Sexual segregation in African elephants, *Loxodonta africana*, in the Associated Private Nature Reserves, Limpopo, South Africa

Tarryn Chapman

315686

Supervisor: Prof. Neville Pillay

Supervisor: Prof. Francesca Parrini

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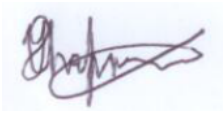
Declaration

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



Tarryn Chapman

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Abstract

The African elephant, *Loxodonta africana* displays sexual segregation, a phenomenon which describes males and females of the same species living separately, except during the mating season. Despite it occurring in many sexually dimorphic species, the factors that govern sexual segregation are still poorly understood. The aim of my study was to investigate whether or not African elephants in the 1825 km^2 Associated Private Nature Reserves (APNR), Limpopo Province were sexually segregated as a result of habitat segregation. I tested the Forage Selection Hypothesis (FSH) which, based on the Jarman-Bell principle, predicts that smaller females are more selective foragers as a result of their high energy demands and poor digestive capabilities in comparison to the larger males. Using the GPS location data of 18 collared adult elephants (12 male and 6 female) from November 2008 to November 2010, I plotted both the total (95% isopleth) and core (50% isopleth) home ranges of individual elephants. I used these home ranges to i) confirm sexual segregation in the APNR, ii) determine whether or not there was a difference in vegetation composition of the home ranges between males and females, and iii) to establish how frequently male and female elephants were associated with each of the vegetation types located within their home ranges. All analyses were done at both the total and core home range level. Home range overlaps were rare between male and female home ranges, particularly at the core home range level, confirming sexual segregation of elephants in the APNR. The vegetation composition data of the home ranges as well as the frequency of association by elephants with each of the available vegetation types (using GPS locations) revealed no significant difference between male and female elephants. Therefore, habitat segregation did not explain sexual segregation by elephants in the APNR. I propose that future studies should consider: i) temporal distribution of elephants to assess how much time each sex spends in each of the available vegetation types; ii) other resources, particularly the availability of water, in addition to the availability of forage, since water limits elephant movements; and iii) social segregation in conjunction with habitat segregation, since elephants display sex-specific differences in social organisation. A comprehensive understanding of the factors that govern sexual segregation of elephants might contribute to conservation management of elephants in the APNR and other small reserves.

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In loving memory of my father, David Charles Chapman, who sadly passed away within the duration of my studies. Although at times I found it really difficult to keep on going, I did it and now I dedicate this to you.

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Introduction

The African elephant, *Loxodonta africana*, was listed as Endangered on the IUCN Red List of Threatened Species in 1996 (Blanc 2008) as a result of poaching for ivory and bushmeat in a large portion of its range. Due to subsequent intensive conservation of the species in parts of its former range, African elephants are today listed as Vulnerable but this relaxing of the status depends on a bigger threat, that of habitat fragmentation (Blanc 2008). With the ever increasing human population will come an increase in the demand to convert natural landscapes into artificial landscapes, severely decreasing and fragmenting the ranges of elephants as well as increasing the probability of human-elephant interaction and conflict (Davis 1976; Blanc 2008). It is for this reason that elephants need to be formally conserved in protected areas, ensuring their persistence into the future.

It has been suggested that to ensure the best conservation practice of a species, it is essential to understand the behaviour of the species (Caro 1998; Rubin & Bleich 2005), yet the role of behaviour in the past has been much debated and questioned (Caro 2007). As there is sufficient evidence to suggest that African elephants are sexually segregated (a behaviour exhibited by a variety of mammal species), understanding the factors that influence this segregation will be beneficial in determining why they remain segregated in the environment. In turn, this would allow for the design of reserves that account for sexual segregation behaviour, best ensuring the most successful conservation of elephants in the face of the decreasing land available for conservation (Stokke & Du Toit 2000; Shannon *et al* 2006a; Shannon *et al* 2006b; Shannon *et al* 2008).

Despite the fact that sexual segregation is a widespread phenomenon in a variety of taxonomic groups (mammals, birds, fish), the factors governing this segregation are still poorly understood and often debated (Ruckstuhl & Neuhaus 2000; Wearmouth & Sims 2008). My study will provide insight into some of the factors governing sexual segregation in African elephants.

Sexual segregation

Outside of the breeding season, there are a number of species in which males and females live either solitarily or in groups of the same sex (Conradt 2005; Wearmouth & Sims 2008). This behaviour is more commonly referred to as sexual segregation and has been observed in large ungulates and also whales, seals, monkeys, elephants and in bird and fish species

(Wearmouth & Sims 2008). There are a number of explanations proposed for sexual segregation, which fall into two broad classes: habitat segregation (Clutton-Brock *et al* 1982) and social segregation (Conradt 2005). Habitat segregation occurs when individuals have different spatial distributions and thus have different habitat utilisation. Social segregation occurs when individuals group together with others of the same social category (e.g. age or sex) which are separated from other social categories (Conradt 2005). Social segregation can occur independently of habitat segregation. When testing whether or not social segregation was merely a by-product of habitat segregation, Conradt (1999) found that the weather parameters that influenced habitat segregation in Red deer, *Cervus elaphus*, did not affect the social segregation. She also found that the degree of social segregation in both *C. elaphus* and feral Soay sheep, *Ovis aries* was significantly greater than habitat segregation (Conradt 1999).

Sexual segregation has been most commonly explained by i) the forage selection hypothesis, ii) the predation risk hypothesis, iii) the social factors hypothesis, and iv) the activity budget hypothesis (Ruckstuhl 2007; Ruckstuhl & Neuhaus 2000; Ruckstuhl & Neuhaus 2002). The first two align with the habitat segregation class while the last two fall into the social segregation class.

The forage selection hypothesis predicts that sexes segregate as a result of differing body sizes and hence differing nutritional requirements that lead them to use different quality food types (Illius & Gordon 1987; Barboza & Bowyer 2000; Conradt 2005). In a number of ungulate species, males are larger than females, a phenomenon referred to as sexual dimorphism. As a result of the allometric relationship between body size and metabolic requirements, smaller individuals (in this case females) often need to access forage of a better quality while larger individuals (i.e. males) can persist on larger quantities of poorer quality forage (Illius & Gordon 1987), referred to as the Jarman-Bell principle (Demment and van Soest 1985, Bell 1971). Lactation in females would also result in their selecting better quality forage to meet the energetic requirements of milk production (Clutton-Brock *et al* 1982). Sexually dimorphic ungulate species may therefore have different diets and consequently use different vegetation types in order to maintain their nutritional requirements which in turn results in them segregating in space (Clutton-Brock *et al* 1982; Conradt 2005). When assessing sex differences in forage quality of white-tailed deer, *Odocoileus virginianus,* Beier (1987) found that diets of female consisted of better quality forage than did male diets which was used to explain why the two sexes were seldom observed together. Ciuti *et al.* (2004), on

the other hand, found that the forage selection hypothesis could not be used to explain sexual segregation in fallow deer, *Dama dama*¸ at San Rossore, Italy, as there were no differences in foraging found between the sexes.

The predation risk hypothesis (otherwise referred to as the reproductive strategy hypothesis – Main and du Toit 2005) suggests that one of the two sexes may be more vulnerable to the risk of predation than the other. Females with offspring, for instance, are often more vulnerable to predation than are their male counterparts which would result in females and their offspring needing to first select areas that offer the most protection against predators (Conradt 2005). As predation is less of threat to males, they may be able to utilise areas of little protection and better forage quality and it is in this way that segregation of the sexes would occur (Conradt 2005). Main & Coblentz (1996) found that female Mountain mule deer, *Odocoileus hemionus hemionus,* used areas of low coyote, *Canis latrans,* activity and increased security benefits to enhance offspring survival while males used areas to enhance their reproductive fitness and to maximise foraging opportunities for preferred forage items, irrespective of Coyote density. This differing behaviour between the two sexes indicates that the predation risk hypothesis might explain the sexual segregation observed in this species. In contrast, since predators have been absent from Nordenskiöld land, Svalbard for over 5000 years, the predation risk hypothesis was discarded as a reason for explaining the sexual segregation exhibited now by Svalbard reindeer, *Rangifer tarandus platyrhynchus* (Loe *et al.* 2006).

The social factors hypothesis proposes that segregation of the sexes occurs as a result of either social attraction or social avoidance (Conradt 2005). The social avoidance hypothesis proposed by Main *et al. (*1986) suggests that males and females may avoid each other socially as a result, for example, of aggression between the sexes, while the social attraction hypothesis suggests that segregation of the sexes occurs as a result of an attraction between individuals of the same sex to benefit learning (Bon & Campan 1996). In male only groups, for instance, males may learn from one another how to behave in the presence of rivals and also learn to fight, two skills that would be beneficial in the breeding season when the competition for mates is high. The acquisition of these two skills would promote the aggregation of males into single sex groups (Ruckstuhl & Neuhaus 2000; Ruckstuhl & Neuhaus 2002).

The activity budget hypothesis predicts that differences in activity budgets and movement rates between the sexes are the most important factors influencing sexual segregation in

sexually dimorphic social ungulates (Conradt 1998; Ruckstuhl 1998; Ruckstuhl & Neuhaus 2002). Sexual dimorphism may result in sexes spending differing amounts of time foraging and travelling to meet energy requirements and, as activity synchrony is important for group cohesion, these differences may result in the fission of mixed groups into unisex groups (Ruckstuhl & Neuhaus 2000; Ruckstuhl & Neuhaus 2002; Conradt 2005). On the Isle of Rum, sexual segregation exhibited by sexually dimorphic feral goats, *Capra hircus*, was most effectively explained by the activity budget hypothesis (Calhim *et al.* 2006). The opposite was found for sexually dimorphic Bison, *Bison bison*, at the National Bison Range and Fort Niobrara National Wildlife Refuge, Nebraska, where single-sex male groups were no more synchronised in their activities than the female groups (Mooring *et al.* 2005).

Home ranges

The area that an animal normally traverses over a period of time (i.e. a month, season, or year) in order to find food, water, shelter, mates and protection is defined as a home range (Burt 1943). Home ranges do not have particular shapes or concrete boundaries and there are a number of factors that influence the extent of an animal's home range. These include intrinsic (e.g. body size, sex) and extrinsic (e.g. herd size, season) factors which influence the nutritional requirements of an animal (Burt 1943; Anderson *et al.* 2005). For instance, herbivores that live in herds have larger home ranges than solitary herbivores and body size correlates positively with home range size (Owen-Smith 1988).

Seasonal changes in resources influence the size and the extent of the home range and often results in an animal having a distinct wet and dry season home range (Burt 1943). Such seasonal differences have been observed both in the white rhinoceros, *Ceratotherium simum*, and the African buffalo, *Syncerus caffer*: both had larger home ranges in winter (dry season) when resources were limited and smaller home ranges in summer (wet season) when resources were abundant (Owen-Smith 1988; Ryan *et al.* 2006).

