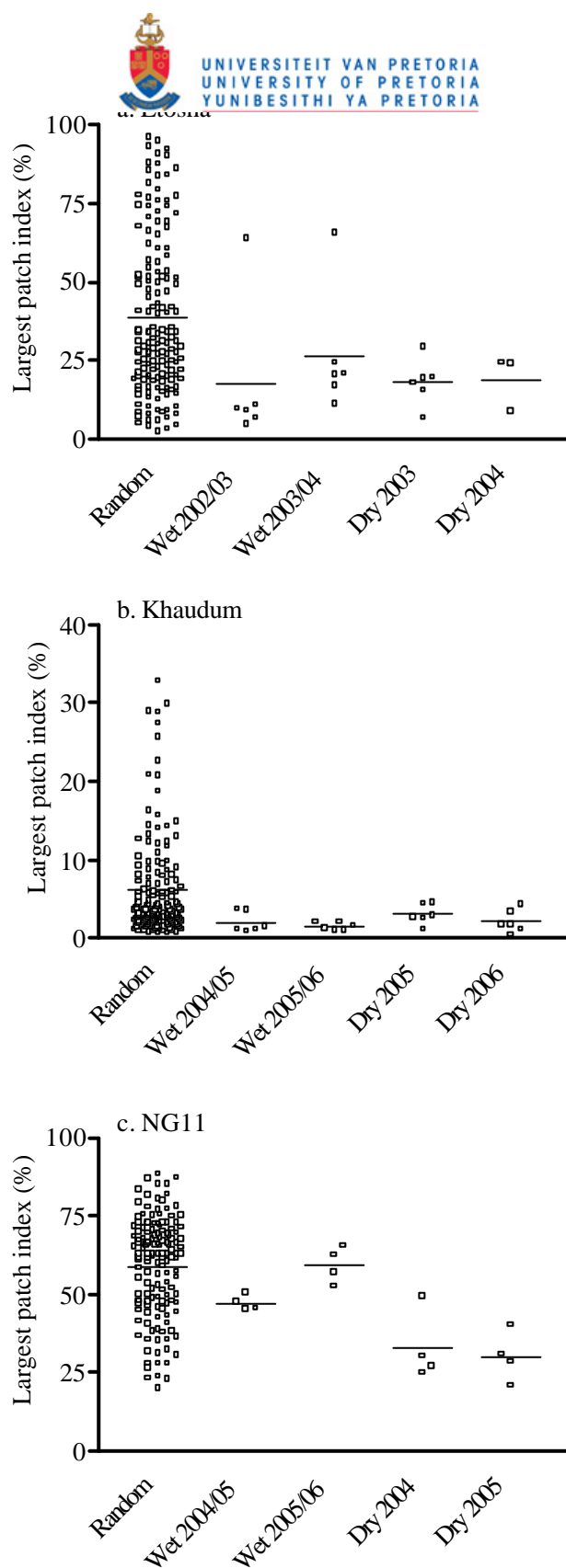
Figure 8. The values obtained for Largest patch index measured within randomly located ranges and elephant home ranges during two wet and two dry seasons in a) Etosha National Park, b) Khaudum Game Reserve and c) Ngamiland District 11. The horizontal lines indicate the means.
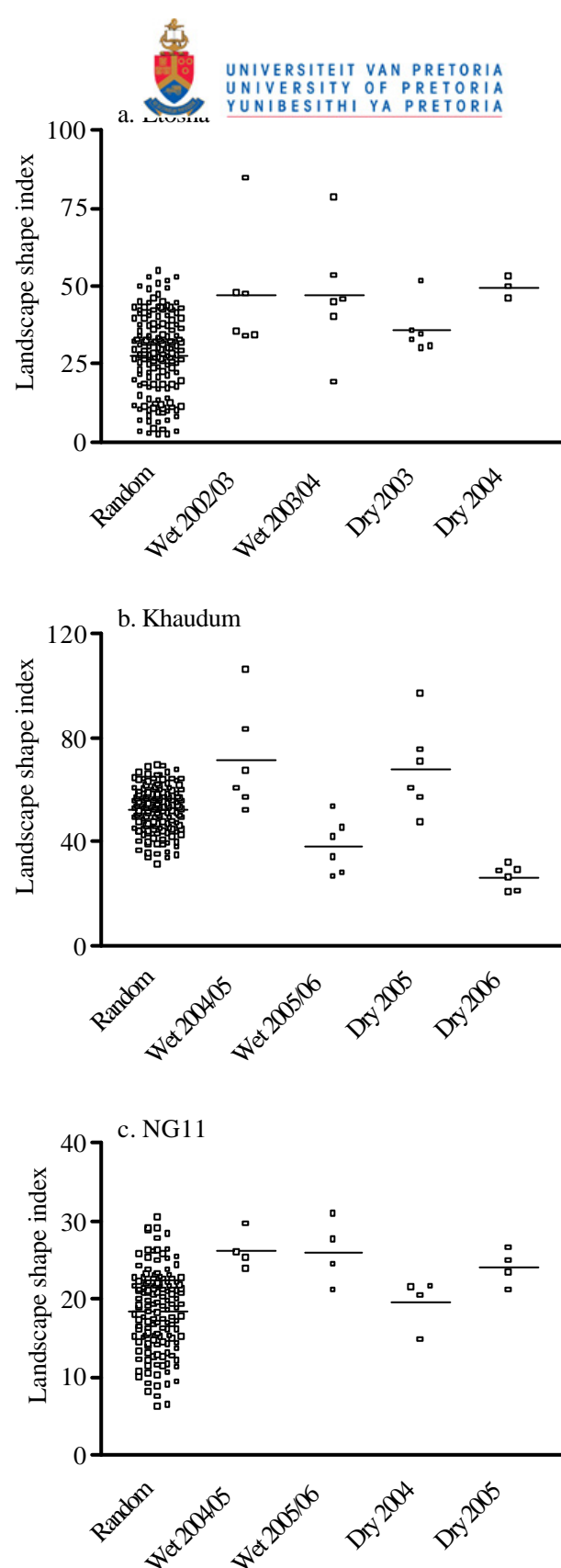
Figure 9. The values for Landscape shape index measured within randomly located ranges and within elephant home ranges during two wet and two dry seasons in a) Etosha National Park, b) Khaudum Game Reserve and c) Ngamiland District 11. The horizontal lines indicate the means.
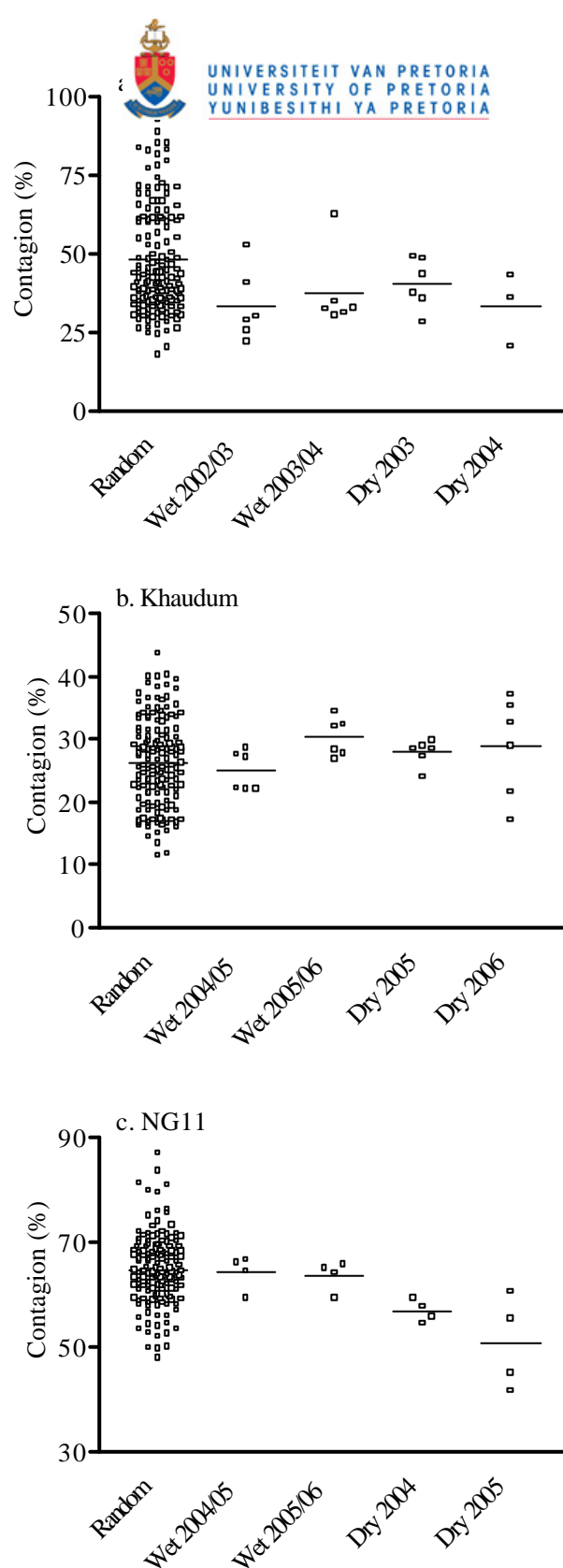
Figure 10. The values for Contagion measured within randomly located ranges and within elephant home ranges during two wet and two dry seasons in a) Etosha National Park, b) Khaudum Game Reserve and c) Ngamiland District 11. The horizontal lines indicate the means.
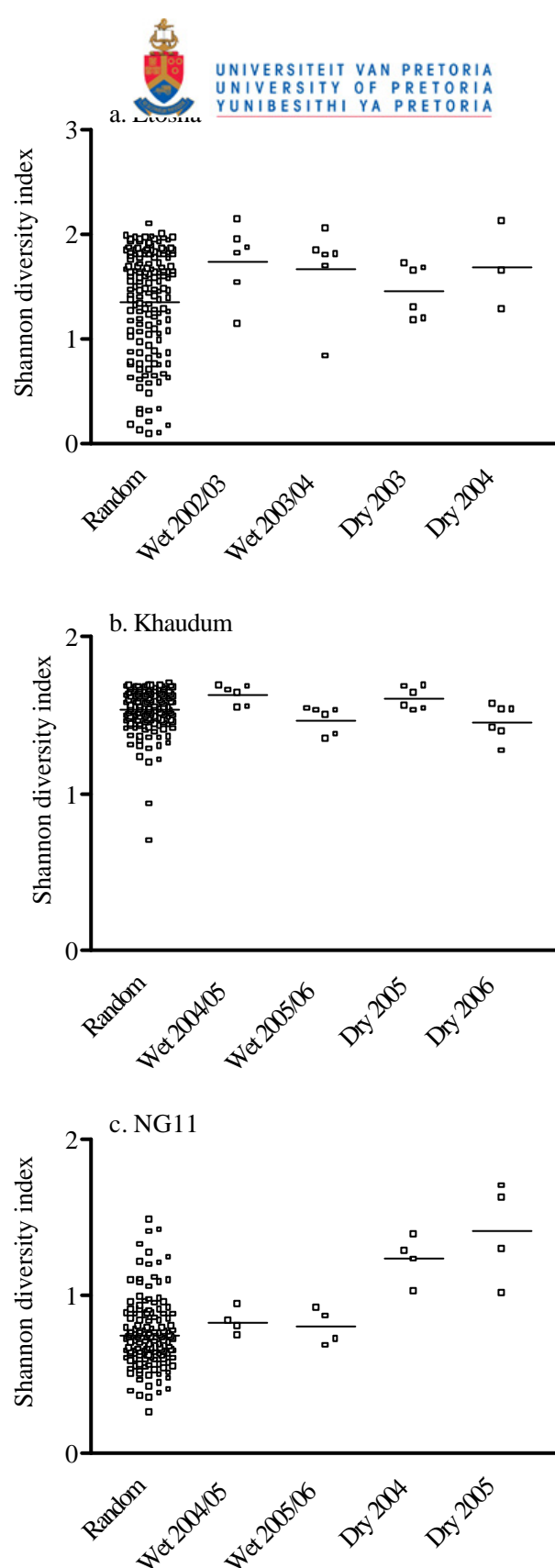
Figure 11. The values for Shannon diversity index measured within randomly located ranges and within elephant home ranges during two wet and two dry seasons in a) Etosha National Park, b) Khaudum Game Reserve and c) Ngamiland District 11. The horizontal lines indicate the means.

