Do anthropogenic and natural features act as barriers to African elephant (*Loxodonta africana*) space use?

Kristy Robertson

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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.

Kristy Robertson

25/03/13

Abstract

The degree that different landscape features influence elephants use of space in the Kruger National Park and surrounding private game reserves (Balule, Timbavati, Klaserie and Umbabat) is not known. The aim of my study was to assess landscape features which influence elephant space use at two different spatial scales: at a large scale representing home range selection within the landscape and a small scale representing core area selection within the total home range. I investigated the space use of 15 male and 6 female adult elephants over a three year period (June2007-May 2010), using GPS data and satellite mapping analysis. The features selected for analysis as possible barriers to elephant space use were anthropogenic (fences, roads, railway lines and infrastructure) and natural features (rivers, geological features and vegetation). I also investigated the total and core home range size of elephants and whether elephant space use differed by sex and season. Males had larger total home range sizes than females irrespective of season, but there were no size or seasonal differences of core home range size between the sexes. Elephants used features differently at the two spatial scales, differed in the use of features between seasons, and there was a difference between the sexes in the use of features. Fences, railways, rivers (in the wet season), geological features and vegetation types were the features that influenced elephant space use, and could be possible barriers at the large scale. Elephants occurred close to fences which possibly restricted their space use. Elephants also occurred close to railway lines but they might not have crossed these. As expected, elephants occurred less often at close distances to rivers in the wet season which could possibly be as a result of higher rainfall in this season, preventing elephants from crossing their usual riverbed corridors. Male and female elephants differed in the use of vegetation types found on particular geological features: males selected basalt and females selected granite areas for both the dry and wet seasons. Both male and female elephants were associated with a wider variety of vegetation types in the dry season, possibly because the limited food availability causes elephants to cover larger areas in search of food. Elephant space use was therefore governed by several features that may or may not restrict space use. My study, using satellite mapping analysis, can suggest what hinders movements of elephants and what is essential for assisting elephant space use, which could help conservation efforts for reserve design and corridor formation between reserves.

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Introduction

Research problem

There are several mechanisms responsible for driving African elephant (*Loxodonta africana*) movements, but the extent of avoidance of particular landscape features such as railway lines or fences is unknown. There is an important need to understand elephant space use, for future conservation efforts and planning. With the newly increased interest in game reserve expansion and design, reserve managers will need to know what factors influence elephant presence in a particular area (Whyte 1996; Duffy *et al*. 2011); for example, resources such as vegetation type influence where elephants select their home range (Grainger *et al*. 2005). By knowing the influence of features that promote or deter the occurrence of elephants, new areas for conservation can be designed that take into consideration the features that promote and restrict movement to ensure effective conservation of the African elephant (Whyte 1996; Margules and Pressey 2000; Boettiger *et al*. 2011). My study will analyse the space use of both male and female elephants over a three year period in the Kruger National Park (KNP) and surrounding private game reserves (Balule, Timbavati, Klaserie and Umbabat).

Motivation for study

An increased concern for elephant conservation began after the 1970s when elephant numbers drastically decreased throughout Africa because of poaching for ivory (Kangwana 1996). Since then, conservation of elephants has been a goal of protected game reserves. To achieve successful conservation of elephants, it is important to understand distribution, population density, movement, behaviour and impacts on the ecosystem (and sometimes impacts on human settlements) (Dublin and Taylor 1996; Kangwana 1996). My study will focus on the movement behaviour of elephants and how they utilise the space provided to them. There have been some studies that have investigated space use by elephants and the factors that affect space use (Grainger *et al*. 2005; Druce *et al*. 2008; Cushman *et al*. 2010); however, few studies have investigated space use across different scales (Cushman *et al*. 2010; Marshal *et al.* 2011). Elephant home ranges could extend over landscape features (e.g. roads, railways, rivers), and perhaps elephants are not utilising the entire area of their home range equally because they avoid these features.