There are sections of an animal's home range referred to as the core home range, defined as the area within an individual's total home range that is utilised more often than the rest of the home range (Samuel *et al.* 1985). Individuals frequently return to core parts of their home range, indicating that the resources necessary for the survival and reproduction of the animal must be concentrated in these areas (Cederlund & Okarma 1988). Examples that demonstrate the value of core home ranges include Lehmann *et al.* (2008) who found that on Karongwe Game Reserve, where water availability is limited, male lions concentrated their core home

ranges around the few available water points. When there was high competition of mates, red squirrels, *Scuirus vulgaris*, showed little within-sex core home range overlap, defending their core areas against same sex individuals (Wauters & Dhondt 1992).

The African Elephant

Having been removed from parts of its historical range through poaching and illegal hunting, the African elephant, *L. africana*, can only be found in 37 sub-Saharan African countries today (Blanc 2008). Being extensive in its range, *L. africana* can be found throughout a number of different landscape units including dense forest, open and closed savanna, grasslands and even in the arid deserts of Namibia and Mali (Blanc 2008).

African elephants are sexually dimorphic with adult males reaching a maximum weight of up to 6000kg and adult females reaching approximately 3000kg (Laursen & Bekoff 1978). In addition, bulls have a curved, wide forehead while females have a narrow, angular forehead (Laursen & Bekoff 1978). In accordance with the Jarman-Bell hypothesis and sexual dimorphism, male elephants should be able to persist on larger quantities of lower quality forage while females would need to have access to better quality forage, especially during periods of lactation. This has in fact been found to be true in a number of elephant studies where female elephants were found to exploit a much better quality diet than males, even in instances where body size between males and females was similar (Stokke 1999; Stokke & du Toit 2000; Greyling 2004; Woolley *et al.* 2009).

The diet of the African elephant consists of bark, grass, herbs, fruit and foliage from a number of different tree species and, when available, African elephants can drink approximately 225 litres of water per day (Laursen & Bekoff 1978). Because of their large size, African elephants have very few natural predators. It is only calves younger than two years of age that may be predated upon, usually by lions, *Panthera leo*, wild dogs, *Lycaon pictus*, hyena, *Crocuta crocuta*, and crocodiles, *Crocodylus niloticus* (Laursen & Bekoff 1978).

Sexual segregation is well documented for African elephants because females and their offspring live together in permanent groups and mature males live either solitarily or in loosely associated male-only/bachelor groups (Shannon *et al.* 2008). Female groups or clans can number from six to 70 individuals and are made up of families of sisters and daughters and their associated offspring, all of which are led by a single mature female, the matriarch

(Laursen & Bekoff 1978; Poole 1995). Young male offspring are tolerated in these female clans but are forced to leave at around the age of 12 to 15 years at which time they join other sexually immature or mature bulls (Laursen & Bekoff 1978; Poole 1995). There is no defined mating season due to an unusually long inter-calving period (3-5 years), and male elephants older than 30 years of age enter 'musth' (Laursen & Bekoff 1978; Poole 1995). During musth, androgen levels are higher than normal and males seek out and associate with females for mating (Laursen & Bekoff 1978). The period of musth differs for each individual male but, on average, can last for up to 2-3 months of the year (Laursen & Bekoff 1978; Poole 1995). It is only during this period that mature males may be tolerated by the females, which is why male elephants will be found in the presence of female elephants at certain times of the year (Laursen & Bekoff 1978; Poole 1995).

African elephants are not territorial and occupy large home ranges that vary in size from 54km^2-2178 km^2 (Laursen & Bekoff 1978; Ngene *et al.* 2009; Roux & Bernard 2007). As previously mentioned, variance in home range size and shape are dependent on a number of factors and for African elephants these include seasonal availability of food and water, landscape heterogeneity, amount of available space and also the sex of the individuals (De Villiers & Kok 1997; Stokke & du Toit 2000; Roux & Bernard 2007; Woolley *et al.* 2009). Although there have been a number of studies that have found that due to their roaming behaviour, male elephant home ranges are larger than female elephant home ranges (Jackson & Erasmus 2005;; Druce *et al.* 2008), there have also been studies that found no differences in home range size between the sexes (De Villliers & Kok 1997; Whitehouse & Schoeman 2003; Roux & Bernard 2007). In a number of studies, it has been noted that there is a marked seasonal difference in home range size (Viljoen 1989; Legget 2006; Shannon *et al.* 2006c; Roux & Bernard 2007; Thomas *et al.* 2011). Although most studies have found that elephant home range size increases in the dry winter months when resources are limited and the distance travelled to find resources increases (Viljoen 1989; Shannon *et al.* 2006c, there have also been other studies that have found that home ranges are smaller in winter months as elephants aggregate around the few available water points (Legget 2006; Thomas *et al.* 2011).

Aims and objectives

The aim of my study was to investigate whether or not African elephants, *L. africana,* in the Associated Private Nature Reserves (APNR), Limpopo Province are sexually segregated as a result of habitat segregation (particularly that of the forage selection hypothesis (FSH)), using the GPS locations of 18 collared elephants from November 2008 to November 2010.

Objective 1: To investigate the degree of overlap between male and female elephant monthly total and core home ranges in the APNR to confirm sexual segregation.

Prediction: I predicted that there would be little overlap between male and female elephant monthly total and core home ranges in the APNR.

Objective 2a: To ascertain the vegetation composition of male and female elephant monthly total and core home ranges

Prediction: Although elephants have a catholic diet and ingest a variety of vegetation types, based on the previously mentioned studies that found females select vegetation types of a better quality in contrast to males, I predicted that there would be a difference in the vegetation composition of monthly total and core home ranges of female and male elephants in the APNR.

Objective 2b: To establish how frequently male and female elephants are associated with each of the vegetation types located within their monthly total and core home ranges.

Prediction: Based on the Jarman-Bell hypothesis as well as on the findings of the previously mentioned studies, I predicted that the females would be associated with fewer vegetation types within their monthly total and core home ranges in contrast to males which I predicted would be associated with a greater proportion of the vegetation types located within their monthly total and core home ranges.

Materials and Methods

Study Site

This study was conducted using data collected in the 1825 km^2 Associated Private Nature Reserves (APNR), Limpopo, South Africa. The APNR forms part of the greater Kruger National Park and is comprised of four nature reserves, three of which were amalgamated in 2003 and the fourth which became amalgamated in 2006. The four reserves include Timbavati Private Nature Reserve, Klaserie Private Nature Reserve, Umbabat Private Nature Reserve and Balule Private Nature Reserve. The first three of these reserves share an eastern boundary fence with the Kruger National Park (KNP) that was dismantled to create an open system between the APNR and KNP (Figure 1). Average annual precipitation for the region is approximately 550mm and most of this rain falls between the months of December and February while the dry months occur between May and August. The APNR is situated within the summer rainfall region of South Africa with average annual temperature for the area ranging between 20°C min and 32°C max in the wet season and between 10°C min and 27°C max in the dry season (Turner 2007). Falling within the semi-arid savanna biome of Southern Africa, the APNR is classified as Granite Lowveld (Mucina & Rutherford 2006), and the vegetation, as defined by Low & Rebelo (1996) is Mopani Bushveld, Mixed Lowveld Bushveld and Sweet Lowveld Bushveld.

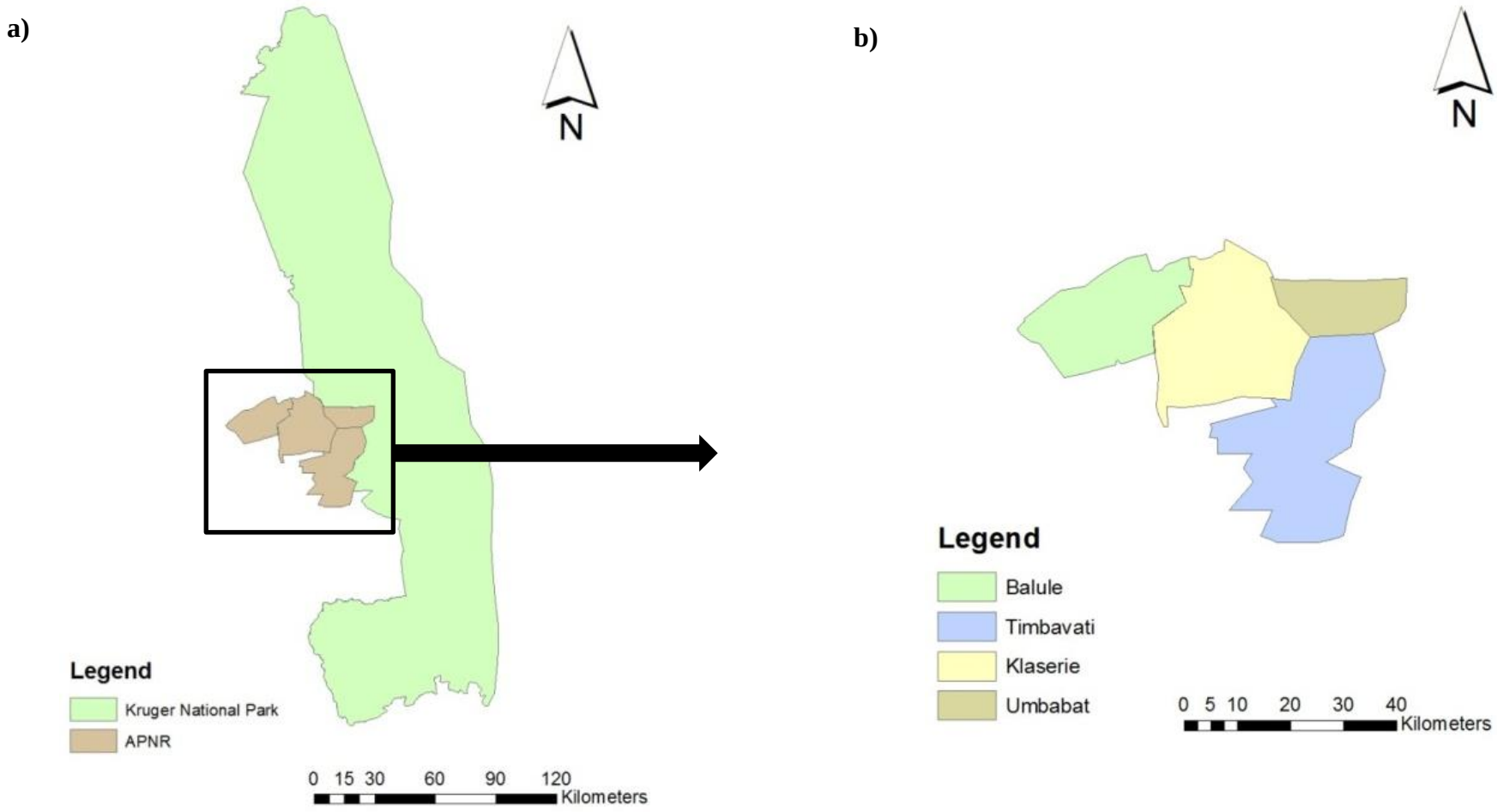

Figure 1: (a) The study site (APNR) in relation to the Kruger National Park, and (b) the four Private Nature Reserves comprising the APNR.