Relationships between home range size and landscape heterogeneity metrics

In Etosha, elephant home range size decreased with increasing Patch density during the 2003 dry season (Fig. 12b – exponential relationship; df = 3, r^2 = 0.81) and the 2004 dry season (Fig. 12d – linear relationship; $F_{1,1}$ = 56.01, r^2 = 0.98, p = 0.085). In Khaudum, elephant home range size decreased exponentially with increasing Patch density during the 2004/05 wet season (Fig. 12f – df = 3, r^2 = 0.94) and during the 2004/05 wet season (Fig. 12h – df = 3, r^2 = 0.94). During both wet seasons of Khaudum (Fig. 12e & g), home range size seemed to decrease exponentially with increasing Patch density, however, curves could not be fitted.

The negative relationship between home range size and Patch density was also apparent during the 2004 dry season (Fig. 12i – exponential relationship; df = 1, r^2 = 0.97), the 2004/05 wet season (Fig. 12j – linear relationship; $F_{1,2}$ = 6.594, r^2 = 0.77, p = 0.124) and the 2005/06 dry season (Fig. 12k – linear relationship; $F_{1,2}$ = 39.32, r^2 = 0.95, p < 0.05) of NG11. During the 2005/06 wet season, a similar trend of elephant home range size decreasing with increasing Patch density was noted, although no curves were fitted (Fig. 12*l*).

Largest patch index explained variability in elephant home range size only during the 2004/05 wet season (Fig. 13e – df = 3, r^2 = 0.55) and the 2005 dry season (Fig. 13f – df = 3, r^2 = 0.95) of Khaudum where range size decreased exponentially with Largest patch index.

A positive linear relationship was noted between home range size and Landscape shape index during the 2002/03 wet season (Fig. 14a – $F_{1,4}$ = 15.54, r^2 = 0.80, p < 0.05) and the 2003/04 wet season (Fig. 14c – $F_{1,4}$ = 42.09, r^2 = 0.91, p < 0.01) of Etosha and during the 2005 dry season of Khaudum (Fig. 14f – $F_{1,4}$ = 22.12, r^2 = 0.85, p < 0.01). Similarly, the positive linear relationship was noted for both wet

seasons of NG11, but the trend was significant only for the 2005/06 wet season (Fig.

14l – $F_{1,2}$ = 9.710, r^2 = 0.83, p = 0.089).