The rapid elephant population growth in protected areas of southern African is becoming a concern for reserve managers because of the resulting impact on biodiversity (Harris *et al*. 2008; Vanak *et al*. 2010; Duffy *et al*. 2011). Various methods are currently being used to reduce elephant's impact on the ecosystem, including translocations, birth control and culling (Harris *et al*. 2008). However, there might be a more natural solution to the problem: the elimination of features that restrict elephant space use in current reserves or in the design of future reserves (Vanak *et al*. 2010; Duffy *et al*. 2011). If elephants were provided with more space in their environment, their impact would be diluted over a wider area (Harris *et al*. 2008). Therefore, my study will investigate the impacts that landscape features have on elephant space use and how elephants respond to barriers. Reserve planning could consider these issues when analysing landscape connectivity and designing new corridors (Cushman *et al*. 2010).

Barriers, both artificial and natural, influence large mammalian herbivore movements by causing more complex movement paths, such as repetitive encounters with a feature and then turning around to avoid the feature or by spending little time near the feature, in which timing and speed of movement can be investigated (Graham *et al*. 2009; Vanak *et al*. 2010; Boettiger *et al*. 2011). Artificial barriers include fences, roads, railways, and villages (Forman and Alexander 1998; Benítez-López *et al*. 2010; Cushman *et al*. 2010; Vanak *et al*. 2010). Barriers can also be natural, such as rivers, mountains, vegetation type and geological features (Munyati *et al*. 2009; Vanak *et al*. 2010), although these can also be influenced by anthropogenic activities.

Research questions

The aim of my study is to investigate the effects of anthropogenic (fences, roads, railway lines, and infrastructure) and natural features (rivers, geological features and vegetation) on the space use of both male and female elephants in the Kruger National Park and surrounding Associated Private Nature Reserves (Balule, Timbavati, Klaserie and Umbabat) over a three year period (June 2007-May 2010). I asked four research questions. What is the size of the seasonal core and total home ranges for male and female elephants? Do anthropogenic features (specifically fences, roads, railways and villages) and natural features (specifically rivers, geological features and vegetation) restrict elephant space use? Does season influence space use in relation to the above mentioned features? Do the above mentioned features have different effects on male and female elephants?

Literature review

Study animal

The African elephant is the largest living terrestrial animal, with cows weighing between 2800-3500 kg and bulls between 5000-6300 kg (Langman *et al*. 1995; Skinner and Chimimba 2005; Duffy *et al*. 2011). There are two subspecies of the African elephant: the savanna elephant (*Loxodonta africana africana*) and the forest elephant (*Loxodonta africana cyclotis*) (Poole 1996). In areas where forests and savannas merge, there is hybridisation of these two subspecies (Poole 1996). The African elephant is restricted to sub-Saharan Africa and populations that occur in South Africa are mostly those in protected areas; 80% of elephants in South Africa occur in Kruger National Park and surrounding private game reserves (Skinner and Chimimba 2005). The remaining 20% is found in the Addo Elephant National Park (Eastern Province), the Pilanesberg National Park and Madikwe Game Reserve (North West Province), and Tembe Elephant Reserve, the Hluhluwe-Imfolozi Park and Ithala Nature Reserve (the north-eastern KwaZulu-Natal; Skinner and Chimimba 2005).

Elephants have dynamic social systems, comprising of fluid or fission-fusion groups instead of stable groups (Poole 1996; Archie *et al*. 2006). Males and females live separately but in the same area (Poole 1996). The sexes differ in habitat use and requirements (Stokke and Du Toit 2002). Females and their associated immature offspring form groups of about 2-30 individuals called family units in which all females are related and there is usually one matriarch which leads the group (Poole 1996). Mature males are solitary or form small groups with other bulls (Poole 1996). Males experience musth, a period of heightened sexual and aggressive activity from about 29 years of age in free-living individuals (Poole 1996; Hollister-Smith *et al*. 2008). During musth, males search for receptive females and increase roaming behaviour (Poole 1996; Hollister-Smith *et al*. 2008).

Elephants have a wide habitat tolerance meaning that they can live in a variety of vegetation types but like most animals, are limited by an adequate supply of food, water and shade (Skinner and Chimimba 2005). They are mixed feeders, with a diet that includes grass and trees (Codron *et al*. 2006; Duffy *et al*. 2011). Their daily intake of food is about 4-7% of their bodyweight resulting in elephants travelling long distances to obtain a constant supply of new food (Poole 1996). African elephants are mostly active at dusk and dawn (crepuscular), although they are more active at night during dry conditions (Loarie *et al*. 2009).