Elephant spatial data

The data that I used for this study were collected and provided by Dr Michelle Henley and Save the Elephants-South Africa (STE-SA). Save the Elephants is a non-profit organisation focussed on understanding the behaviour and ecology of African elephants using GPS tracking. The organisation was founded in 1993 by Dr Iain Douglas-Hamilton.

Between 1998 and 2011, 34 elephants were collared by "STE - SA" in the APNR, comprising of six females and 28 males. The males were both immature and mature bulls that had left their maternal herds while the collared females were matriarchs of different clans. Because of the social nature of female African elephants, I assumed that the GPS locations and movement patterns exhibited by the matriarch included the rest of her clan. The collars fitted to the elephants were GSM-GPS collars obtained from African Wildlife Tracking (AWT) which recorded the location of the elephants via cell phone networks in real-time. Depending on the type of collar fitted to each elephant, the GPS locations were recorded and transmitted either hourly or every four hours.

For the purpose of this study, only data from November 2008 to November 2010 were used, representing the period when the largest numbers of both female and male elephants were collared at the same time. In total, data from 18 elephants (12 males, 6 females) were used in the analyses below (Table 1).

Table 1: The 12 male and 6 female elephants used in this study and the time (in months) that each was collared prior to the study.

Sex	Individual elephant	Time collared prior to study (months)
Male	Big Al	36
	Captain Hook	18
	Classic	28
	General	41
	Gower	24
	Intandwamela	6
	Mac	77
	Matambu	3
	Mellow	18
	Proud	35
	Tussle	25
	Wessa	23
Female	Diney	37
	Joan	45
	Lapajuma	24
	Mandy	41
	Umbabat	36
	Yvonne	15

Normalised Difference Vegetation Index (NDVI) is a measure of vegetation greenness and biomass. Since NDVI reflects the phenology trends that are a response to rainfall, the NDVI for the years 2008, 2009 and 2010 was used to divide each of the study years into both a wet and dry. For the period of this study, two wet and two dry seasons were identified (Table 2).

Table 2: The seasons of the study period as defined by the NDVI of the APNR from 2008 until the end of 2010.

Season	Time period
Wet season 1	15/11/2008-14/05/2009
Dry season 1	15/05/2009-30/11/2009
Wet season 2	01/12/2009-31/05/2010
Dry season 2	01/06/2010-14/11/2010

Home ranges

There have been a number of different methods used previously to calculate the home range of an animal, such as minimum convex polygons, Local Convex Hull (LoCoH), adaptive kernels and fixed kernels (Harris *et al.* 1990, Getz & Wilmers 2004). It has been suggested that the LoCoH methods are best used when calculating home ranges as they represent gaps and boundaries within a home range and also excludes locations from the home range where the animal was not recorded (Getz & Wilmers 2004). This method is used more often than the other abovementioned methods in modern home range studies (Getz & Wilmers 2004). LoCoH is also used to determine core home ranges which are better known as the 50% isopleth (as opposed to entire home ranges which are referred to as 95% isopleths) (Getz & Wilmers 2004). Determining the core home range using LoCoH methods is done by using utilisation distributions (UDs), which, as defined by Van Winkle (1965) are "the two-dimensional relative frequency distributions for the points of location of an animal over a period of time". Because they assess the probability of an animal occurring at any one point in the landscape, UDs are important in home range studies (Van Winkle 1965).

Analyses were performed using the monthly home ranges (hereafter referred to as home ranges) of each of the study elephants. I calculated these home ranges using the "K-LoCoH" method in R version 2.15.2 (http://www.r-project.com). The K-LoCoH method is a powerful method to use when calculating home ranges as it accurately reflects animals locations while at the same time creating indicators of density (Getz & Wilmers 2004). Two GPS location time points (08:00 and 16:00) were used per day per elephant to calculate the monthly home ranges of each elephant. The use of only these two location points is based on findings in the literature that these are the times of the day when elephants move and forage most (Laursen & Berkoff 1978; Loarie, van Aarde & Pimm 2009). As the main aim of this research was to assess sexual segregation in terms of the habitat segregation hypotheses, as discussed earlier, it was important to rule out the use of vegetation for other purposes (e.g. shading or cover during sleep). In instances where location data were unavailable for these two times of the day, I used locations that were the closest to these times provided that they were within three hours of 08:00 and 16:00. Both the core (50% isopleth) and total (95% isopleth) home ranges were calculated for each elephant for each month of the study period by entering the two location points into the "K-LoCoH" method in R version 2.15.2 (http://www.r-project.com).

Procedure

Home range overlap

To determine the percentage overlap between male and female elephant home ranges, the home range of each male was overlaid with the corresponding home range of each female for every month in ArcGIS version 10. In instances where an overlap of the home ranges occurred, the area of the overlap was calculated in square kilometres and the percentage of overlap was calculated as a proportion of the area of both the male and female home range. These calculations were done for both the core and the total home ranges and for comparison purposes, were done for male-female and female-male overlap and also for male-male overlap and female-female overlap.

Vegetation composition of home ranges

To ascertain the vegetation composition of both the core and total home ranges for each of the elephants, each home range was intersected with a vegetation map of the APNR. These intersections were done using the "Geoprocessing -> Intersect" tool in ArcGIS version 10. The area of each of the vegetation types available in the home range was then calculated in square kilometres. The vegetation map that was used in the analyses was an adaptation of the vegetation map constructed for the APNR by Van Rooyen (2005). The 24 vegetation types that were described by Van Rooyen (2005) were collapsed into seven vegetation types (referred to as 'biotopes') and were provided by Dr Michelle Henley and STE-SA. The vegetation map was inclusive of the Timbavati, Klaserie and Umbabat Private Nature Reserves, but did not include the Balule Private Nature Reserve as well as the vegetation of the neighbouring Kruger National Park. Figure 2 shows the Reserves included in the vegetation map as well as the vegetation types making up the map.

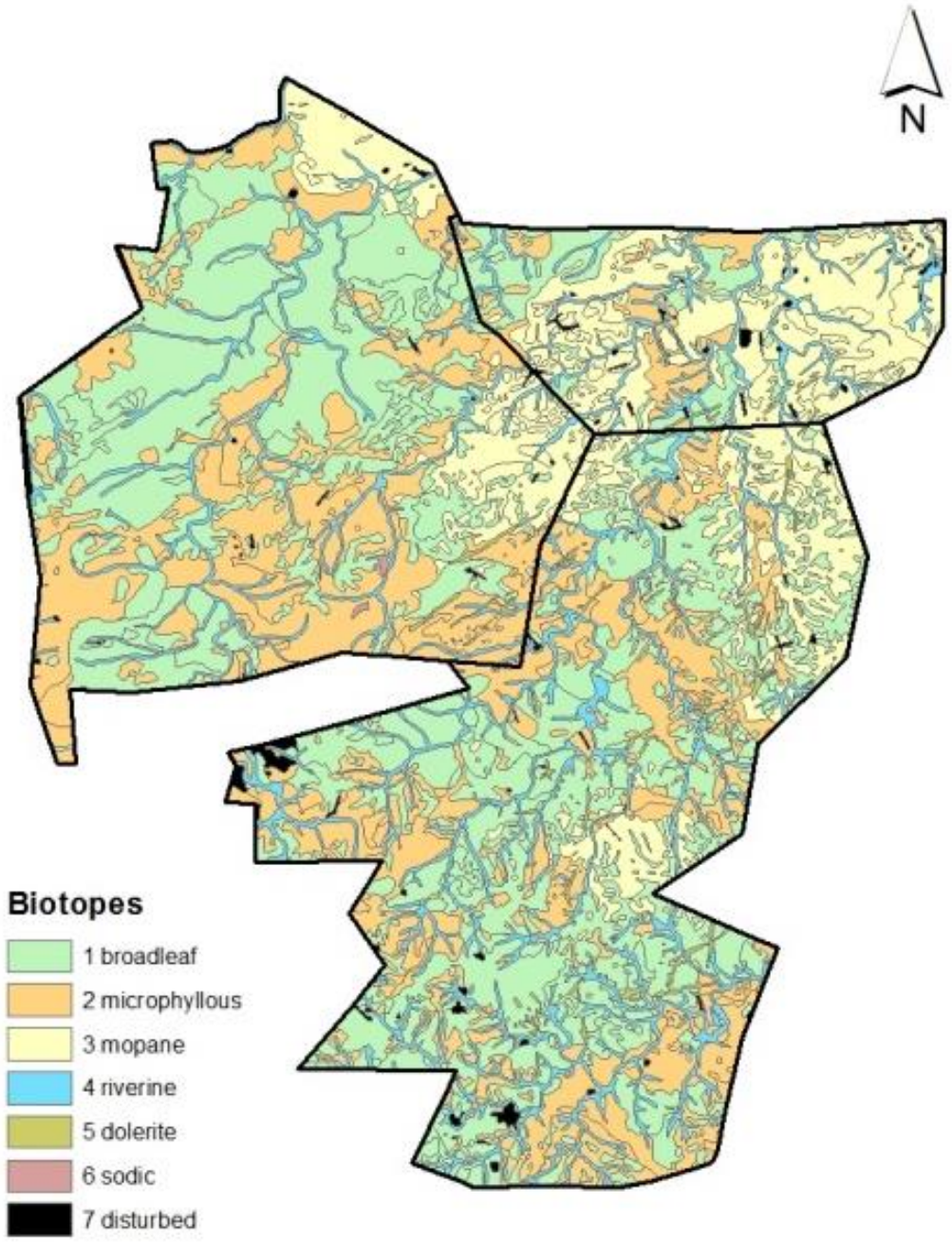

Figure 2: Vegetation map of the APNR (excluding Balulue Private Nature Reserve) displaying the seven biotopes as defined by Save the Elephants-South Africa. Adapted from Van Rooyen (2005).

The vegetation type in each of the home ranges was calculated as a proportion of the area of the home range, as well as a proportion of the total area of each vegetation type available in the APNR (Table 3). In instances where more than 20% of the home range fell outside of the boundaries of the provided vegetation map, the home range for that particular elephant for that month was discarded from the analysis. These included the instances where 80% or more of the home ranges fell within the boundaries of Balule Private Nature Reserve and Kruger National Park.

Table 3: The total area of each vegetation type available in the APNR (km^2) and the proportion of each of these in relation to the area of the APNR.