Elephant home range size did not have any significant relationship with Contagion (Fig. 15) or Shannon diversity index (Fig. 16) in any of the three study areas.
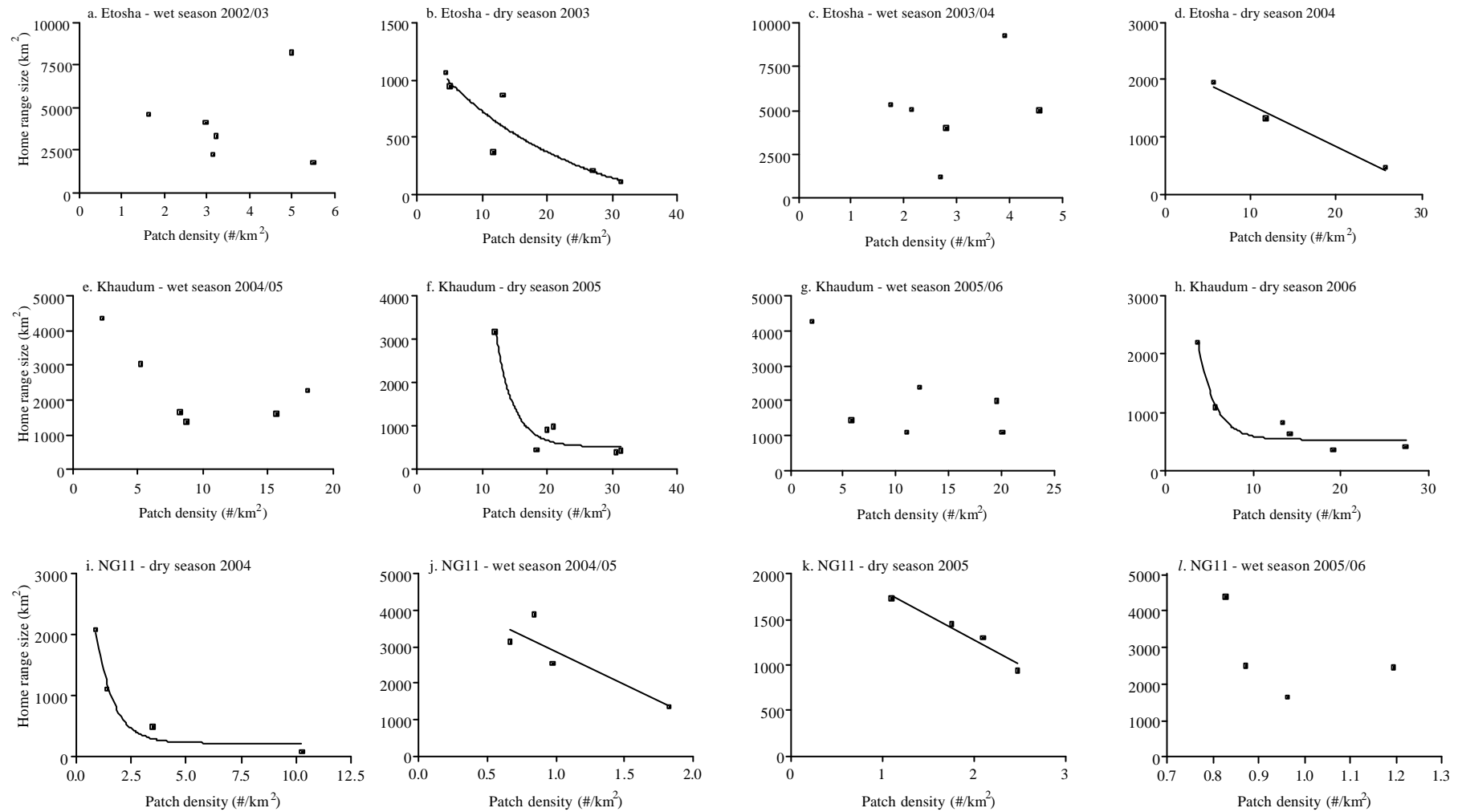
Figure 12. Elephant home range size as a function of Patch density during two wet and two dry seasons of Etosha National Park, Khaudum Game Reserve and the Ngamiland District 11. Curves were fitted only in cases where a significant relationship was identified.
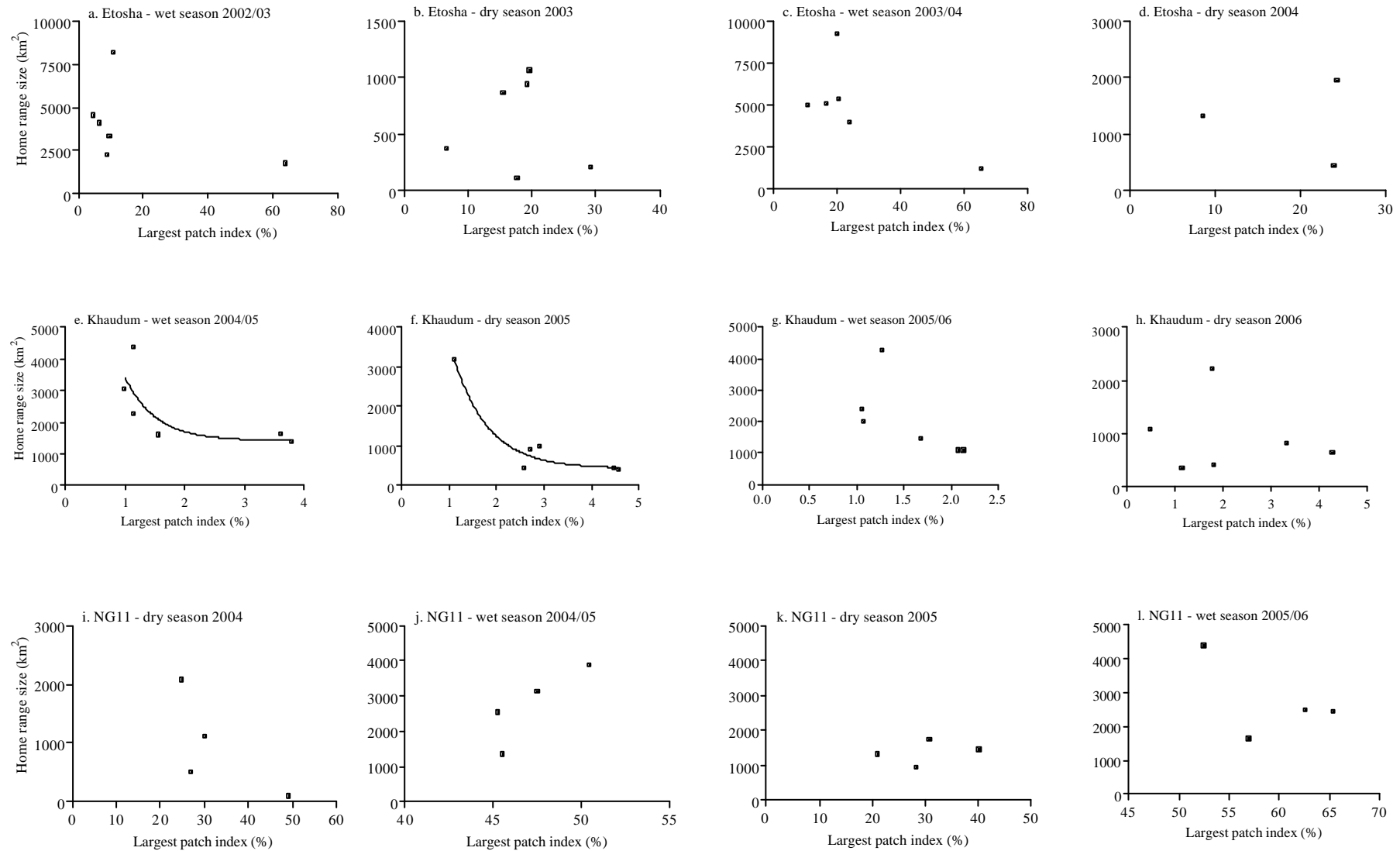
Figure 13. Elephant home range size as a function of Largest patch index during two wet and two dry seasons of Etosha National Park, Khaudum Game Reserve and the Ngamiland District 11. Curves were fitted only in cases where a significant relationship was identified.
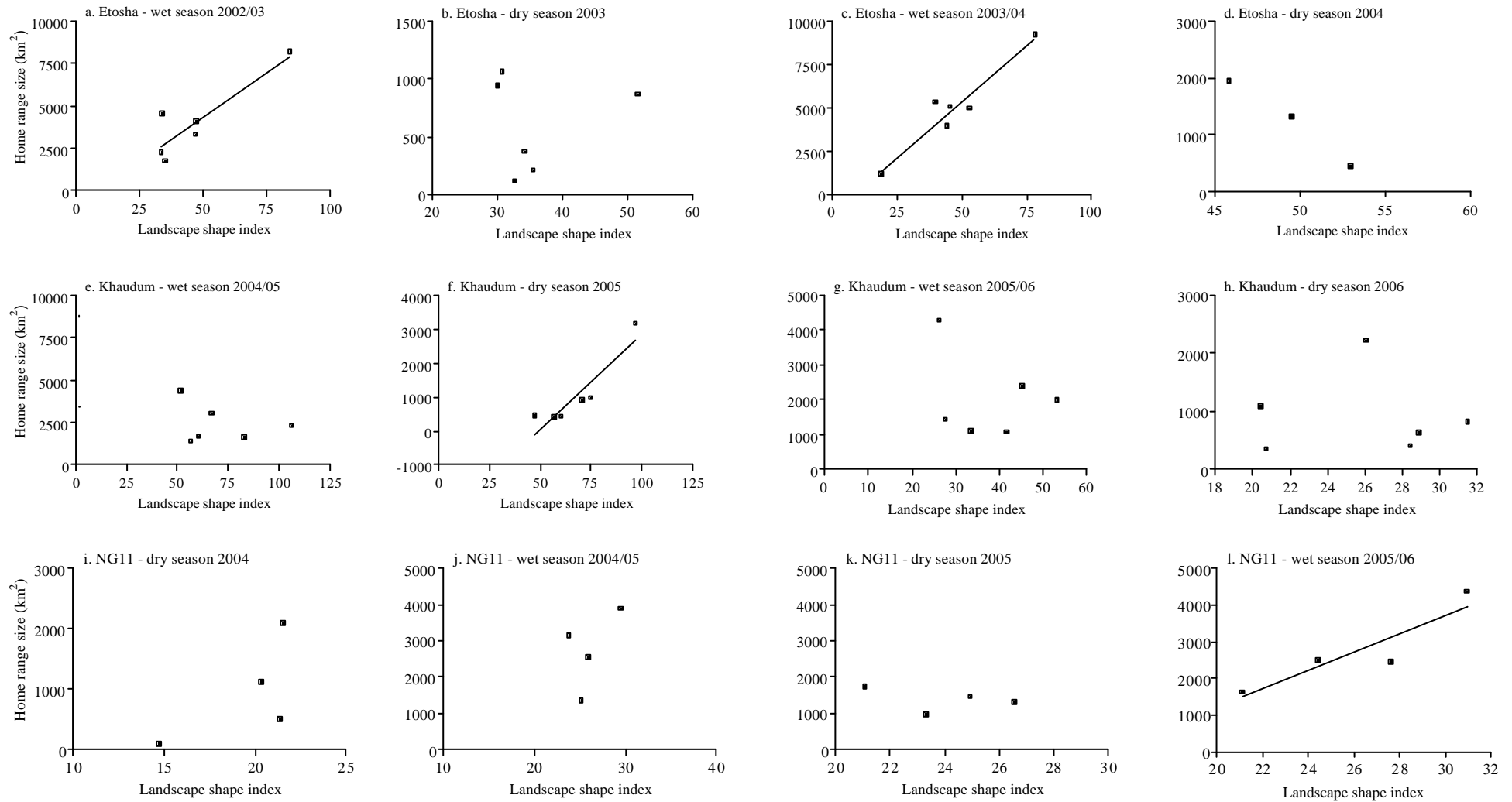
Figure 14. Elephant home range size as a function of Landscape shape index during two wet and two dry seasons of Etosha National Park, Khaudum Game Reserve and the Ngamiland District 11. Curves were fitted only in cases where a significant relationship was identified.
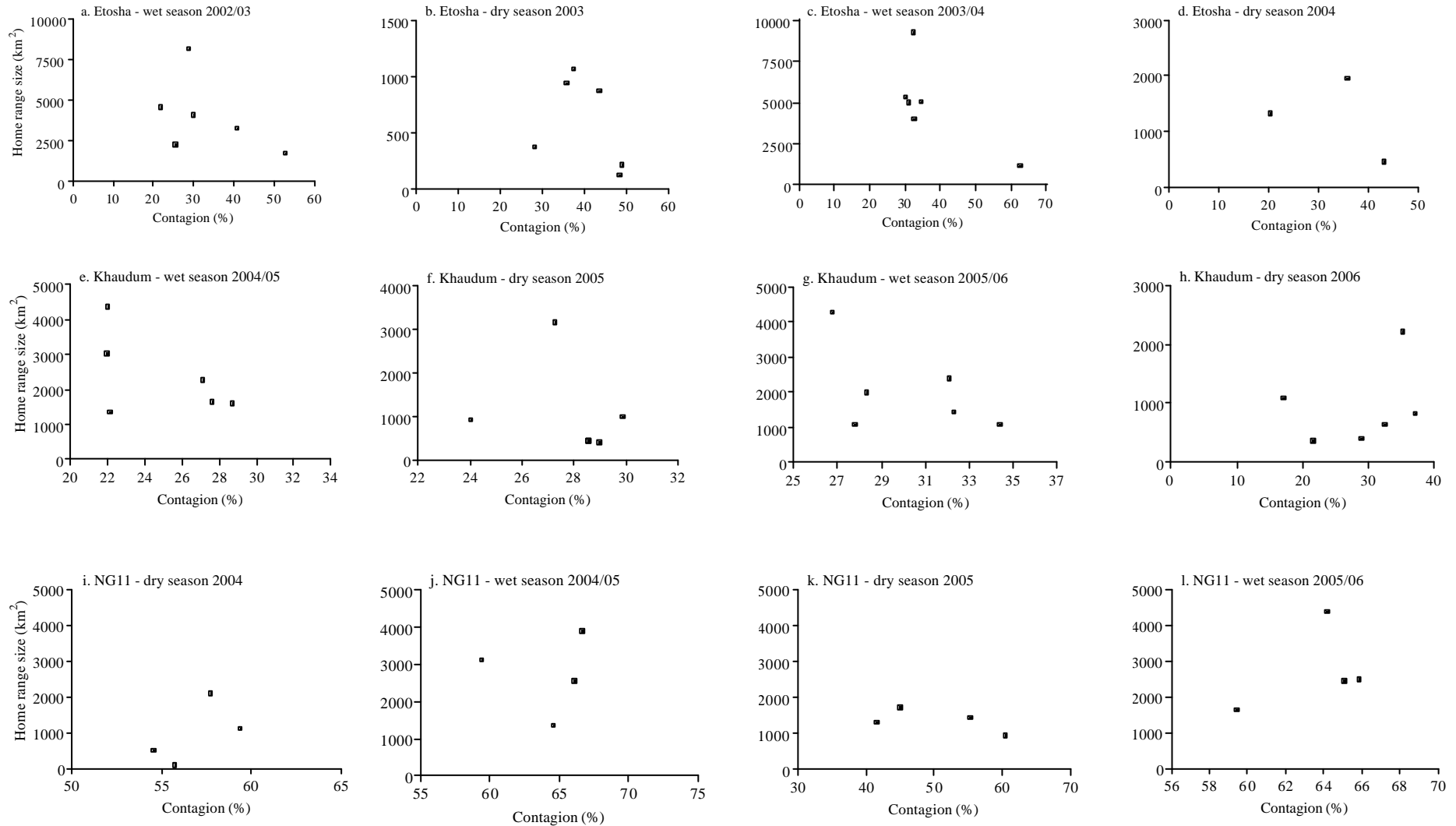
Figure 15. Elephant home range size as a function of Contagion during two wet and two dry seasons of Etosha National Park, Khaudum Game Reserve and the Ngamiland District 11. Curves were fitted only in cases where a significant relationship between home ranges size and Contagion was identified.
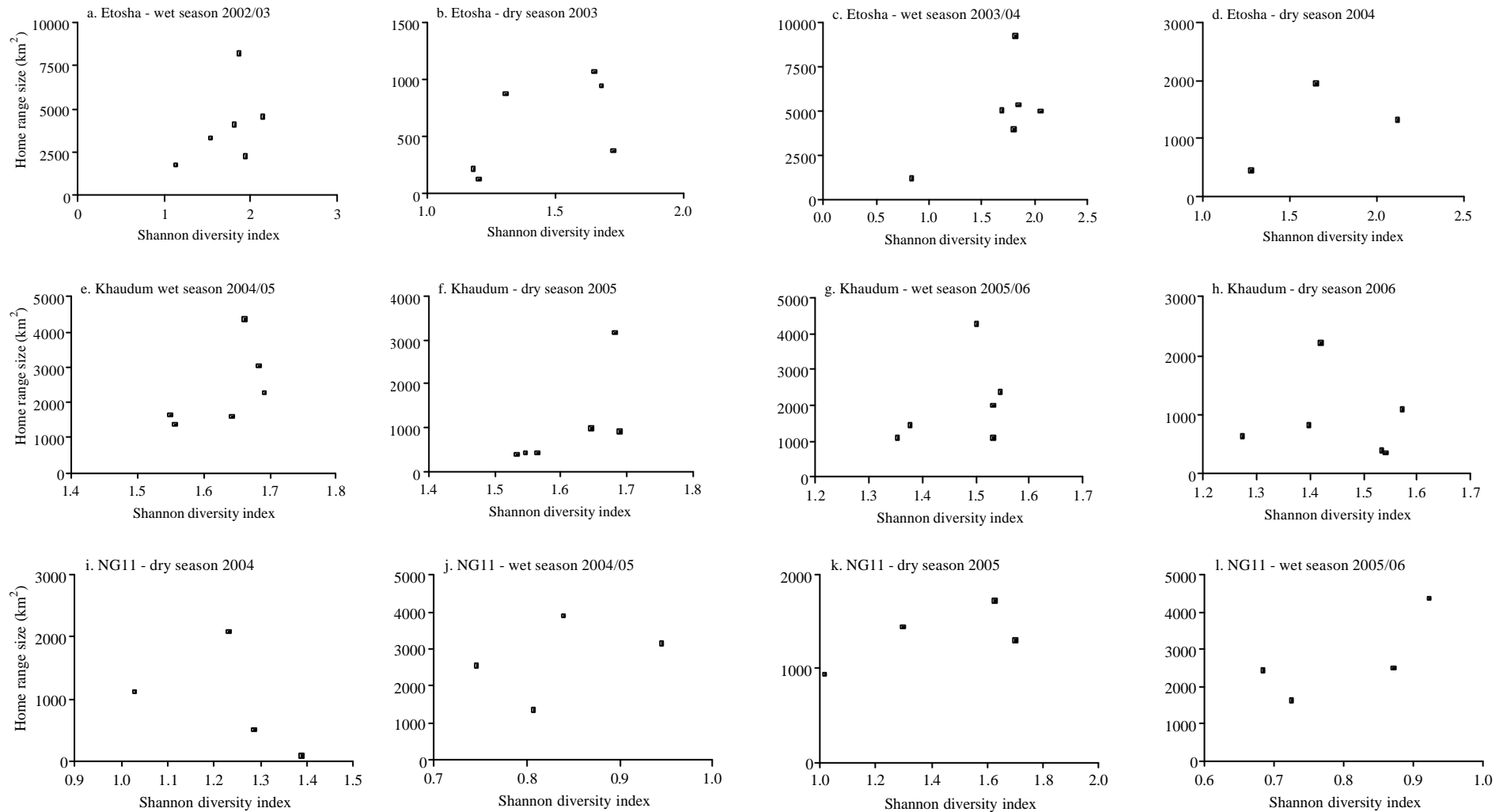
Figure 16. Elephant home range size as a function of Shannon diversity index during two wet and two dry seasons of Etosha National Park, Khaudum Game Reserve and the Ngamiland District 11. Curves were fitted only in cases where a significant relationship was identified.