The distribution and abundance of resources determines the seasonal home range size, shape and location (Shannon *et al*. 2006), and thus space use varies seasonally (Vanak *et al*. 2010). The size of an elephant's home range is also an indication of how much the area is disturbed or restricted by certain features (Whyte 1996). Home ranges for elephants are small in the Kruger National Park, about 909 km^2, compared to larger home ranges of about 5860-8693 km^2 in more arid environments such as Namibia (Whyte 1996), which is a result of landscape heterogeneity and water distribution in the arid region (De Beer and van Aarde 2008). In the dry season, elephant home ranges tend to be smaller than the wet season because they stay closer to rivers and water holes (Loarie *et al.* 2009; Vanak *et al*. 2010).

Space use across multiple spatial and temporal scales

Animals select for an area to live that is suitable to them in terms of achieving survival and reproductive success (Orians and Wittenberger 1991). Animal space use is driven by a variety of processes that differ across temporal and spatial scales (Hansson *et al*. 1995; Nathan *et al*. 2008). Temporal scale refers to changes in animal space use over time such as between seasons (Orians and Wittenberger 1991; Boyce 2006). Spatial scale refers to animal space use at different hierarchical levels including feeding stations (fine scale), plant communities, landscapes, and regional systems (large scale) (Senft *et al.* 1987).

Multiscale studies of selection are important because features that influence selection occur at different spatial scales (Senft *et al.* 1987). For example, Cushman *et al*. (2010) showed that elephants differed in avoidance behaviour of towns at different spatial scales. Elephants had a stronger avoidance of towns at a finer scale compared to a larger scale (Cushman *et al*. 2010). By comparing between two spatial scales (such as fine and large scale), it can be seen if animals are preferring close areas to a feature; for example, Cushman *et al*. (2010) showed that elephants preferred areas closer to rivers after multi-scale analysis.

Several studies have investigated movements of animals and the drivers for these movements (reviewed in Mueller and Fagan 2008). The behavioural motivation to travel by an animal results from the interaction between internal or external factors that affect the physiological and psychological state of an animal, resulting in the behavioural decision to leave an area/site (Reiners and Driese 2004; Nathan *et al*. 2008). Internal factors include individual characteristics, such as age, sex, genetic composition and physiological state (Reiners and Driese 2004). There are several external factors that bring about animal movement, including resource availability (such as food and water), predator avoidance, searching for mates, and competition with conspecifics for limiting resources (Reiners and Driese 2004; Nathan *et al*. 2008). For example, in herbivores, young individuals (internal factor) will avoid predators (external factor) by travelling to areas where predators are absent. Another example specific to elephants could be that older bulls (internal factor) travel far distances to search for mates (external factor).

My study will focus on daily locations of elephants to establish elephant space use. My study does not involve movement pattern analysis which uses elephant path movements (Cushman *et al*. 2010). Over a longer time period, animals can make 2 types of movements: dispersal and migration. 1) Dispersal is defined as the decision made by an animal to leave an area, that was previously its living area (home range), to a new living area or home range, which is some distance away. Dispersal does not happen very often in an individual's lifespan (Reiners and Driese 2004) and usually occurs once after weaning in most mammals (O'Donoghue and Bergman 1992; Favre *et al*. 2007). 2) Migration is defined as a seasonal movement with repeated back and forth movements between regions of favourable conditions, one of these regions usually being the breeding site (Dingle and Drake 2007).

Space use and barriers to movement

There are various definitions of barriers to animals, so it is therefore important to define what constitutes as a barrier to elephant space use in my study. A well-known definition of a barrier is when a physical structure causes populations to fragment and reduced gene flow (McDonald and St. Clair 2004), but this is not the intended definition for my study. I consider barriers as features, artificial or natural, that an elephant completely avoids or uses rarely; for example, the railway line in Pongola Game Reserve acts as a functional barrier to the female elephant herd because they deliberately avoid crossing it (Shannon *et al*. 2006). If elephants occur close to a feature, I assume that this indicates an attraction to a feature or avoidance of another feature.

Barriers have different effects on different sized animals (Coffin 2007). For small mammals, arthropods and amphibians, different road characteristics might be responsible for influencing movement, such as road surface type, road width and traffic volume (Forman and Alexander 1998; McDonald and St. Clair 2004). In contrast, road width and road surface type have not been found to be barriers to large mammals because they actually use roads to travel more easily through the landscape (Coffin 2007). Large rivers are barriers to small animals such as reptiles and rodents, but large animals, such as wildebeest and zebra, are able to cross rivers (Gereta and Wolanski 1998; Vences *et al*. 2009). The effects of artificial and natural barriers on elephants will be discussed, below.