Vegetation Type	**Area (km^2)**	**Proportion of APNR**
Broadleaf	586.484	0.405
Microphyllous	421.347	0.291
Mopane	271.288	0.188
Riverine	140.801	0.097
Dolerite	12.486	0.009
Sodic	1.347	0.001
Disturbed	12.939	0.009

Frequency of association with each available vegetation type in the home range

To establish how often the elephants were associated with each of the available vegetation type in their home ranges, the GPS locations of each elephant for each month was overlaid with the corresponding intersected home range-vegetation type designed above. The number of points located in each of the vegetation types was calculated and the proportion of points in each of the vegetation types was calculated as a proportion of the total number of available points in the home range. This was done for both male and female elephants for the months that were included in the previous analysis.

Data analysis

Home range size

To analyse the difference in monthly total and core home range size between male and female elephants, I used a Generalised Linear Model (GLM) with a repeated measures design where month was the repeated measure and sex was the fixed effect. Tests were two-tailed and the model level alpha was 0.05. Fisher's post hoc tests were used to test for differences in the significant fixed effects.

Home range overlap

I used transition matrices to compare the frequency of home range overlaps between the sexes as well as within the sexes for the core and total home ranges. I transformed the tables of overlaps between the home ranges into transition matrices for each month using Matman^{TM} (Noldus Information Technology). I used the matrices to calculate the positive adjusted residuals (overlaps occurring more often than expected by chance). Expressed according to a Z-distribution, the adjusted residuals represent the differences between the observed and expected values for the transition frequency. I considered only the positive associations in the matrices to assess whether overlaps occurred greater than chance.

Vegetation composition of elephant home ranges in the APNR

To analyse the difference in vegetation composition of male and female total and core home ranges in relation to the size of the home ranges themselves, I used a Generalised Linear Model (GLZ) with a *logit* or *probit* link function, in which the seven vegetation types were the dependent variables, sex was the independent variable and the proportion of each vegetation type available in each home range was the count variable.

I used a GLZ with a *logit* or *probit* link function to analyse the differences in vegetation composition of male and female total and core home ranges in relation to the proportion of each vegetation type available in the entire APNR. Again, the seven vegetation types were the dependent variables, sex was the independent variable but here, the proportion of each vegetation type in relation to what was available in the entire APNR was the count variable.

Frequency of association with each available vegetation type in the home range

Again, I used a GLZ with a *logit* or *probit* link function to analyse the differences in the use of available vegetation types by male and female elephants in the APNR. The seven vegetation types were the dependent variables, sex the independent variable, the proportion of GPS locations within each vegetation type available in the home range, the count variable and the proportion of each vegetation type available within the entire APNR was the continuous predictor.

When required, I arcsine transformed the data. All analyses were made using STATISTICA^{TM} (version 7.1).

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Results

Home range size

At the total (95% isopleth) home range level, male elephant home ranges ranged, on average, from 10.4 km^2 to 93.00 km^2 and female elephant home ranges from 18.6 km^2 to 92.3 km^2 (Figure 3a). A GLM with a repeated measures design revealed that sex ($F_{1, 16}$= 0.003, p = 0.956), month ($F_{24, 384}$ = 1.27, p = 0.181) and month*sex ($F_{24, 384}$= 0.98, p = 0.495) did not affect home range size of elephants in the APNR from November 2008 to November 2010 (Figure 3a).

At the core (50% isopleth) home range level, male elephant home ranges ranged from, on average, 1.5 km^2 to 13.3 km^2 and female elephant home ranges from 3.9 km^2 to 8 km^2 (Figure 3b). The GLM revealed that there was no trend for sex predicting home range size ($F_{1, 15}$ = 4.04, p = 0.063). However, both month ($F_{24, 360}$ = 3.13, p < 0.001) and month*sex ($F_{24, 360}$= 3.1364, p < 0.001) affected home range size from November 2008 to November 2010. A Fisher's post-hoc test revealed that there was a general increase in core home range size from November 2008 to November 2010 (Figure 3b). Considering these patterns in relation to the defined wet and dry seasons above, core home ranges in dry season 1 (December 2009-May 2010) were the larger compared to wet season 1 (November 2008 – May 2009). In addition, dry season 2 core home ranges (June 2010 – November 2010) were larger than wet season 2 core home ranges (May 2009 – November 2009) (Figure 3b). Female core home ranges were larger in late 2009 and in 2010 than male core home ranges for this time period, as well as larger than both male and female core home ranges in the late 2008 and early 2009.

Home range overlap

At the total home range level, over the entire 25 month study period, male/male elephant home range overlaps occurred more frequently than female/female, male/female (where male home ranges overlapped with female home ranges) and female/male (where female home ranges overlapped with male home ranges) elephant home range overlaps. Female/female home range overlaps occurred the least (Table 4a).

Male/female and female/male home range overlap occurred mostly from January to May 2009 and least in October 2010, June 2009 and October 2009 (Figure 4b). The highest occurrence of male/male home range overlaps was in May 2010, November 2009 and May 2009 and the lowest occurrence was in November 2008, December 2009 and February 2010 (Figure 4a). Female/female home range overlaps occurred mostly in November 2009, March 2009 and April 2009 whereas in December 2008, August 2009, December 2009, June 2010, July 2010 and September 2010, there were no overlaps (Figure 4a).

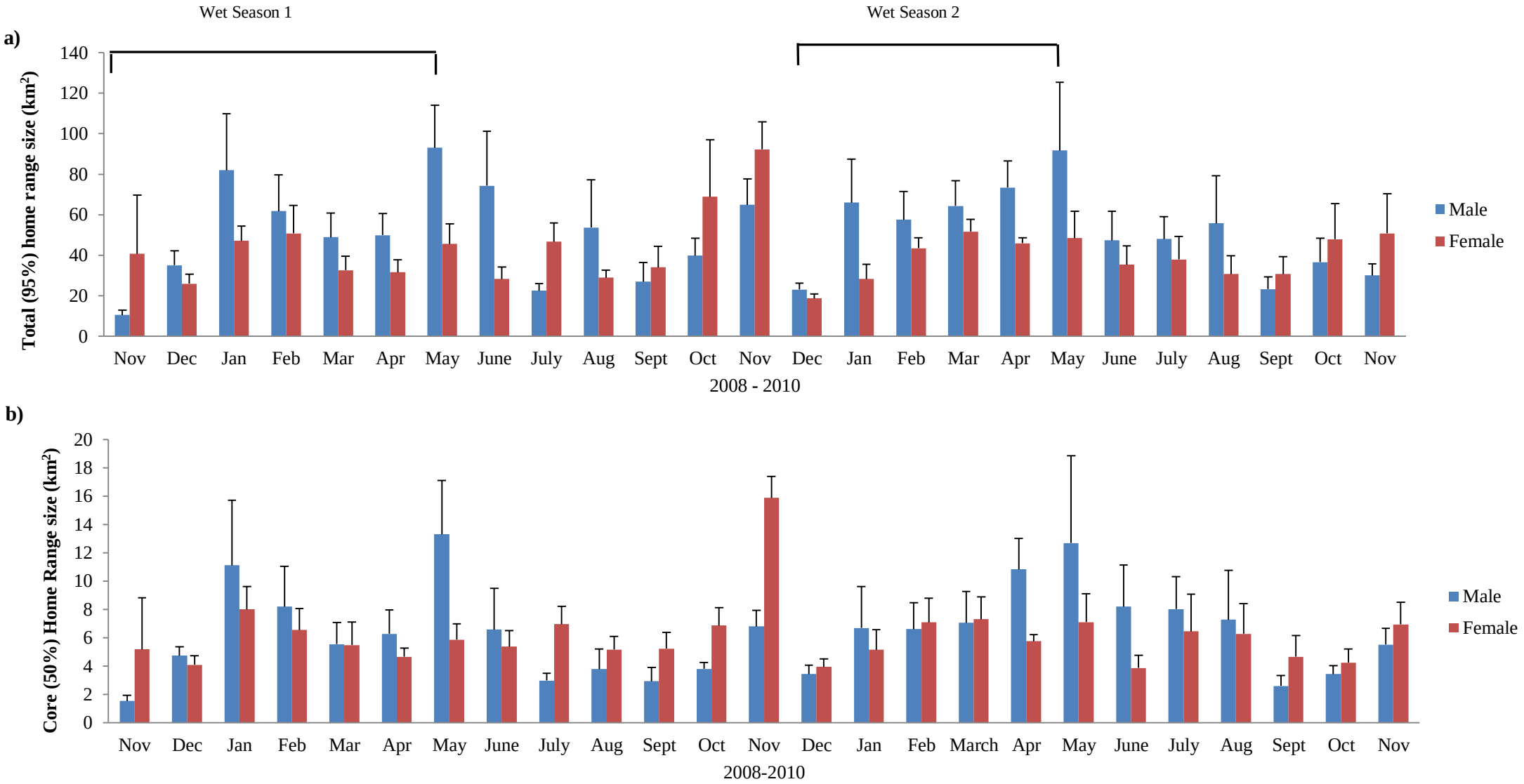


Figure 3: Total (a) and core (b) monthly home range size (km^2) of male and female elephants in the APNR from November 2008 to November 2010. Error bars indicate standard error of the mean.

Compared to the total home range level, at the core home range level, there was a marked decrease in male/male, female/female, male/female and female/male home range overlaps (Table 4b). Male/male home range overlaps still occurred most frequently at this level while female/female home range overlaps occurred the least (Table 4b). Male/female and female/male home range overlaps occurred the most in February 2009 and April 2009 and did not occur at all for 13 of the 25 month study period (Figure 4d). The highest occurrence of male/male overlaps at this level were in November 2009, April 2010 and May 2010 while male/male home range overlaps did not occur at all for January 2009 (Figure 4c). Female/female home range overlaps only occurred in November 2008, March 2009 and February 2009 (Figure 4c).