Seasonal differences in the landscape metrics measured for the elephant home ranges

Elephants in Etosha had similar values for Largest patch index (Fig. 17b – $F_{5,17} = 0.365$, p = 0.78), Landscape shape index (Fig. 17c – $F_{5,17} = 0.831$, p = 0.49), Contagion (Fig. 17d – $F_{5,17} = 0.537$, p = 0.66) and Shannon diversity index (Fig. 17e – $F_{5,17} = 0.727$, p = 0.55) during the wet and dry season home ranges. Patch density values differed significantly (Fig. 17a – $F_{5,17} = 4.805$, p < 0.05) between the seasons with higher values of Patch density during the 2003 dry season than during the 2002/03 wet season (Unequal sample *post-hoc* test; p < 0.05) and the 2003/04 wet season (Unequal sample *post-hoc* test; p < 0.05) of Etosha.

For Khaudum, an ANOVA showed seasonal differences for Patch density (Fig. 18a – $F_{5,20} = 3.271$, p < 0.05), Landscape shape index (Fig. 18c – $F_{5,20} = 13.91$, p < 0.0001) and Shannon diversity index (Fig. 18e – $F_{5,20} = 6.756$, p < 0.01), but not for Largest patch index (Fig. 18b – $F_{5,20} = 1.720$, p = 0.19) and Contagion (Fig. 18d – $F_{5,20} = 1.414$, p = 0.27).

Specifically, Patch density values was higher during the 2005 dry season than during all of the other seasons of Khaudum but the difference was only significant when compared to the 2004/05 wet season (Tukey *post-hoc* test; p < 0.05). Values of Landscape shape index for the 2004/05 wet season were significantly higher than for the 2005 dry season (Tukey *post-hoc* test; p < 0.01) and 2005/06 wet season (Tukey *post-hoc* test; p < 0.01) of Khaudum. The 2005 dry season also had significantly higher values of Landscape shape index than the 2005/06 wet season (Tukey *post-hoc* test; p < 0.001) and the 2006 dry season (Tukey *post-hoc* test; p < 0.001). Shannon diversity index for the

2004/05 wet season of Khaudum were significantly higher than for the 2005 dry season (Tukey *post-hoc* test; $p < 0.05$) and 2005/06 wet season (Tukey *post-hoc* test; $p < 0.05$) of Khaudum, while higher values of Shannon diversity index were obtained for the 2005 dry season than for the 2006 dry season (Tukey *post-hoc* test; $p < 0.05$).

In NG11, seasonal differences occurred for all of the landscape heterogeneity metrics, except for Patch density (Fig. 19a – $F_{3,12} = 1.685$, $p = 0.22$). Largest patch index values (Fig. 19b – $F_{3,12} = 12.95$, $p < 0.001$) were higher during the wet seasons than during the dry seasons but the difference was only significant between the 2004/05 and 2005/06 wet seasons and the 2005 dry season (Tukey *post-hoc* test; $p < 0.05$ and $p < 0.001$, respectively) as well as between the 2005/06 wet season and the 2004 dry season (Tukey *post-hoc* test; $p < 0.01$). An ANOVA yielded higher values for Landscape shape index (Fig. 19c – $F_{3,12} = 3.850$, $p < 0.05$) during the 2004/05 and 2005/06 wet seasons and the 2005 dry season than for the 2004 dry season (Tukey *post-hoc* test; $p < 0.05$, respectively).

Contagion values (Fig. 19d – $F_{3,12} = 6.433$, $p < 0.01$) was significantly higher during the 2004/05 and 2005/06 wet seasons of NG11 than during the 2005 dry season (Tukey *post-hoc* test; $p < 0.05$, respectively). Values of Shannon diversity index (Fig. 19e – $F_{3,12} = 10.18$, $p < 0.001$) were significantly higher for the 2004 dry season than for the 2004/05 and the 2005/06 wet seasons (Tukey *post-hoc* test; $p < 0.05$, respectively). Similarly, higher values of Shannon diversity index were obtained for the 2005 dry season than for both wet seasons (Tukey *post-hoc* test; $p < 0.01$, respectively) in NG11.
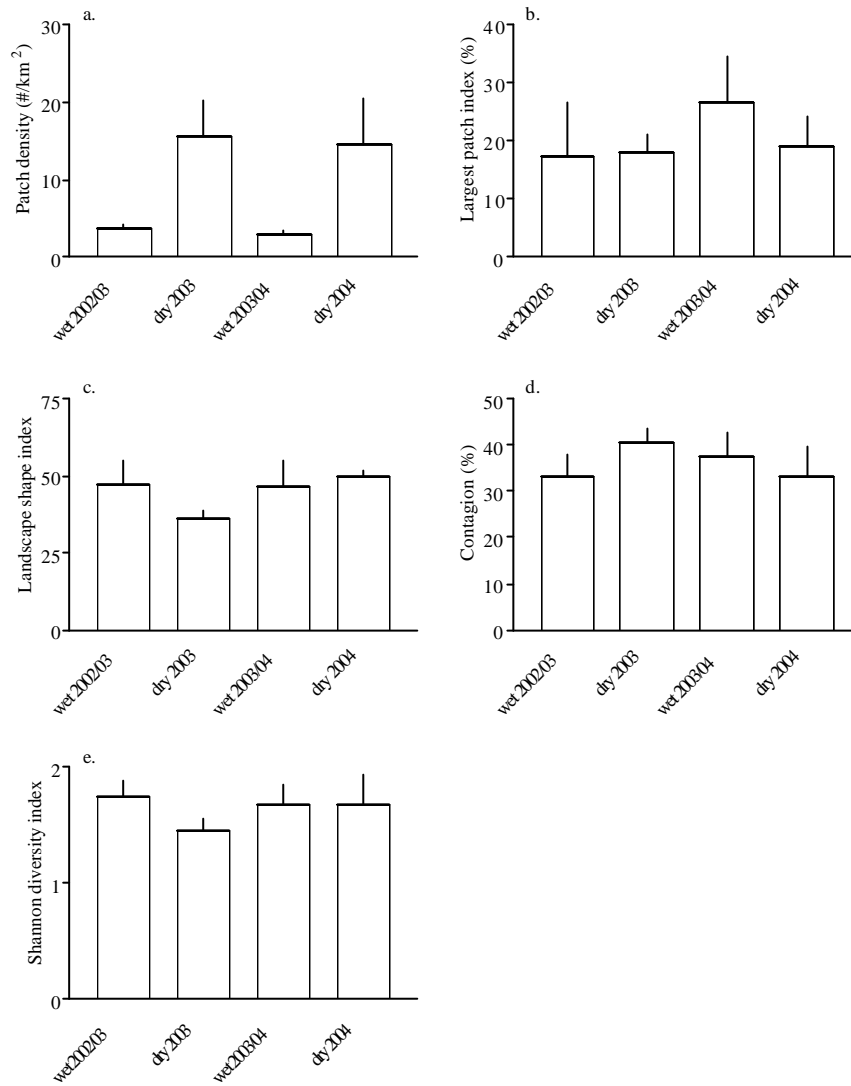
Figure 17. The season-specific landscape metric values (mean + SE) for elephant home ranges in Etosha National Park.