Anthropogenic features

Anthropogenic features are man-made structures that occur either around a protected area or inside a protected area (Blake *et al*. 2008; Vanak *et al*. 2010). These features are not always barriers to animals - sometimes they impact animals through habitat loss, edge effects or mortality (Richardson *et al*. 1997; Benítez-López *et al*. 2010; Vanak *et al*. 2010). It is suggested that animals view anthropogenic features as barriers when they cannot move over the feature, they avoid the feature, or they spend limited time near the feature (Jaeger *et al*. 2005; Graham *et al*. 2009). Therefore, the feature might prevent animal movement from one area to another or the animal might avoid the feature because it causes stress, such as disturbance through noise, visual stimuli or danger (Jaeger *et al*. 2005; Benítez-López *et al*. 2010). Examples of these structures include fences, roads, railways, powerlines, pipelines, hydroelectric developments, seismic lines, and villages (Benítez-López *et al*. 2010; Cushman *et al*. 2010; Vanak *et al*. 2010). The four features that are being tested to influence elephant space use in my study are fences, roads, railways, and villages.

Fences are known to act as barriers to elephant space use (Druce *et al* 2008; Vanak *et al*. 2010; Ferguson *et al*. 2011). Fences cause an edge-effect, especially in the wet season, because the expansion in home range size causes elephants to revisit the fence more often (Vanak *et al*. 2010). Thus the edge-effect is related to seasonality and fences do constrain elephant spaces use (Loarie *et al.* 2009). However, the edge-effect is more likely to occur in small fenced reserves (Loarie *et al.* 2009; Vanak *et al*. 2010). There are instances where elephants are “habituated” to or familiarized with electrified fences where they learn to associate fencing with electric shock in an electrified boma before introduction to a reserve (Slotow 2012) and many of these elephants avoid fences later in their life or are cautious when exploring areas where fences have been removed (Vanak *et al*. 2010). It is usually groups of female elephant that do not attempt to cross into new areas after fences are removed (Druce *et al* 2008). Elephant bulls move sooner into a new area and travel further than females, thereby indicating that older mature bulls are more prepared to explore new areas and travel far from known resources compared to female groups (Druce *et al* 2008).

There is no research on avoidance of roads by African elephants. Protected roads within reserves do not appear to influence elephant movement (Blake *et al*. 2008). All elephants in South Africa are located in protected areas so the exposure to unprotected roads is very low, unless an elephant breaks out of a fenced area. Protected roads are usually sand roads and are easier for elephants to move along instead of travelling through savanna bush (Vanak *et al*. 2010).

Some national parks have been developed over old railway lines in South Africa and some might still consist of active railway tracks. There has not been sufficient research done on how railways affect animal movements in South Africa. However, in some areas such as the Tsavo East National Park in Kenya, elephants do cross over railway lines (McKnight 2004) and in other areas they do not, such as in Pongola Game Reserve in South Africa (Shannon *et al*. 2006). Shannon *et al* (2006) showed that herds of female elephants avoided railway lines because they occasionally approached the line and then turned away but male elephants crossed the line freely. In India, railways contribute to the mortality of Asian elephants (*Elephas maximus*) in Rajaji National Park (Joshi and Singh 2011). However, in South Africa, most railway lines (in and outside protected areas) have been out of use for many years and no literature explores whether and why these railway lines are barriers to elephants.

Elephants have been found to avoid human settlements such as villages, huts and small towns (Cushman *et al*. 2010). Elephants avoid rest camps and staff villages, which are disturbed areas in the natural environment in game parks (Freitag-Ronaldson and Foxcroft 2003; Jaeger *et al*. 2005; Benítez-López *et al*. 2010). A study showed that female elephants tend to stay further away from human settlements compared to male elephants, so elephants found near villages or camps are most probably males but the possible reason for this was not stated (Harris *et al*. 2008). A possible reason for why elephants are found inside or near villages/camps could be as a result of searching for food, and this could be in both the wet and dry season, but possibly more in the dry season when resources are scarce (Foxcroft *et al*. 2008; Hema *et al*. 2010).