Table 4: The number of months and percentage of the study period where home range overlaps occurred between same and different sex elephants at the a) total and b) core home range levels. Male/female overlaps refer to male home ranges overlapping with female home ranges while female/male overlaps refer to when female home ranges overlap with male home ranges.

a)

Sex combination	Number of months where home range overlaps occurred (/25)	% of study period
Male/Male	25	100
Female/Female	18	72
Male/Female	25	100
Female/Male	25	100

b)

Sex combination	Number of months where overlaps occurred (/25)	% of study period
Male/Male	24	96
Female/Female	3	12
Male/Female	12	48
Female/Male	12	48

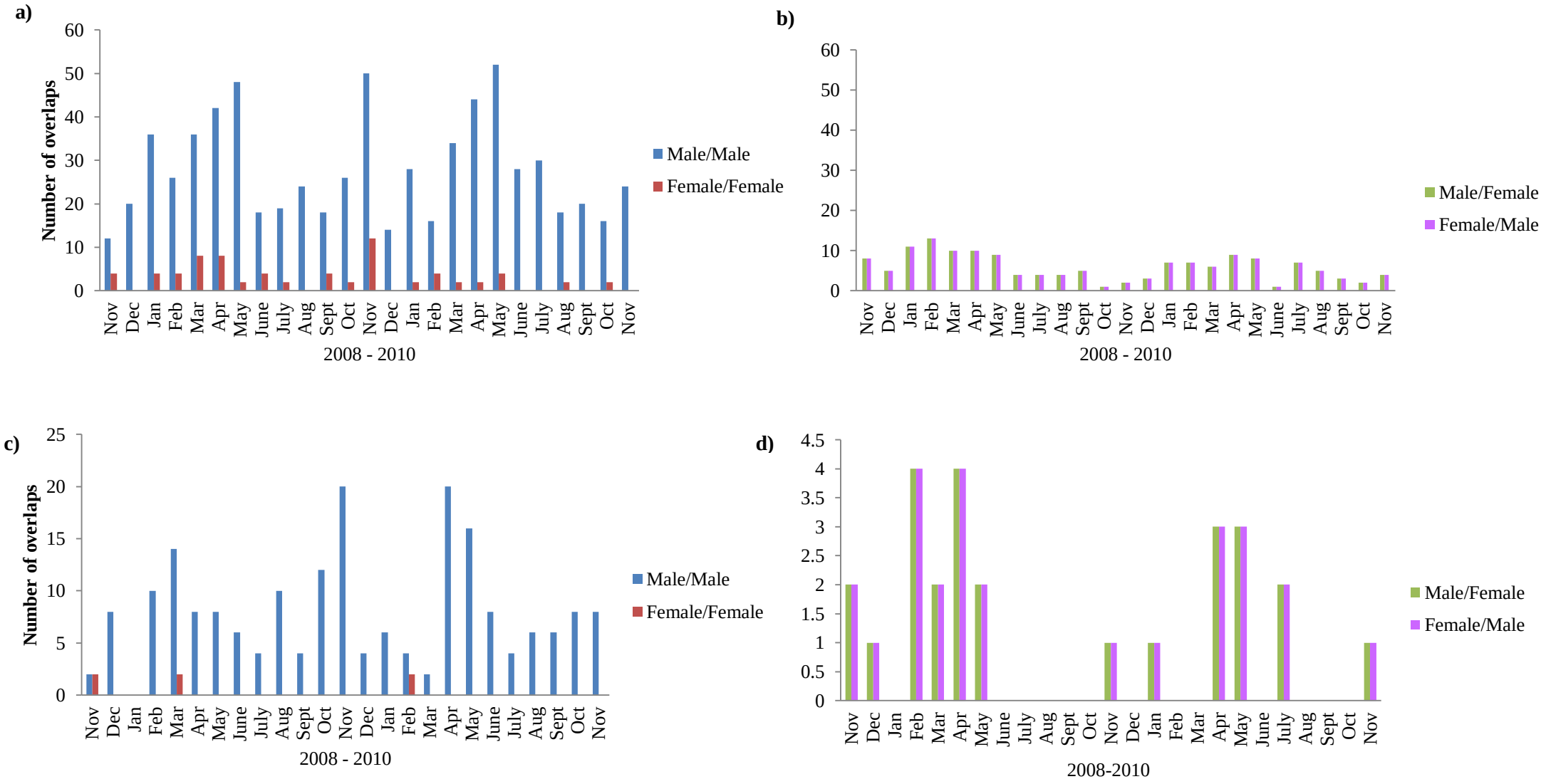


Figure 4: The number of same sex a) total and b) core and opposite sex b) total and d) core monthly home range overlaps for the elephants of the APNR from November 2008 – November 2010.

Looking at the positive associations between elephant total and core home ranges yielded by the transition matrices (Table 5a & b), the following patterns were evident. The greatest number of positive associations at the total home range level was between male/male home ranges (Table 5a). Positive associations between male/female home ranges were the next highest, followed by female/male home ranges and lastly by female/female home ranges, which for 10 non-consecutive months of the study period had no positive associations at all (Table 5a).

At the core home range level, there was a marked decrease in the number of positive associations for all of the sexual combinations compared to the total home range level. Again, the greatest number of positive associations was between male/male home ranges followed by male/female and female/male home ranges. Female/female home range associations only occurred in 3 of the 25 months (Table 5b).

Table 5: The number of positive associations (overlaps greater than expected by chance) between same sex and opposite sex elephants for a) total and b) core home ranges from Nov 2008 to Nov 2010

a)

	2008		2009												2010										
Sex combination	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**
Male/Male	5	8	14	15	12	14	14	7	10	10	16	15	13	9	10	11	10	12	12	9	7	13	8	7	15
Female/Female	4	0	2	4	3	4	2	2	0	0	2	0	0	0	2	4	1	2	2	0	0	2	0	2	0
Male/Female	2	3	5	6	6	9	6	1	4	2	3	1	5	2	2	3	1	4	6	1	4	3	1	2	2
Female/Male	3	2	6	5	8	6	5	1	3	3	5	3	4	2	4	3	4	5	4	1	3	3	2	1	2

b)

	2008		2009												2010										
Sex combination	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**
Male/Male	0	7	8	6	5	9	5	0	0	7	2	11	13	4	6	4	0	8	10	0	5	0	6	6	6
Female/Female	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Male/Female	0	1	0	0	2	4	2	0	0	0	0	0	1	0	1	0	0	3	2	0	1	0	0	0	0
Female/Male	0	0	0	2	1	4	2	0	0	0	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0

Vegetation composition of elephant home ranges in the APNR

The APNR is made up of seven broad vegetation types including Broadleaf, Microphyllous, Mopane, Riverine, Dolerite, Sodic and Disturbed (Figure 2). Of these, Broadleaf makes up the greatest area of the APNR while Dolerite, Disturbed and Sodic make up the smallest area (Table 3).

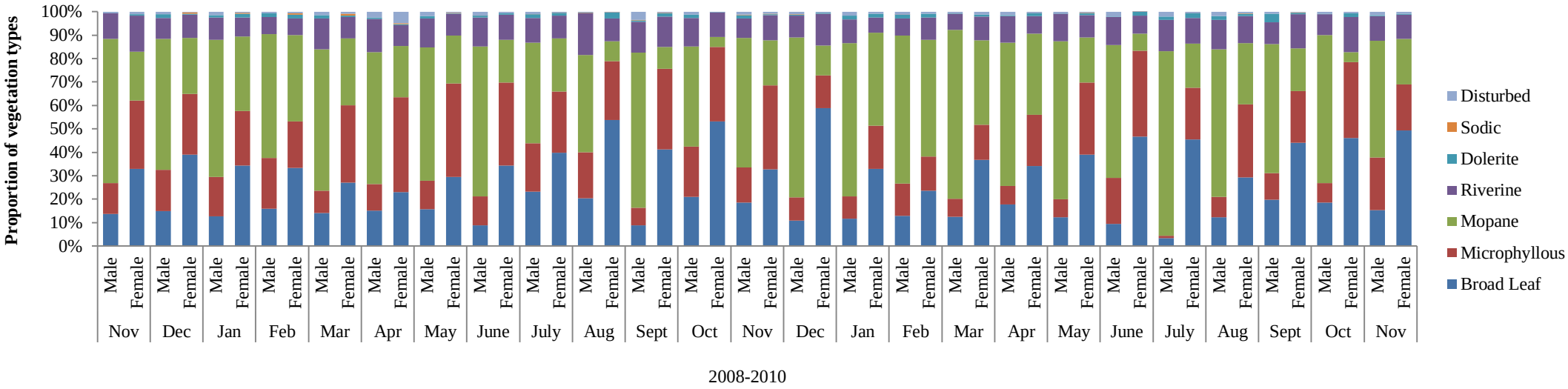
Area of the home ranges

Both at the total and core home range level; sex did not predict vegetation composition of elephant home ranges from November 2008 to November 2010 (Figure 5a; Table 6a).

Proportion of each vegetation type available in the entire APNR

For the entire 25 month study period at the total and core home range level, there were no sex differences in the vegetation composition as a proportion of the total available vegetation in the APNR (Figure 6a; Table 7a) except at the total home range level for February 2009 which was the only month where a significant difference in vegetation composition of male and female elephant home ranges occurred. In this month, female home ranges comprised more of the Sodic and Dolerite vegetation types and male home ranges of Mopane (Figure 6; Table 7).

a)



b)

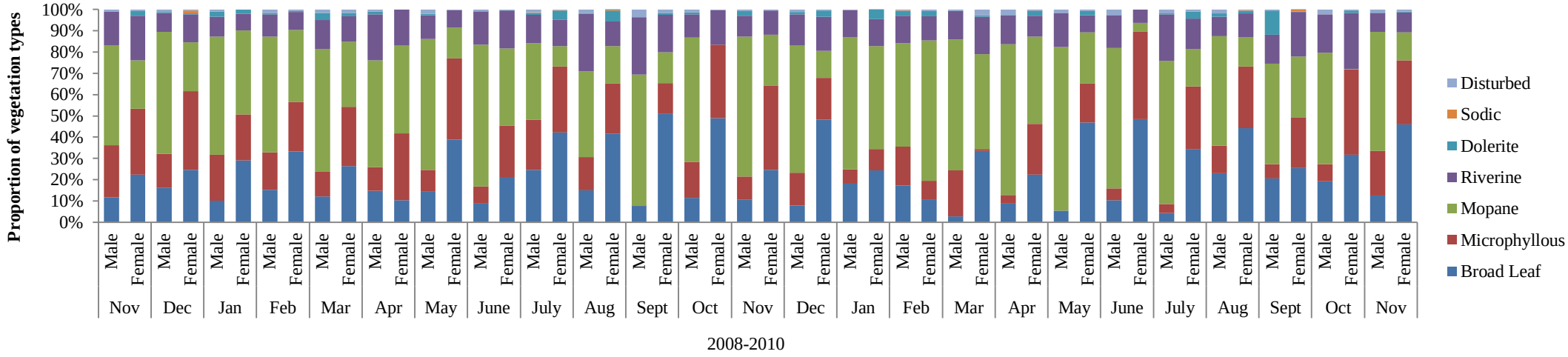


Figure 5: The proportion of each vegetation type found within the total (a) and core (b) monthly home ranges of male and female elephants in the APNR from November 2008 – November 2010. The proportion of vegetation types are in relation to home range size (km^2).