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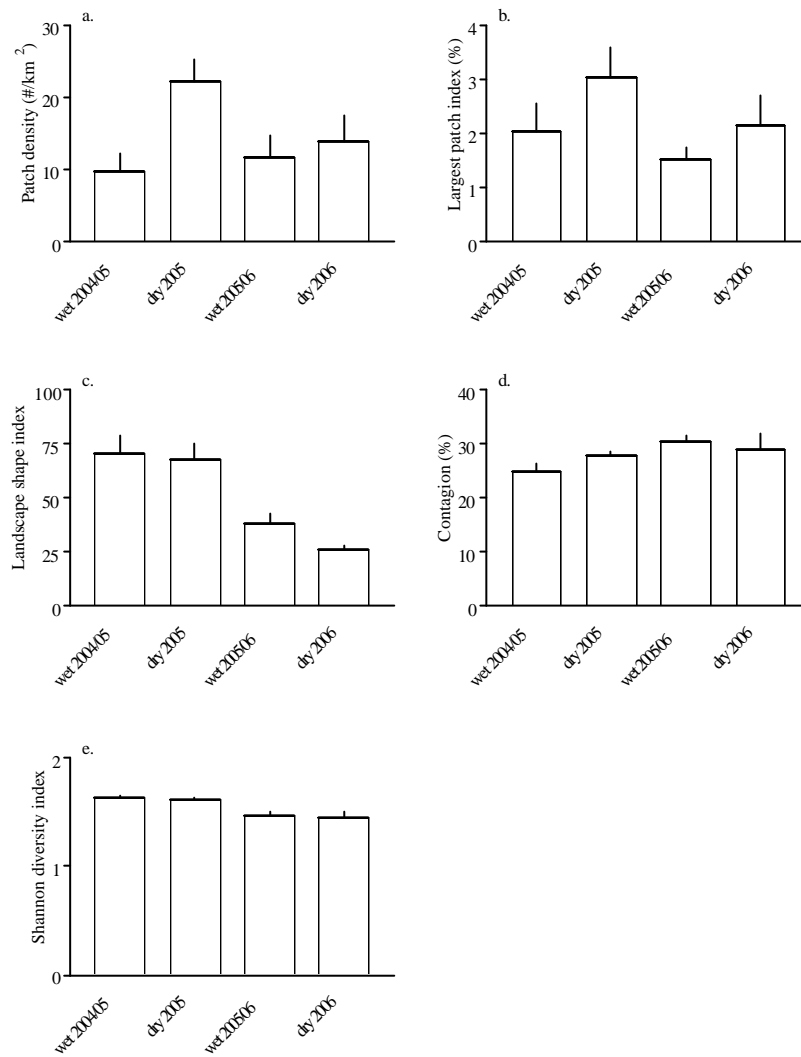
Figure 18. The season-specific landscape metric values (mean + SE) for elephant home ranges in Khaudum Game Reserve.
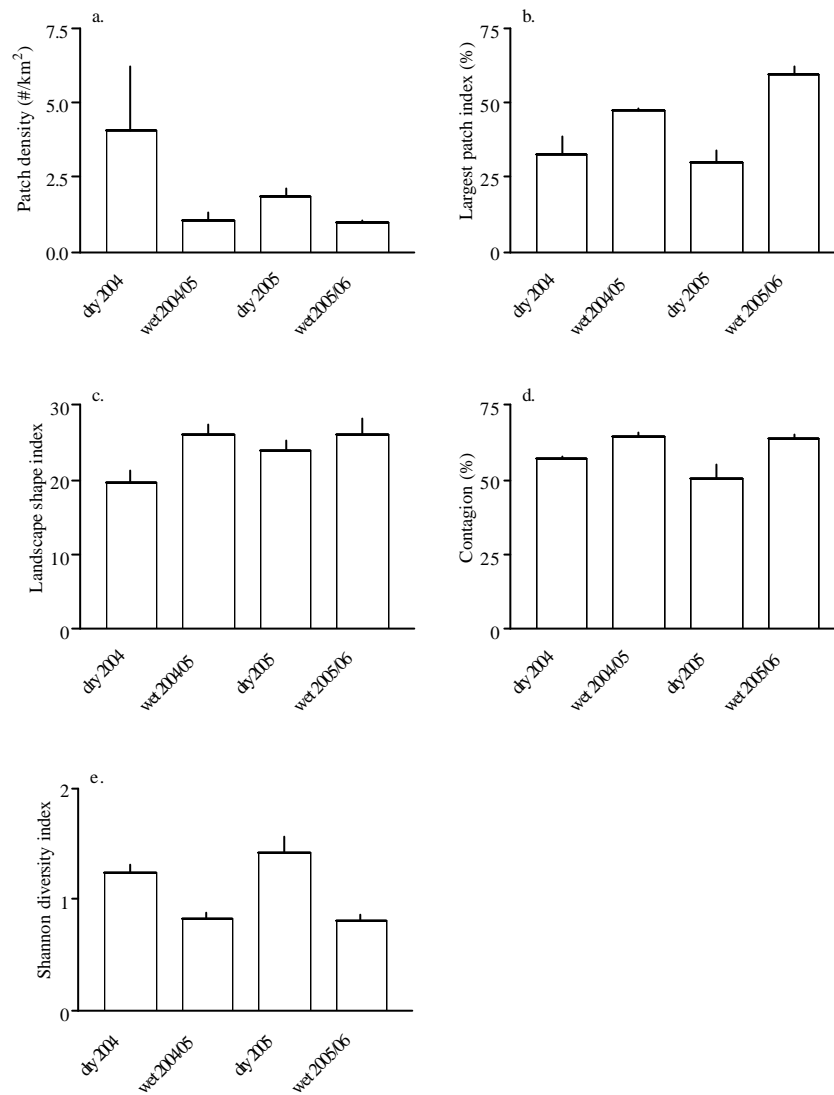
Figure 19. The season-specific landscape metric values (mean + SE) for elephant home ranges in Ngamiland District 11.

Elephant selection for structural classes

Etosha National Park

Elephants in Etosha did not show any specific pattern in their preferences (Table 7) for the structural classes that made up the landscape map. During the 2003 dry season, the preference ranking suggested that elephants highly preferred *Acacia* **dominant savanna**, *Catophractes alexandri* **savanna**, **Mopane woodland savanna** and **Steppe & grass**. This also holds for the 2002/03 wet season, but preferences were ranked much lower. Then, during the 2004 dry season and the 2003/04 wet season, elephants did not show any preferences except for a ranking of 1 for *Catophractes & Acacia* **savanna** and **Mopane woodland savanna,** respectively.

Table 7. Relative preference rankings of elephants derived from a second-order (Johnson, 1980) compositional analysis (Aebischer *et al.*, 1993) for structural classes in Etosha National Park during two wet and two dry seasons.

Structural class	Dry season 2003	Dry season 2004	Wet season 2002/03	Wet season 2003/04
Acacia dominated savanna	8	0	1	0
Catophractes & *Acacia* savanna	0	1	1	0
Catophractes alexandri savanna	5	0	2	0
Dolomite rock savanna	0	0	1	0
Broad-leafed savanna	1	0	0	0
Mopane shrub savanna	0	0	0	0
Mopane woodland savanna	4	0	1	1
Pan	0	0	0	0
Steppe & grass	4	0	1	0

The greater the absolute value the greater the preference

Khaudum Game Reserve

Elephants in Khaudum consistently showed relatively high preference rankings for *Baikiaea* **woodland savanna**, *Terminalia prunioides* **woodland**, and *Acacia* **woodland savanna** during the two wet and the two dry seasons (Table 8). The compositional analysis also showed relatively lower preference rankings for the remaining structural classes, except for *Terminalia sericea* **woodland** for which there was no preference ranking during any of the seasons.

Table 8. Relative preference rankings of elephants derived from a second-order (Johnson, 1980) compositional analysis (Aebischer *et al*., 1993) for structural classes in Khaudum Game Reserve during two wet and two dry seasons.

Structural class	Dry season 2005	Dry season 2006	Wet season 2004/05	Wet season 2005/06
Baikiaea woodland savanna	4	4	4	5
Acacia woodland savanna	2	3	3	3
Burkea woodland savanna	1	2	2	2
Terminalia sericea woodland	0	0	0	0
Terminalia prunioides woodland	3	5	5	4
Grassland	1	2	2	2
Pan	1	1	1	1

The greater the absolute value the greater the preference

Ngamiland District 11

During all the seasons in NG11, the compositional analysis indicated relatively high preferences rankings for the structural classes that represent most woodlands and the grasslands (Table 9). Additionally, the preference rankings were even higher for **Swamp** and **Dry floodplains and island interiors** during the dry seasons but not for the wet seasons.

Table 9. Relative preference rankings of elephants derived from a second-order (Johnson, 1980) compositional analysis (Aebischer *et al.*, 1993) for structural classes in Khaudum Game Reserve during two wet and two dry seasons.

Structural class	Dry season 2004	Dry season 2005	Wet season 2004/05	Wet season 2005/06
Terminalia and *Baphia* savanna	3	3	2	1
Burkea and *Baikiaea* savanna	3	1	2	3
Grasslands with sagebush	2	1	3	3
Acacia dominated savanna	1	1	1	2
Riparian zones	2	1	1	0
Swamp	6	1	0	0
Dry floodplains and island interiors	6	6	0	0
Mopane woodland	0	0	0	0
Former floodplain	1	1	0	0

The greater the absolute value the greater the preference

Water point density as a determinant of elephant spatial use

In this section, I present the results of the analysis in which I related elephant home range size to water point density for Etosha and Khaudum. This analysis was not done for NG11 because the Okavango River serves as the only source of water during the dry season.

In Etosha, the sizes of the elephant home ranges decreased exponentially with an increase in water point density during the 2003 dry season (Fig. 20b – df = 3, r^2 = 0.92). During the 2004 dry season, elephant home range size decrease linearly with increasing water point density (Fig. 20d – $F_{1,1}$ = 5.040, r^2 = 0.83, p = 0.2668). During both the wet seasons there was no relationship between water point density and elephant home range sizes (Fig. 20a & c).