Table 6: The Wald statistics and p-values for the proportion of vegetation types in the (a) total and (b) core monthly home ranges of the male and female elephants. Degrees of freedom for all months = 1. There were no significant outcomes.

a)

Month/year	Wald Stat	p
Nov 08	0.45	0.058
Dec 08	0.82	0.503
Jan 09	0.52	0.470
Feb 09	0.02	0.898
March 09	0.71	0.399
April 09	0.39	0.534
May 09	0.88	0.349
June 09	1.84	0.176
July 09	0.39	0.533
Aug 09	0.87	0.351
Sept 09	1.44	0.230
Oct 09	0.75	0.385
Nov 09	0.47	0.495
Dec 09	1.14	0.285
Jan 10	0.54	0.461
Feb 10	0.06	0.801
March 10	0.23	0.631
April 10	0.49	0.482
May 10	0.93	0.336
June 10	1.37	0.242
July 10	1.80	0.179
Aug 10	0.66	0.418
Sept 10	0.48	0.490
Oct 10	0.30	0.582
Nov 10	0.59	0.443

b)

Month/year	Wald Stat	p
Nov 08	0.16	0.693
Dec 08	0.27	0.601
Jan 09	0.49	0.485
Feb 09	0.39	0.531
March 09	0.55	0.459
April 09	0.43	0.511
May 09	1.33	0.250
June 09	0.61	0.438
July 09	0.34	0.562
Aug 09	0.97	0.325
Sept 09	1.71	0.191
Oct 09	1.65	0.199
Nov 09	1.75	0.186
Dec 09	1.04	0.309
Jan 10	0.00	0.994
Feb 10	0.06	0.800
March 10	0.08	0.784
April 10	0.64	0.424
May 10	1.83	0.176
June 10	1.97	0.160
July 10	1.04	0.308
Aug 10	0.47	0.494
Sept 10	0.17	0.682
Oct 10	0.20	0.652
Nov 10	0.87	0.351

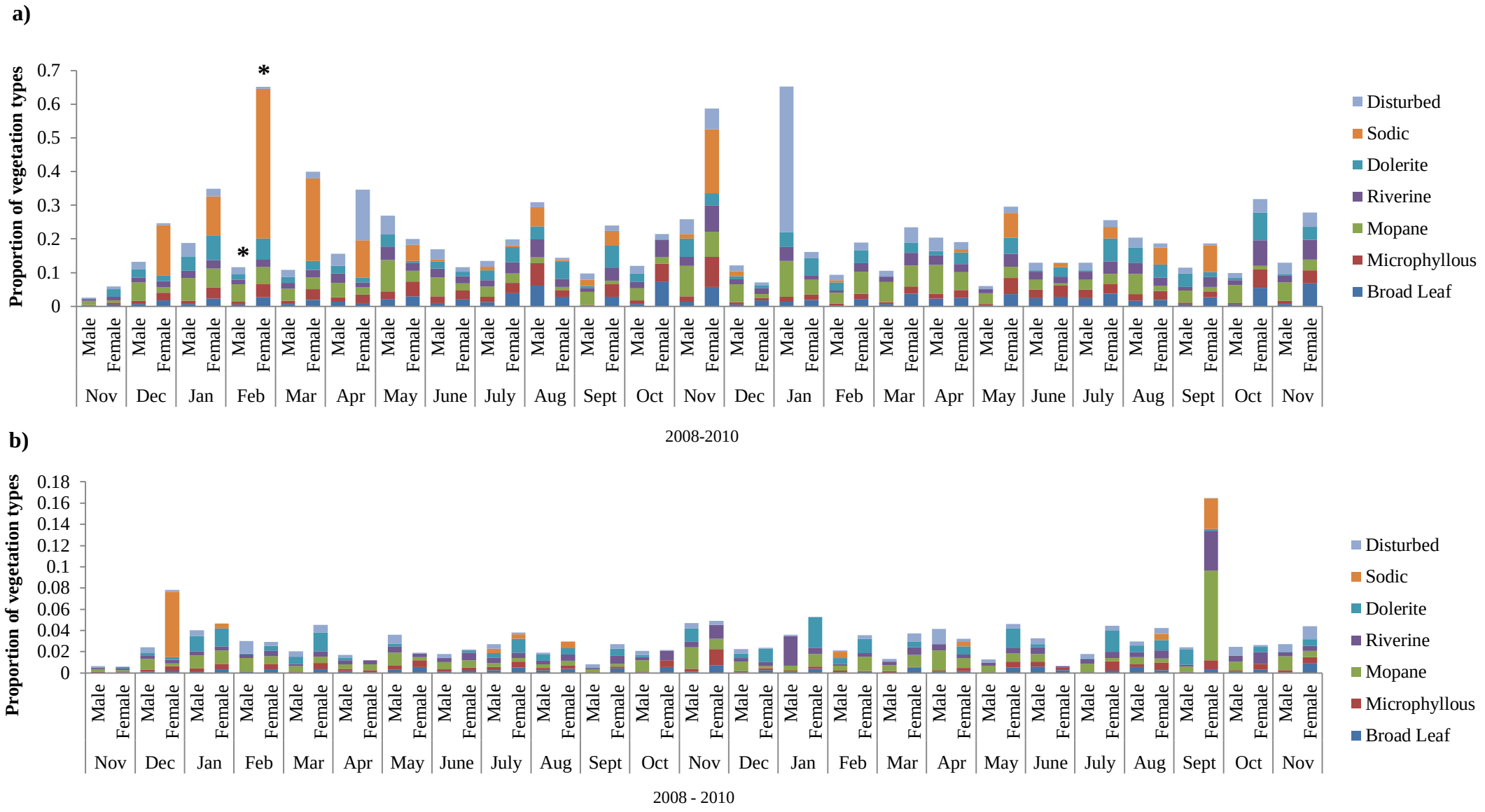


Figure 6: The proportion of each vegetation type found within the a) total and b) core monthly home ranges of male and female elephants in the APNR from November 2008 – November 2010. The proportion of vegetation types is in relation to the total area of each vegetation type available in the APNR. Significant differences marked by asterisks (*).

Table 7: The Wald statistics and p-values for the proportion of vegetation types in the (a) total and (b) core monthly home ranges of the male and female elephants. Degrees of freedom for all months = 1. Significant months indicated in bold.

a)

Month/year	Wald Stat	p
Nov 08	0.02	0.886
Dec 08	0.05	0.817
Jan 09	0.00	0.983
Feb 09	**8.53**	**0.003**
March 09	0.07	0.784
April 09	0.29	0.589
May 09	0.02	0.876
June 09	0.06	0.808
July 09	0.05	0.827
Aug 09	0.00	0.972
Sept 09	0.03	0.855
Oct 09	0.11	0.736
Nov 09	0.01	0.943
Dec 09	0.02	0.892
Jan 10	0.23	0.630
Feb 10	0.03	0.852
March 10	0.00	0.989
April 10	0.00	0.977
May 10	0.00	0.971
June 10	0.41	0.523
July 10	0.03	0.866
Aug 10	0.01	0.917
Sept 10	0.00	0.996
Oct 10	0.00	0.993
Nov 10	0.03	0.868

b)

Month/year	Wald Stat	p
Nov 08	0.00	0.982
Dec 08	0.03	0.867
Jan 09	0.01	0.928
Feb 09	0.03	0.862
March 09	0.00	0.947
April 09	0.00	0.963
May 09	0.05	0.827
June 09	0.01	0.942
July 09	0.02	0.927
Aug 09	0.00	0.985
Sept 09	0.01	0.922
Oct 09	0.03	0.861
Nov 09	0.05	0.825
Dec 09	0.00	0.997
Jan 10	0.00	0.944
Feb 10	0.00	0.960
March 10	0.00	0.990
April 10	0.00	0.949
May 10	0.00	0.973
June 10	0.01	0.931
July 10	0.00	0.987
Aug 10	0.01	0.934
Sept 10	0.03	0.873
Oct 10	0.00	0.951
Nov 10	0.00	0.959

Frequency of association with each vegetation type in the home range

At the total home range level, both male and female elephant location points were randomly distributed across their individual home ranges, regardless of the proportion of each vegetation type, for 24 months of the 25 month study period (Figure 7a; Table 8). The only exception was for August 2009 where the observed non–random distribution was the result of elephants occurring more frequently in Broadleaf vegetation and the least frequently in Sodic vegetation (Figure 7a, Table 8).

Similarly, at the core home range level, elephant location points were randomly distributed across their individual home ranges for 24 months of the 25 month study period (Figure 7b, Table 9). June 2010 was the only month in which elephant location points were not randomly distributed across their home ranges, as a consequence of elephants, particularly males, occurring more frequently in Mopane vegetation and least frequently in Sodic vegetation (Figure 7b).

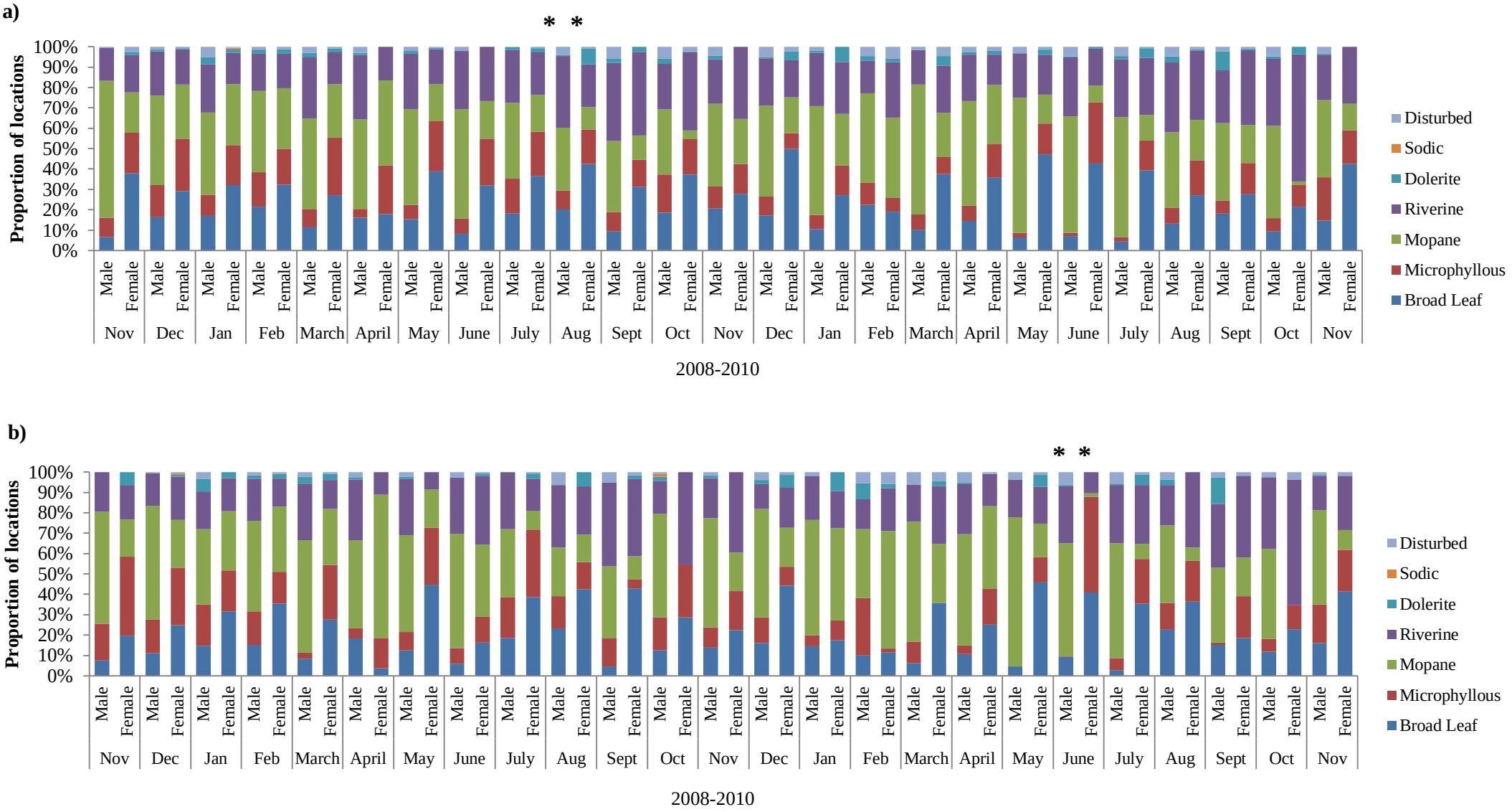


Figure 7: The proportion of male and female elephant location points within each available vegetation type in the a) total and b) core monthly home ranges. Significant differences indicated by asterisks (*).