In Khaudum, elephant home range size decreased exponentially with increasing water point density during the 2004/05 wet season (Fig. 21a – df = 3, r^2 = 0.87), the 2005 dry season (Fig. 21b – df = 3, r^2 = 0.99) and the 2005/06 wet season (Fig. 21c – df = 3, r^2

= 0.98). During the 2006 dry season, the relationship between home range size and water point density appeared to follow a similar trend, however, I could not fit a curve to the data.
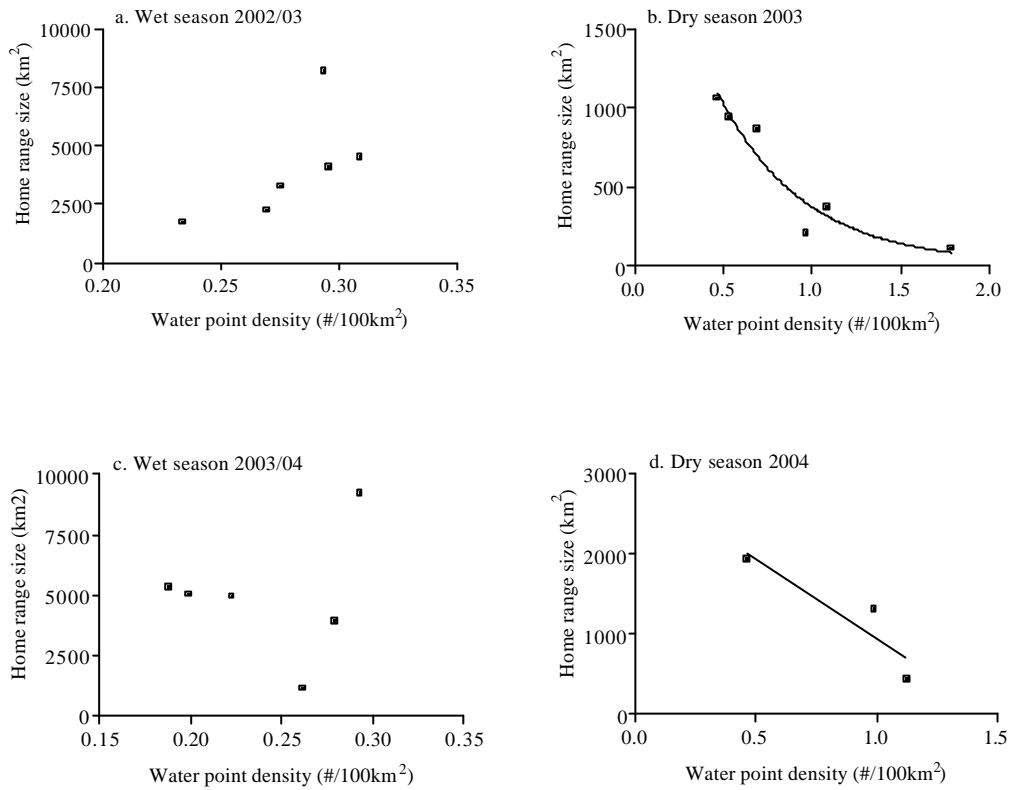
Figure 20. The sizes of the elephant home ranges as a function of water point density during two wet and two dry seasons for Etosha National Park. Curves were fitted only in cases where a significant relationship between home ranges size and water point density were identified.
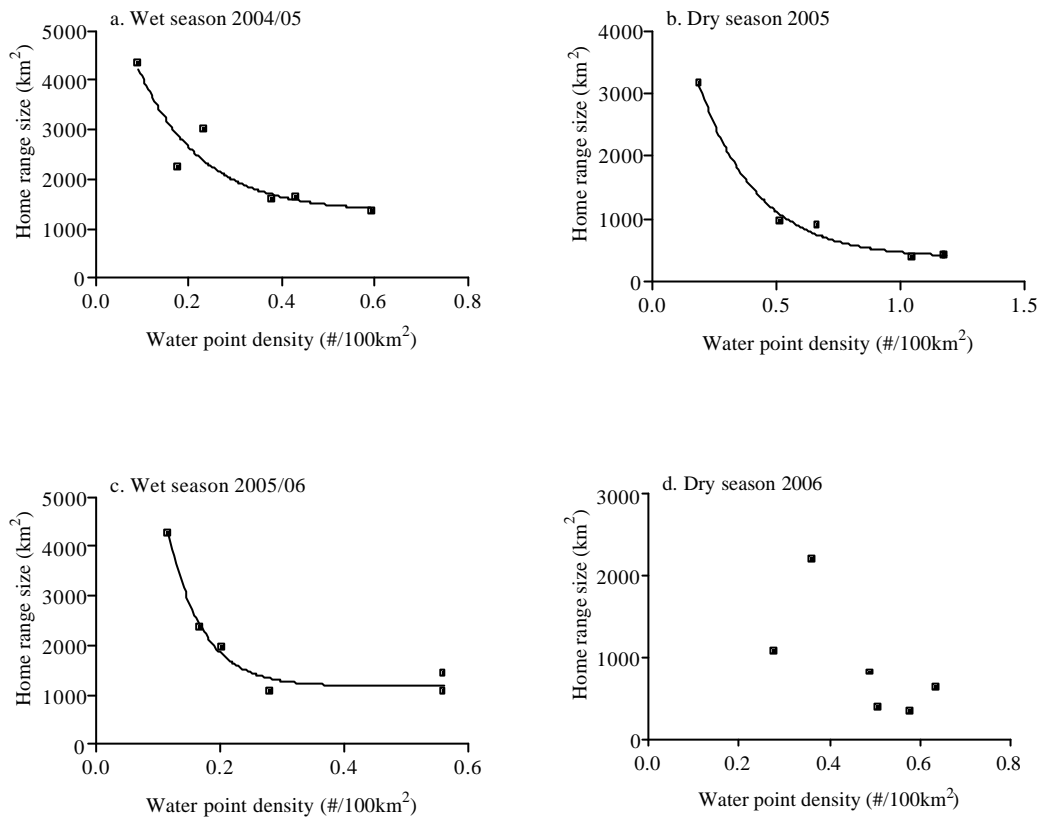
Figure 21. The sizes of the elephant home ranges as a function of water point density during two wet and two dry seasons for Khaudum Game Reserve. Curves were fitted only in cases where a significant relationship between home ranges size and water point density was identified.

CHAPTER 5

DISCUSSION

Elephants live in heterogeneous landscapes where their preference for certain habitats can be explained by their selection for nutrient-rich habitats (Ruggiero & Fay, 1994; Verlinden & Gavor, 1998; Houston *et al*., 2001), their preference for plants with higher palatability (Owen-Smith & Cooper, 1987; de Boer *et al*., 2000; O'Connor *et al*., 2007), their avoidance of rugged terrain (Nelleman *et al*., 2002), sexual segregation in habitat use (Stokke, 1999; Stokke & du Toit, 2002; Shannon *et al*., 2006) and their thermoregulatory needs (Kinahan *et al*., 2007). Primary productivity as measured by NDVI may also play a role in habitat preference (Young *et al*., in review).

Optimal foraging theory (Emlen, 1966; MacArthur & Pianka, 1966) implies that elephants will select certain resources above others (Illius & Gordon, 1993; Morris, 2003). My hypothesis that landscape heterogeneity determines variability in elephant home range location and size follow from the home range being the area that an elephant will use to meet its resource requirements (see Ford, 1983; Morris, 2003; Mitchell & Powell, 2004). However, the apparent selection for areas within the landscape that are relatively more heterogeneous can only be speculated upon since a link between resource quality and landscape heterogeneity, to the best of my knowledge, still needs to be verified.

Many different aspects of the spatial structure and the configuration of patches within the landscape need to be considered when quantifying landscape heterogeneity. For instance, heterogeneity at the landscape scale may increase as the amount of edge habitat increases or when patch density and the area among different

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structural classes become more equally distributed (McGarical & Marks, 1995; Tufto *et al.*, 1996).

I relied on five landscape metrics to measure different aspects of heterogeneity within elephant and randomly located ranges in three areas across the arid savannas of southern Africa. I also determined whether these metrics for elephant home ranges differed from those of equally sized randomly located ranges in each of the three study areas. I assumed that home ranges with higher levels of Patch density, Landscape shape index and Shannon diversity index, but lower values of Contagion and Largest patch index than for randomly located ranges, implied selection.

The significant differences in the five metrics for the randomly located ranges of the study areas may be ascribed to differences in abiotic factors (see Wiens *et al.*, 1993; Turner *et al.*, 2001). For instance, Khaudum was consistently more heterogeneous than Etosha and NG11, while the latter was the least heterogeneous. Indeed, different patterns of vegetation structure and composition are primarily the product of differences in the geomorphology and soil characteristics as well as the rainfall of the areas (see Chapter 2 for more detail). Factors, such as the distribution of water, incidence of fire and animal foraging may further alter the structure of patches within the landscapes (Dublin *et al.*, 1990; Vandvik *et al.*, 2005; Smit *et al.*, 2007). I therefore treated the landscape metrics separately for the elephant home ranges in each of the study areas.

The location of elephant home ranges in all three study areas may be explained by at least some of the landscape metrics. Patch density was the only metric that could not explain any of the variability in home range location. In this case, elephants selected against Patch density during the wet seasons of all three study areas, but during the dry seasons, values for elephant and randomly located ranges

were similar. This suggests that elephants consistently preferred areas where the number of patches per unit area (see Table 4, p.35) was less or similar to that typical for each study area. Elephants, however, may not select for this metric, since Patch density does not reflect on the different types of patches but rather on the number of patches, some of which may be of the same structural classes.

Largest patch index measures the percentage of the total area made up by the largest homogenous patch (or structural class) (see Table 4, p.35). In both Etosha and Khaudum, the Largest patch index values in elephant home ranges were consistently lower than those in randomly located ranges during all seasons. In NG11, values for the Largest patch index was lower in the elephant home ranges during both dry seasons and one of the wet seasons. Only during one of the wet seasons were the values of Largest patch index for the elephant and the randomly located ranges similar in NG11. Elephants therefore seemed to prefer areas that comprise of relatively small patches.

Landscape shape index is a measure of the amount of edge within an area (see Table 4, p.35). Elephants in Etosha and NG11 appeared to select for Landscape shape index during both wet seasons and one of the dry seasons. In both these areas, values for Landscape shape index were similar to that for the randomly located ranges only during one of the dry seasons. In Khaudum, elephants appeared to prefer areas with higher values of Landscape shape index during the 2004/05 wet and dry season, while they seemed to prefer areas with lower values of the metric during the 2005/06 wet and dry season. In Etosha and NG11 the areas selected by elephants had relatively high amounts of edges during both the wet seasons. Edges are often referred to as transition zones where an increase in resource diversity is a result of more than one habitat patch types adjoining each other (Ries & Sisk, 2004). Conceivably, foraging

by elephants may be more efficient in these transition zones than in non-edges (patch interiors) because being at the edge offers better access to the resources of more than one patch type (Fagan *et al.*, 1999; Ries & Sisk, 2004).

Contagion is a measure of the interspersion and aggregation of patches within the landscape and lower values of the metric implies higher heterogeneity (see Table 4, p.35). The patterns observed for Contagion were not consistent. For instance, elephants in Etosha preferred areas within the landscape that were more interspersed and less aggregated than were represented by the randomly located ranges. Those in NG11 showed a similar preference though only during the dry seasons. In Khaudum, however, elephant preferences could not be explained by this metric.