Table 8: The Wald statistics and p-values for the proportion of vegetation types in the home ranges and the sex of the elephants at the total home range level. Degrees of freedom for all months = 1. Significant months indicated in bold.

Month/year	Variable	Wald Stat	p
Nov 08	Proportion of Vegetation Type	1.51	0.219
	Sex	1.68	0.195
Dec 08	Proportion of Vegetation Type	0.61	0.434
	Sex	0.31	0.578
Jan 09	Proportion of Vegetation Type	1.29	0.256
	Sex	0.40	0.525
Feb 09	Proportion of Vegetation Type	0.04	0.835
	Sex	0.56	0.453
March 09	Proportion of Vegetation Type	1.19	0.275
	Sex	1.27	0.260
April 09	Proportion of Vegetation Type	1.39	0.238
	Sex	0.39	0.535
May 09	Proportion of Vegetation Type	1.08	0.298
	Sex	1.46	0.228
June 09	Proportion of Vegetation Type	2.99	0.084
	Sex	3.04	0.081
July 09	Proportion of Vegetation Type	1.71	0.191
	Sex	0.45	0.502
Aug 09	**Proportion of Vegetation Type**	**3.90**	**0.048**
	Sex	1.51	0.219
Sept 09	Proportion of Vegetation Type	2.59	0.107
	Sex	1.27	0.260
Oct 09	Proportion of Vegetation Type	3.73	0.054
	Sex	0.67	0.412
Nov 09	Proportion of Vegetation Type	1.71	0.191
	Sex	0.06	0.803

(Table 8 continued…)

(…Table 8 continued)

Month/year	Variable	Wald Stat	p
Dec 09	Proportion of Vegetation Type	1.08	0.298
	Sex	0.50	0.479
Jan 10	Proportion of Vegetation Type	0.71	0.401
	Sex	0.25	0.621
Feb 10	Proportion of Vegetation Type	0.20	0.653
	Sex	0.06	0.807
March 10	Proportion of Vegetation Type	0.57	0.451
	Sex	0.26	0.612
April 10	Proportion of Vegetation Type	1.17	0.279
	Sex	1.26	0.261
May 10	Proportion of Vegetation Type	2.03	0.154
	Sex	1.91	0.167
June 10	Proportion of Vegetation Type	2.68	0.102
	Sex	2.62	0.106
July 10	Proportion of Vegetation Type	2.89	0.089
	Sex	2.19	0.139
Aug 10	Proportion of Vegetation Type	1.89	0.169
	Sex	0.18	0.671
Sept 10	Proportion of Vegetation Type	2.07	0.151
	Sex	0.88	0.347
Oct 10	Proportion of Vegetation Type	1.98	0.160
	Sex	0.11	0.742
Nov 10	Proportion of Vegetation Type	1.21	0.272
	Sex	0.89	0.346

Table 9: The Wald statistics and p-values for the proportion of vegetation types in the home ranges and the sex of the elephants at the core home range level. Degrees of freedom for all months = 1. Significant months indicated in bold.

Month/year	**Variable**	**Wald Stat**	**p**
Nov 08	Proportion of Vegetation Type	0.16	0.685
	Sex	0.39	0.533
Dec 08	Proportion of Vegetation Type	0.33	0.563
	Sex	0.23	0.628
Jan 09	Proportion of Vegetation Type	0.40	0.525
	Sex	0.40	0.526
Feb 09	Proportion of Vegetation Type	1.31	0.252
	Sex	0.56	0.453
March 09	Proportion of Vegetation Type	0.71	0.399
	Sex	1.27	0.260
April 09	Proportion of Vegetation Type	0.48	0.487
	Sex	0.00	0.992
May 09	Proportion of Vegetation Type	1.21	0.271
	Sex	2.54	0.111
June 09	Proportion of Vegetation Type	2.25	0.134
	Sex	0.94	0.333
July 09	Proportion of Vegetation Type	3.37	0.066
	Sex	1.51	0.219
Aug 09	Proportion of Vegetation Type	1.00	0.317
	Sex	0.37	0.542
Sept 09	Proportion of Vegetation Type	1.50	0.220
	Sex	1.20	0.274
Oct 09	Proportion of Vegetation Type	1.32	0.251
	Sex	0.39	0.532
Nov 09	Proportion of Vegetation Type	1.04	0.307
	Sex	0.20	0.651

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(Table 9 continued on next page…)

(Table 9 continued…)

Month/year	Variable	Wald Stat	p
Dec 09	Proportion of Vegetation Type	0.57	0.448
	Sex	0.40	0.527
Jan 10	Proportion of Vegetation Type	0.75	0.388
	Sex	0.00	0.948
Feb 10	Proportion of Vegetation Type	0.40	0.527
	Sex	0.16	0.694
March 10	Proportion of Vegetation Type	2.19	0.139
	Sex	0.02	0.901
April 10	Proportion of Vegetation Type	0.57	0.451
	Sex	1.02	0.312
May 10	Proportion of Vegetation Type	3.23	0.072
	Sex	1.80	0.180
June 10	**Proportion of Vegetation Type**	**3.93**	**0.047**
	Sex	**4.61**	**0.032**
July 10	Proportion of Vegetation Type	2.61	0.106
	Sex	1.27	0.260
Aug 10	Proportion of Vegetation Type	1.89	0.169
	Sex	0.18	0.671
Sept 10	Proportion of Vegetation Type	2.56	0.110
	Sex	0.53	0.466
Oct 10	Proportion of Vegetation Type	0.94	0.332
	Sex	0.03	0.857
Nov 10	Proportion of Vegetation Type	0.62	0.432
	Sex	0.61	0.434

Discussion

The aim of my study was to investigate whether or not African elephants, *L. africana,* in the Associated Private Nature Reserves (APNR), Limpopo Province, South Africa are sexually segregated as a result of habitat segregation. I did so by using the GPS locations of 18 collared elephants from November 2008 to November 2010 to calculate the total (95% isopleth) and core (50% isopleth) home ranges of the elephants in the APNR.

Home range size

The sex of the individual, the temporal variation of the available resources in the area as well as the interaction between these variables are just a few factors that determine the size of an individual's home range (Burt 1943; Harestad & Bunnell 1979; Anderson *et al.* 2005). Since, in accordance with the Jarman-Bell hypothesis, smaller females limit their movements to areas of high quality forage and larger males forage over a larger area as they can forage on lower quality forage, there should be a distinct difference in the home range size of males and females of sexually dimorphic species (Bell 1971; Jarman 1974). Based on this hypothesis, as well as the fact that male elephants can weigh up to 3000 kg more than females, it can be assumed that male elephant home ranges would be larger than female elephant home ranges. In support, it has been found that male elephant home ranges were larger than female elephant home ranges in Tanzania (Kikoti 2009) and in Chobe, Botswana (Stokke and du Toit, 2002).

This was not the case for my study with home range sizes of male and female elephants in the APNR being similar in size at both the total and core home range level. Although my results contradict the prediction of the Jarman-Bell hypothesis, my findings are supported by another study by De Villiers & Kok (1997). These authors assessed home ranges of elephants in the same location as my study and found no sex difference in elephant home range size in the Klaserie Private Nature Reserve (KPNR), which they attributed to the large perennial bodies of water (Klaserie and Olifants Rivers) running through the reserve. Since the perennial bodies of water are equally available to each of the sexes, neither male nor female elephants would have to range further to find water (De Villiers & Kok 1997). Since these rivers formed part of my study area, it too could be the availability of perennial rivers that results in the observed lack of sex differences in the home range size of the elephants in the APNR.

The lack of difference in home range size between male and female elephants of the APNR may be attributed to the fact that, for this study, the collared females were part of a herd (as mentioned in Materials and Methods). Since female elephants are constrained to areas of higher quality forage, which are generally limited in an environment, a herd of elephants might be expected to cover a larger area to provide sufficient high quality forage to satisfy the needs of the herd (Demment & van Soest 1985; Mysteraud 2000).

In South Africa, winter months are usually characterised by periods of low rainfall which are generally the primary periods of resource constraints in the environment (Mysterud 2000; Symes *et al.* 2008). It has been hypothesised that as the available resources in an environment decline, an individual would have to range further to find the resources to meet the nutritional requirements necessary for their survival, which would lead to an increase in the individual's home range (Shannon *et al.* 2006c). For example, the winter home ranges of elk, *Cervus elaphus*, were larger than the summer home ranges because they had to range further in order to find forage of adequate quality and quantity (Anderson *et al.* 2005).

In my study, elephant home ranges were measured monthly. Since elephants have been reported to change the size of their home ranges in the wet and dry seasons (De Villiers & Kok 1997; Stokke & du Toit 2000; Roux & Bernard 2007; Woolley *et al.* 2009), I would have expected that there would be months of the study period where home ranges were larger than at other times, particularly in the winter/drier months. In my study, total home range (95% isopleth interval) size did not change for the entire 25 month study period (November 2008 – November 2010). There was, however, a general increase in the size of the core home range for all elephants from the beginning of the study period (November 2008) until the end of the study period (November 2010). The monthly core home ranges falling under Dry Season 1 and Dry Season 2 were larger than core home ranges falling under Wet Season 1 and Wet Season 2 respectively, fitting the prediction that dry season home ranges are larger than wet season home ranges. A study of elephant home range and habitat selection in Pongola Game Reserve, South Africa, by Shannon *et al.* (2006a) found that the dry season/winter home ranges were larger than the wet season/summer home ranges, explained with the limited food availability in the dry season which would force individuals to move over a wider area in search of resources.

Since core home ranges are areas of concentrated use, changes in core home range size might be more revealing of the changing ecological and nutritional needs of animals (Whauters &

Dhondt 1992). For sexually dimorphic species, during periods of constrained resources, larger males would not need to roam as far to find resources to survive than would smaller females (Illius & Gordon 1991; Mysterud 2000). For sexually dimporhic species in temperate regions, this has been attributed to the greater amount fat reserves of the larger males that are deposited during the summer months (Mysterud 2000). The depletion of fat reserves takes longer in larger individuals, in this case males, and in periods of limited resources, males would not need to range far to find resources but could live off these fat reserves while foraging on the fewer remaining amounts of poorer quality forage (Mysterud 2000). In my study, female elephant core home ranges were larger than male core home ranges at the start of Wet Season 2 (late 2009) as well as throughout the following dry and wet seasons (2010). These findings suggest that forage quality and quantity was limited during these periods of the study forcing females to expand their core areas to areas with the higher quality forage needed to ensure the survival of themselves and their young.