In my study, the Shannon diversity index measures the proportional distribution of area among patch types (see Table 4, p.35). Conceivably, elephants would select for areas within the landscape where the equal distribution of a larger number of different patch types implies better access to a greater diversity of resources (Honnay *et al.*, 2003; Ortega *et al.*, 2004). In the wet seasons, the elephants of Etosha and in the dry seasons, the elephants of NG11 seemed to select for areas where the area occupied by different structural classes was more even than in randomly located ranges. In Khaudum, values for Shannon diversity index were similar to those for the randomly located ranges.

The consistent apparent selection for areas with relatively lower values of Largest patch index and Contagion and relatively higher values of Landscape shape index and Shannon diversity index across both wet and/or dry seasons by elephants in Etosha and NG11 suggests that landscape heterogeneity can explain landscape utilisation by elephants. The natural water distribution in NG11 may however be correlated with the structural classes and increased heterogeneity close to the

Okavango river. The seemingly greater selection for heterogeneity metrics by elephants during the dry seasons may therefore be a result of such a correlation. The relationship between heterogeneity and water requires further investigation.

Elephants in Khaudum inconsistently selected for Largest patch index and Landscape shape index. A possible explanation for this may be that Khaudum represents a much more heterogeneous landscape (as measured by the metrics) than Etosha and NG11. Thus, the level of heterogeneity may be above a threshold at which selection could be noted using my approach. In this case, selection for water also may govern the pattern of spatial use, especially when noting the near uniform distribution of water across Khaudum. This opens the way for further research.

My evaluation of seasonal differences in landscape heterogeneity within elephant home ranges followed on my expectation that selection for higher levels of heterogeneity would be accentuated in the wet season when the distribution of water may not restrict roaming (de Beer *et al*., 2006; Jackson *et al*., 2007). This did not hold for elephants in Etosha where Patch density was the only metric that was higher for the dry season than for the wet season home ranges. In Khaudum and NG11, selection for the landscape metrics varied between seasons but did not show any season-specific trends. Harris *et al.* (in review) on the habitat selection by elephants suggests that selection is not consistent and differs between individuals and seasons. Verlinden & Gavor (1998) also found no large differences between wet and dry season selection for habitats. This certainly differs from the general trends noted by others - elephants tend to be more selective during the rainy season when their movements are less restricted by the availability of water (e.g. Western & Lindsay, 1984; Osborn, 2004; Ntumi *et al*., 2005).

Based on compositional analyses elephants in Etosha showed strong

preferences for *Acacia* **dominant savanna**, *Catophractes alexandri* **savanna**, **Mopane woodland savanna** and **Steppe & grass** during the 2003 dry season. The following dry season, elephants only showed a very low preference ranking for *Catophractes & Acacia* **savanna**. This contradiction in preference rankings also occurred during the two wet seasons, where low preference rankings were obtained for six of the nine structural classes of landscapes during the 2002/03 wet season and a low preference ranking only for **Mopane woodland savanna** during the 2003/04 wet season. The lack of any regular pattern in elephants' preferences for structural classes suggests that their use is dictated by their proportional availability.

In Khaudum the preference rankings for structural classes during both the wet and dry seasons were similar, but the *Baikiaea* **woodland savanna** and *Terminalia prunioides* **woodland** were ranked higher than the other structural classes. These varying degrees of preference rankings for the structural classes were consistent across all seasons and suggest that elephants in Khaudum prefer some structural classes above others. However, only *Terminalia sericea* **woodland** was avoided through all of the seasons, which contradicts the findings of Jachmann & Croes (1991) and Verlinden & Gavor (1998) that suggests that elephants selected for woodlands dominated by *Terminalia sericea*. The results for Khaudum suggested that elephants were not exceptionally specific in their preferences for structural classes.

During the dry seasons, elephants in NG11 showed stronger preferences for the structural classes associated with areas close to the Okavango River (**Dry floodplains and island interiors** and **Swamp**) than for those classes further from the river. During the wet seasons, elephants preferred structural classes away from the river. It therefore seems that the apparent preferences by elephants in NG11 are also determined by their selection for water.

Elephants in all three study areas did not seem to be habitat-specific although some structural classes were preferred above others. This implies that elephants require multiple habitats to fulfil their needs (see Law & Dickman, 1998) and may support the idea that elephants would select for aspects of heterogeneity that might reflect on better accessibility of multiple habitats.

Elephant home range sizes in the three study areas varied between individuals (see Table 5, p.40). The question arises whether home range size would be determined by measures of landscape heterogeneity. Tufto *et al*. (1996) and Kie *et al*. (2002) show that landscape heterogeneity is a factor that explains variability in home range size for roe deer and mule deer. Within seasons, I therefore expected elephants to decrease their home range sizes in response to increased landscape heterogeneity as favoured resources become more abundant (Tufto *et al*., 1996; Kie *et al*., 2002). Moreover, if any significant relationships existed I expected elephant home range sizes to decrease with an increase in the landscape metrics, except for Contagion and Largest patch index, for which I would expect an increase in home range size.

Elephant home range sizes showed inconsistent inter-seasonal differences across the study areas. In Etosha and NG11, home range sizes were significantly larger during the wet seasons than during one dry season, while home range sizes were similar for the wet and dry seasons in Khaudum. If landscape metrics explained variability in home range size, I expected that these relationships would be accentuated during the wet seasons for Etosha and NG11, but similar for the wet and dry seasons of Khaudum.

In Etosha, Khaudum and NG11 elephant home range size was inversely related to Patch density during the dry seasons. Overall, it seemed that areas with relatively high Patch densities tended to support small home ranges. Patch density is

related to Patch richness density (McGarical & Marks, 1995), which explains variability in home range sizes (see Grainger *et al.*, 2005). However, Patch richness density does increase with area and this relationship is therefore not surprising. The relationship may be the product of an intrinsic area-effect of the calculation of the metric. This means that an increase in Patch density is inherently dependent on an increase in area. The behaviour of this metric in relation to home range size should be carefully investigated and for the purpose of this study, I could not make any conclusions on the apparent relationship. Patch richness density and Patch density therefore contribute little in understanding variability in home range size.

Largest patch index did not explain differences in home range size, except for the first wet season and the following dry season in Khaudum. This may be due to the lack in variability in this metric for Khaudum. Contrary to the expectation (Tufto *et al.*, 1996), home range sizes did not decrease consistently with increasing edge characteristics. For instance, home range size in the wet seasons of Etosha, one dry season of Khaudum and one wet season of NG11 increased with increasing Landscape shape index. It is possible that elephants may increase the size of their foraging areas to include more edge characteristics, but the pattern is inconsistent and may be ascribed to differences in individual behaviour of elephants. Elephant home range size was further not related to Contagion or Shannon diversity index. Landscape heterogeneity, as measured by the metrics I selected for this study, therefore does not seem to explain the variability in home range size. This finding opposes that of Kie *et al.* (2002) which show that increasing home range size of mule deer is inversely related to metrics that describe heterogeneity.

Elephant home range size, however, is influenced by water point density. Several earlier studies indicate that elephants roam over larger areas during the wet

season when water is widely available, while they tend to concentrate their activities around permanent water sources during the dry season (Owen-Smith, 1988; Verlinden & Gavor, 1998; Wittemyer, 2001; Stokke & du Toit, 2002; Gaylard *et al.*, 2003; Osborn & Parker, 2003; Redfern *et al.*, 2003; de Beer *et al.*, 2006; Smit *et al.*, 2007). Home range size in Etosha and Khaudum decreased with increasing water point density during the dry seasons. A similar relationship also occurred during the wet seasons in Khaudum, which may explain the similarity in wet and dry season home range sizes. These results suggest that water is a strong determinant of elephant spatial use in these two areas. In their study in the NG11, Jackson *et al.* (2007) recently also showed that elephant densities near the Okavango River decreased during the wet season, suggesting a pattern for NG11 similar to that which I noted for Etosha and Khaudum.

Landscapes are templates where resources are distributed unevenly and where elephants search for resources that will optimise their survival (Johnson *et al.*, 1992; Gough & Rushton, 2000). To conclude, I showed that elephants in Etosha and NG11 locate their home ranges in areas with higher landscape heterogeneity than elsewhere. In support, Murwira & Skidmore (2005) show that spatial heterogeneity explains variance in elephant distribution. Moreover, in my study, heterogeneity could not explain variability in home range size of elephants. Home range size however was related to water point density. This selection for water seemed to overrule selection for heterogeneity in Khaudum. These findings may have important implications for the conservation and management of elephants across southern Africa.

CHAPTER 6

SYNTHESIS

Across southern Africa, the conservation and management of elephants present a challenge (see van Aarde *et al.*, 1999; Whyte *et al.*, 2003; Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006; van Aarde & Jackson, 2007; Gillson & Lindsay, 2003). The issue becomes even more complicated as global climate change may induce range expansions for animals (Ogutu & Owen-Smith, 2003; Thomas *et al.*, 2006) that may well be limited by the decrease in space as land use becomes increasingly dominated by human populations (Meadows, 2006). The conservation and management of elephants pose two interdependent challenges, namely 1) how do we manage elephants and their apparent impact on biodiversity?, and 2) how do we manage and conserve elephants in an increasingly fragmented regional landscape?

Confined elephant populations may influence local biodiversity through the modification of vegetation structure and composition within the areas where they occur (see Laws, 1970; Owen-Smith, 1988; Herremans, 1995; Owen-Smith, 1996; Cumming *et al.*, 1997; Guldemond & van Aarde, in review). The management of elephant numbers are therefore often enthused by the negative consequences their impact may have for biodiversity (e.g. Whyte, 2004; Owen-Smith *et al.* 2006). Management options such as culling, contraception and translocation has been discarded as long-term solutions to the underlying problem of locally high elephant numbers (see Whyte *et al.*, 1998; van Aarde *et al.*, 1999; Pimm & van Aarde, 2001; Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006; van Aarde & Jackson, 2007). More recently, however, range expansion has been identified as a possible solution for reducing local impacts of elephants (Gillson & Lindsay, 2003; Bulte *et al.*, 2004; van

Aarde & Jackson, 2007). At the same time, range expansion in the form of sets of megaparks may also benefit biodiversity conservation and the maintenance of ecological processes (e.g. Damschen *et al.*, 2006).

The linking of elephant populations across the southern African region is based on the metapopulation metaphor, where the management of elephants as a metapopulation in a 'source-sink' framework may induce regional stability in elephant numbers (van Aarde *et al.*, 2006). Although attractive in principle, the functioning of the metapopulation paradigm needs to make ecological sense from a more practical perspective. One of the first requirements for the establishment of megaparks is to identify the variables that underpin the current spatial distribution of elephants across the region and the factors that determine movement. These variables could be demographic and spatio-temporal in nature. This study therefore provides the first step towards identifying landscape variables at the landscape scale that may be used in the delineation of megaparks in the arid region of southern Africa.

In this thesis I focussed on the spatial aspect of elephant landscape use over four consecutive seasons within three study areas in the arid savannas of southern Africa. Elephants select for a wide array of resources (see Chapter 5 for detail) within the landscapes they live in. Whether the distribution of sought after resources is reflected in areas of relatively high heterogeneity remains to be demonstrated. However, if elephants selected for areas with higher heterogeneity, it may suggest that such areas provide for their nutritional (Ruggiero & Fay, 1994; Verlinden & Gavor, 1998; de Boer *et al.*, 2000; Houston *et al.*, 2001; O'Connor *et al.*, 2007) and thermoregulatory (Kinahan *et al.*, 2007) requirements. I therefore hypothesized that landscape heterogeneity underlies the location and size of elephant home ranges.

Elephants selected for some aspects of heterogeneity within each of the three

study areas. This was less convincing for Khaudum where selection for heterogeneity seemed to be overruled by their selection for water. My study further indicated that selection for areas with relatively higher levels of heterogeneity within the landscape may be in the form of the locality of the home range rather than the size. The latter variable was however a function of water point density.

Elephants are known to induce considerable changes onto the landscape. It is therefore difficult to isolate the effects of heterogeneity on elephant spatial use from the consequences of elephant spatial use for the heterogeneity within the landscape (Kie *et al*., 2002). The interdependence of spatial use and landscape heterogeneity may further be affected by management actions such as the provisioning of water and fencing of protected areas.

The distribution of water is an important driver of elephant spatial use that may influence the location and the size of home ranges. In our study (de Beer *et al*., 2006) we indicate that elephants in Etosha concentrate their activities within 4 km of water points. Selection for water may therefore co-vary with selection for aspects of heterogeneity. In some cases, as for Khaudum, water may however be overruling the selection for heterogeneity. Here, the relationship between home range size and water point density prevailed during all seasons. The artificial provisioning of water may therefore induce artificial patterns of elephant impact (de Beer *et al*., 2006). Such artificial patterns may prevent impacted areas from recovering as quickly as it would when elephants followed their natural patterns of spatial use and subsequently the landscape becomes increasingly homogenous (Gaylard *et al*., 2003; Smit *et al*., 2007). Fencing may further prevent range shifts and subsequently also the recovery of impacted areas.

My study supports the notion that increasing space, while promoting heterogeneity for elephants may enhance range expansion. This is in accordance with Revilla *et al*., (2004) that show that heterogeneity influences dispersal behaviour of Iberian lynx (*Lynx pardinus*). WallisDe Vries et al. (1999) further suggest that patchiness across all scales is an important driver of herbivore selectivity. The landscape metrics I used to measure heterogeneity is relatively easy to apply and may provide a tool by which it is possible to identify areas of ecological importance to elephants. The management of elephants (and biodiversity) should therefore be directed at managing heterogeneity, which would require reconsideration of water management policies and the construction of fences around protected areas. Consequently, we are presented with a possible solution for the challenges stated above where, 1) local elephant impacts may be alleviated through the re-establishment of metapopulation dynamics at a regional scale and 2) expanding the area available to elephants may further defragment the landscape. Ultimately, this may be beneficial for the conservation of elephants and biodiversity.

Limitations of the study and future research

My study of the influence of landscape heterogeneity on elephant home range location and size was somewhat limited. For instance, the study could be improved by increasing the sample size of elephants. This would probably strengthen certain patterns that I identified here and would make quantitative analyses more feasible. The study could also have benefited from landscape maps that provided higher accuracy statistics. The complexity caused by the differences in habitat types and management practices for the three study areas also made it difficult to incorporate more metrics.

The study provides the first step to identifying variables at the landscape scale that may be important tools in elephant management and conservation. It therefore provides many opportunities for future research. For example, it is important to identify metrics that may be meaningful to elephants. In my study, I used five metrics of which only four seemed to affect elephant home ranges. This type of study will further benefit from establishing a direct link between landscape heterogeneity and the quality and quantity of resources. Moreover, to investigate the relationship between heterogeneity and the distribution of artificial and natural water is essential since many animals are dependent on water. The importance of water as a possible management tool needs to be considered within the landscape context. Understanding how animals functionally respond to heterogeneity at different scales and how these are related between different scales is an important issue that needs thorough research.

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SUMMARY

Resources that can optimize survival are distributed unevenly across landscapes. I assumed that the distribution of these resources is reflected by landscape heterogeneity and that selection for areas with relatively high heterogeneity reflects on selection for resources. I therefore hypothesized that landscape heterogeneity determines variability in elephant home range location and size.

I evaluated home range sizes for elephants living in the Etosha National Park (n = 6), Khaudum Game Reserve (n = 6) and Ngamiland District 11 (n = 4) during two wet and two dry seasons. I used raster grid landscape maps, which were based on structural classes, to superimpose elephant home ranges and to generate randomly located ranges. I then used the FRAGSTATS programme to calculate five landscape metrics that measure aspects of heterogeneity within elephant and randomly located ranges. I compared landscape heterogeneity of the three study areas using the landscape metrics calculated for the randomly located ranges. Assuming that higher values of Patch density, Lanscape shape index and Shannon diversity index, and lower values of Largest patch index and Contagion implies selection for heterogeneity, I qualitatively compared the distribution and the mean of the landscape metric values for the elephant home ranges with those for the randomly located ranges. The influence of season on selection for the landscape metrics was also evaluated. I searched for relationships between home range size and landscape metrics for the three study areas and searched for a possible relationship between home range size and water point density for elephants in Etosha and Khaudum.

Khaudum was consistently more heterogeneous than Etosha and NG11, while the latter was the least heterogeneous. Within these study areas, at least some of the

landscape metrics may explain the location of elephant home ranges. The consistent apparent selection for areas with relatively higher values of Landscape shape index and Shannon diversity index and lower values of Largest patch index and Contagion across both wet and/or dry seasons by elephants in Etosha and NG11 suggests that landscape heterogeneity can explain landscape selection by elephants. This did not hold for elephants in Khaudum where elephants inconsistently selected for Largest patch index and Landscape shape index. This study further suggested that landscape heterogeneity did not determine home range size. However, water was a strong determinant of home range size and may therefore explain the lack of selection for heterogeneity in Khaudum.

Heterogeneity is an inherent characteristic of landscapes and seems to reflect on the availability of resources that may subsequently influence the way elephants use space. My study supported the concept that increasing space, while promoting heterogeneity for elephants may enhance range expansion. The management of elephants should therefore be directed at optimising the availability of heterogeneous landscapes when setting land aside for their conservation. Management also should reconsider water distribution policies since the availability of water influences landscape use and conceivably potential impact on vegetation.

OPSOMMING

Bronne wat oorlewing optimaliseer is oneweredig versprei oor landskappe. Ek het aangeneem dat die verspreiding van hierdie bronne weerspieël word deur landskapsheterogeniteit en dat seleksie vir areas met relatief hoë heterogeniteit ? aanduiding is van seleksie vir sulke bronne. Ek hipoteseer dat landskapsheterogeniteit ? bepaler van tuisgebiedposisie en -grootte van olifante is.

Ek het tuisgebiedgroottes ge-evalueer vir olifante in die Etosha Nasionale Park (n = 6), Khaudum Wildreservaat (n = 6) en Ngamiland Distrik 11 (n = 4) gedurende twee nat en twee droë seisoene. Ek het landskapskaarte gebruik, wat gebasseer is op strukturele klasse om olifant tuisgebiede te superponeer asook ewekansig-geplaasde tuisgebiede te genereer. Ek het die FRAGSTATS program gebruik om vyf indekse te kwantifiseer wat my in staat gestel het om aspekte van landskapsheterogeniteit binne olifant- en ewekansig-geplaasde tuisgebiede te ondersoek. Ek het die indekse bereken vir die ewekansig-geplaasde tuisgebiede om sodoende die landskapsheterogeniteit van die drie studie areas te vergelyk. Die veronderstelling was dat hoër of laer waardes van die indekse (afhangend van die aard van die indeks) seleksie vir heterogeniteit impliseer. Ek het die verspreiding en die gemiddelde waardes van die indekse vir die olifant tuisgebiede met dié vir die ewekansig-geplaasde tuisgebiede kwalitatief vergelyk. Die invloed van seisoen op seleksie vir die indekse was ook ge-evalueer. Die moontlike verband tussen tuisgebiedgroottes en die indekse vir die drie studie areas is ondersoek. Verder het ek ook die afhanklikheid van tuisgebiedgroottes van waterpuntdigtheid vir olifante in Etosha en Khaudum bepaal.

Khaudum was konsekwent meer heterogenies as Etosha en NG11, terwyl laasgenoemde die minste heterogenies was. Binne hierdie studie areas kon die posisie

van olifant tuisgebiede deur sommige van die indekse verduidelik word. Die konsekwente seleksie vir areas met relatief hoër of laer waardes van die indekse as vir die ewekansig-geplaasde tuisgebiede oor beide nat en/of droë seisoene deur olifante in Etosha en NG11 impliseer dat heterogeniteit landskapsgebruik deur olifante kan verduidelik. Hierdie patroon was nie die geval vir olifante in Khaudum nie, waar seleksie vir slegs twee van die indekse ook teenstrydig was binne seisoene. In hierdie studie het ek verder vasgestel dat landskapsheterogeniteit nie bepalend is van tuisgebiedgroottes nie. Waterpuntdigtheid was wel ? faktor wat variasie in tuisgebiedegroottes kon beskryf en bied so ook ? moontlike verduideliking vir die gebrek aan seleksie vir heterogeniteit in Khaudum.

Heterogeniteit is ? inherente eienskap van landskappe wat skynbaar reflekteer op die beskikbaarheid van belangrike bronne wat landskapsgebruik van olifante beïnvloed. My studie ondersteun die konsep dat ? toename in spasie, wat terselftertyd voorsiening maak vir heterogeniteit wat olifante kan bevoordeel, die verspreiding van olifante oor groter areas kan bevorder. Die bestuur van olifante moet dus fokus om die beskikbaarheid van heterogeniese landskappe te optimaliseer wanneer nuwe bewaringsgebiede geïdentifiseer word. Die beleid omtrent die bestuur van water moet heroorweeg word aldus die landskapsgebruik van olifante ook deur die beskikbaarheid van water beinvloed word wat gevolge kan hê vir die plantegroei en uiteraard ook die heterogeniteit van landskappe.