Home range overlap

To confirm sexual segregation in the elephant population of the APNR, I looked at the total and core home range overlaps between male and female elephants, predicting that there would be fewer overlaps between male and female elephants. As previously discussed, adult male and female individuals of sexually dimorphic species might have differing nutritional requirements, resulting in them utilising different parts of the landscape (Demment & van Soest 1985). The smaller females may be constrained to areas of higher quality forage, which are generally limiting in an environment, while the larger male would not be similarly constrained, allowing them to utilise different areas of the landscape (Demment & van Soest 1985; Illius & Gordon 1991; Mysterud 2000). This differing use of environments alone would result in fewer home range overlaps between males and females of sexually dimorphic species. For example, in the Kruger National Park, male and female Kudu, *Tragelaphus strepsiceros*, were found to utilise significantly different habitat types which was used to explain their observed sexual segregation (du Toit 1995). The significant positive associations yielded by the transition matrices in my study showed that although there were significant overlaps between male and female home ranges, these overlaps occurred less frequently than overlaps between male elephants, which had the highest number of significant home range overlaps. Overlaps between female elephants occurred the least of all of the possible combinations. All of these patterns were seen at both the total and core home range level, with a marked decrease in all overlaps at the core home ranges. As core home

ranges are areas used most intensively, it has been suggested that core home range overlaps would provide the best indicator of competition for space within and between the sexes (Wauters & Dhondt 1992).

In elephants, the only time males are tolerated within the range of females is when they are not yet mature enough to leave the matriarchal herd (juveniles) and during mating and periods of musth (Laursen & Bekkof 1978). The few instances in my study where male home ranges overlapped with female home ranges might have been as a result of these periods of musth. I did not have adequate musth data available and therefore could not accurately determine when male/female home range overlaps were the result of musth. However, since most of the males collared in the study were mature bulls, it can be assumed that these observed overlaps were as a result of the musth periods (Laursen & Bekkof 1978). Also, examining the male and female home range overlaps in relation to the wet and dry seasons of the study period, there appeared to be no seasonal pattern to these overlaps, fitting the irregular, non-seasonal pattern of musth cycles observed in mature male elephants (Laursen & Bekkof 1978).

Occurring less frequently than male/male home range overlaps, there were a few instances where female home ranges overlapped with male home ranges. Examining these overlaps in relation to the wet and dry seasons of the study shows a seasonal trend to the overlaps, with majority of the overlaps occurring during the wet seasons and fewer of the overlaps occurring in the dry season. Since the smaller females of sexually dimorphic species utilise high quality forage which is usually limited in an environment (Demment & van Soest 1985), females may overlap with males less in the dry season as they would not range far from areas of known high quality forage.

As already mentioned, male/male overlaps occurred the most frequently at both total and core levels. These overlaps occurred mostly in Wet Season 1 and Wet Season 2. When looking at the movement patterns and habitat utilisation of elephants in Tsavo, Kenya, Leuthold & Sale (1973) found the same trend with male elephant home ranges overlapping more so in the wet season than in the dry season when resource availability was high. In the dry seasons, they found that males restricted their ranges to areas with permanent water sources. Since dry seasons are periods of constrained resources, it can be expected that competition for resources would be high, resulting in same sex animals avoiding areas where they would have to share the limited resources (Mysterud 2000). Although this is true for both of the sexes, it would be

particularly true for females as they have to compete for limited high quality forage (Demment & van Soest 1985). In Amboseli National Park, Moss (1988) found that the two sub-populations of female elephants utilised different dry season ranges but mixed together during the wet season. Martin (1978) also found a similar trend with there being very few overlaps between female elephant groups in the dry season. In my study, female/female overlaps occurred the least frequently of all the sex combinations. Where female/female home range overlaps occurred, there appeared to be a seasonal trend with more overlaps observed during the wet seasons than during the dry seasons, agreeing with the findings of the abovementioned studies.

Vegetation composition of elephant home ranges and frequency of association with each available vegetation type

I predicted that there would be a difference in the vegetation composition of male and female elephant home ranges in the APNR, particularly at the core home range level. I also predicted that male and female location points would not be randomly distributed within their respective home ranges, but rather that male location points would be distributed throughout more of the available vegetation types and female location points throughout fewer of the available vegetation types. My findings, however, do not support this prediction as I found no difference in the vegetation composition of the home ranges at both the total and core home range levels for male and female elephants of the APNR. I also found that male and female elephant location points were generally randomly distributed throughout their home ranges, once again showing no difference in their preference for a particular vegetation type, regardless of the proportion of each vegetation type available.

When assessing whether or not African elephants were sexually segregated at a habitat scale on three South African reserves, Shannon *et al.* (2006a) found no significant differences in habitat preference between male and female elephants. They suggested that due to the fact that elephants thrive in a vast diversity of environments (e.g.. desert and forest) (Laursen & Bekoff 1978), and because elephants are much larger than the temperate ruminant species for which habitat segregation is often studied, elephants, regardless of their sex difference in size, can use most of the vegetation types available to them for foraging (Shannon *et al.* 2006a). Since other studies have found that sexual segregation in African elephants is the result of habitat segregation (Stokke & du Toit 2000; Shannon *et al.* 2006b; Smit *et al.* 2007), Shannon *et al.* (2006a) suggests that it may be necessary to establish which parts (e.g.. stems,

barks, shoots, roots) of the different vegetation types the male and female elephants are using and whether there are differences between the sexes at this scale. In fact, Stokke & du Toit (2000) found that male elephants had a significantly different feeding behaviour to female elephants resulting in their segregation. Although male elephants browsed on fewer plant species than females, they utilised a wider variety of plant parts than the females, which seemed to select plant parts of higher quality from a variety of the available browse species (Stokke & du Toit 2000).In Niger, Caister *et al.* (2003) found that plant tannin constituents were the leading cause for the sexual segregation observed in the giraffe, *Giraffa Camelopardalis peralta*, population. During periods of pregnancy/nursing, female giraffe foraged in different regions to the male giraffe, resulting in their segregation. They found that pregnant/nursing females passed up high quality forage available to them as they contained high levels tannin which they believed made the giraffe's milk unpalatable to their young. (Caister *et al.* 2003).

Previous studies have also suggested that water is one of the more important resources for elephants and that they will establish their home ranges close to water sources (De Villiers & Kok 1997; Ntumi *et al* 2005). In Chobe National Park, Botswana, Stokke & Du Toit (2002) found that the proximity to water sources (as opposed to vegetation type and quality) was a more important factor for male and female elephants when selecting habitats and home ranges. It was suggested that female elephant groups would select home ranges closer to water sources as they, as well as their young, have a high water turnover in comparison to male elephants (Stokke & du Toit 2002). If water is the more important resource determining home range position, the lack of observed difference in vegetation composition of male and female home ranges in the APNR can be better understood. Females in the APNR may be selecting their home ranges in close proximity to the available water sources as opposed to available vegetation types, thereby segregating them from the males. Therefore, the proximity to water points could have resulted in the segregation of the sexes in my study and must be investigated further in the APNR.

Conclusion

The results of my study were evaluated against the theories of habitat segregation, particularly the Forage Selection Hypothesis to determine if it best describes the segregation observed in the elephant population of the APNR. Sexual segregation was evident in the elephant population of the APNR, with there being little overlap between male and female home ranges throughout the 24 month study period, particularly at the core home range level. Based on the methodology and findings of this study, this segregation cannot be ascribed solely to the explanations of the Forage Selection Hypothesis. There was no difference in the vegetation composition as well as the selection for a particular vegetation type within the home ranges between male and female elephants. However, the data used in my study assessed only the spatial distribution of the elephants in the APNR and did not take into consideration the temporal distribution of the elephants. Sexual segregation in the APNR by habitat segregation can therefore not be entirely ruled out. Future studies should assess elephant distributions both spatially and temporally. Assessing how much time an elephant spends at a specific location/feeding on a particular vegetation type would provide a better understanding of their preferences for a particular vegetation type. In addition, it would also be useful to assess whether or not male and female elephants utilise the available vegetation types differently through observations of feeding behaviour. When assessing the sex differences in feeding behaviour of sexually dimorphic giraffe, *Giraffa camelopardalis*, Ginnet & Demment (1997) found that although male and female giraffe made use of similar habitats, their feeding behaviour in these habitats was different. In their study, they found that although male giraffe took larger bites than females, female giraffe cropped bites quicker and also chewed faster than the males (Ginnet & Demment 1997). For African elephants, Stokke (1999) found a significant difference between male and female feeding behaviour with females and their young utilising more woody vegetation species than males. It would also be important to establish whether or not male and female elephants were using the vegetation types in the same way behaviourally. It is possible, for example, that males used a particular vegetation type simply for resting while females used it for foraging, an observation that could not be detected based on the GPS location data used in this study.

Since elephants have very few natural predators due to their large size (Laursen & Bekoff 1978; Ruggerio 1991), predation pressure on females and their young are unlikely to segregate the sexes in the APNR. In support, females did not select different vegetation types (presumably ones that offer more safety) to male elephants.

I also suggest that sexual segregation in African elephants might be a result of social segregation, something that has not been done in the previous studies on sexual segregation in elephants. Social segregation, as defined by Conradt (1998), is the grouping together of same sex animals outside of the mating season. This segregation can be as a result of i) social avoidance, whereby opposite sex individuals would avoid one another due to aggression between the sexes, and ii) social attraction whereby same sex individuals would be attracted to one another for the benefits of learning (Main *et al*. 1986; Bon & Campan 1996). Due to the social nature of elephants where young males leave the matriarchal herd and join groups of sexually mature males (Laursen & Bekoff 1978), I suggest that elephants may be sexually segregated as a result of social segregation, particularly as a result of social attraction. Nonetheless, I believe that the factors influencing sexual segregation in sexually dimorphic species are not mutually exclusive and should be assessed holistically. This idea is supported by numerous authors who have suggested that because social segregation is often associated with sex differences in habitat use, social segregation is merely a by-product of habitat segregation (Clutton-Brock *et al.* 1982; Miquelle *et al.* 1992), but there have been no studies providing evidence of this idea.

In order for African elephants to be managed in their increasingly constrained environments, we need to better understand their behaviour and how they utilise their landscapes, and it would be beneficial to fully understand the mechanisms that drive their sexual segregation (Caro 1998; Rubin & Bleich 2005;Blanc 2008). If segregation of the sexes is due to differing habitat requirements, for example, it will be essential to plan reserves that have habitats that cater for both sexes.

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