Natural features

A game park can include natural features that act as barriers to animals (McDonald and St. Clair 2004; Vanleeuwe 2008). Examples of these features include rivers, mountains, and unsuitable vegetation types which are influenced by the geological features of an area (Vanleeuwe and Lambrechts 1999). These features might hinder movement to another area, cause movement around the feature (where possible), or animals might show a regular pattern of avoidance of a particular feature (Vanleeuwe and Lambrechts 1999; Vanleeuwe 2008). Some examples are discussed below.

There may be natural barriers to elephant movements in areas where geographical features are prominent (Vanleeuwe 2008), such as areas with variable habitat strata (e.g. several deeply incised V-shaped valleys of rivers and streams and numerous hills; Vanleeuwe and Gautier-Hion 1998; Vanleeuwe 2008). In mountainous areas, elephants move to lower altitudes where geographical features are less distinct and easier to travel on (Vanleeuwe and Lambrechts 1999). Rivers can act as barriers to elephant space use in the wet season (Vanleeuwe and Lambrechts 1999; Mpanduji *et al*. 2008), when water levels are high, which causes elephants to avoid crossing the rivers (Hofer and Mpanduji 2004). However, rivers are important movement routes for elephants during the dry season (Hofer and Mpanduji 2004). Thus, elephant space use is influenced by river type and season. Elephants are able swimmers, but will cross rivers only when their feet are near the riverbed surface (West 2001).

Landscape heterogeneity influences habitat selection by elephants (Grainger *et al*. 2005). Resource requirements and the distribution of these resources influence the size of an elephant's home range (Grainger *et al*. 2005). The Kruger National Park consists of a geological divide from west to east (Codron *et al*. 2006; Grant and Scholes 2006). Granite soils in the west consist of nutrient-poor substrates compared to the nutrient-rich substrates of the basaltic soils in the east (Codron *et al*. 2006; Munyati and Ratshibvumo 2010). Granitic areas are undulated catenas or rocky outcrops at the top of catenas that form sandy soils (Grant and Scholes 2006). Basalt areas are less prominent and consist of open plains that form clay soils (Grant and Scholes 2006). The quality of foraging patches is influenced by edaphic factors and elephants prefer vegetation types that have high nutrients growing on high nutrient soils, which are influenced by the geological features of the area (Grant and Scholes 2006).

Other barriers

Elephants could be avoiding particular features which are not physical barriers. There might be another reason unique to an individual elephant or to all elephants in an area that is responsible for their movement behaviour. Psychological barriers occur from stress responses triggered by historic experiences (Jachowski *et al*. 2012). For example, the site of fences can become psychological barriers to elephants even after they are removed (Kioko *et al*. 2008). The continuous negative interaction with electric fences by elephants could result in them learning to avoid these fences and they will avoid such areas even after the electric fences are removed (Kioko *et al*. 2008; Vanak *et al*. 2010).

Elephants might avoid an area associated with a past traumatic event, such as an area where others were culled. The problem though is that psychological barriers are difficult to detect without knowing the history of specific herds/individuals, and often psychological reasons are inferred from the absence of other parsimonius reasons. Moreover, these would require behavioural observations and not computer mapping analysis, as in my study.

Resource selection functions

Resources, both biotic and abiotic, are directly used by an organism and vary spatially (from a home range to the landscape level) and temporarily in terms of seasons (Senft *et al.* 1987; Manly *et al.* 2002). A useful tool for investigating how landscape features influence space use of animals is resource selection functions (RSFs) which estimate the probability of use of a resource unit or feature; this can show which resources are selected and which are avoided (Boyce and McDonald 1999; Boyce 2006). In other words, RSFs provide the tools to assess what the elephants are attracted to and by a process of elimination, determine what they are avoiding. RSFs can be used to develop spatially explicit maps which predict space use by individuals across an area (Harju *et al*. 2011). An RSF model that is useful for space use studies is one which compares the amount of used area versus the available area (Manly *et al*. 2002). Therefore, RSFs are important because they quantify the relative importance of different resources or features to a species (Koper and Manseau 2012).

To develop RSFs, a geographic information system (GIS) is used, showing the GPS animal location points as well as the landscape parameters of interest, for example roads (Koper and Manseau 2012). By generating random points of the area in which the animal can occur, "available" locations are identified, and these are compared with the "used" locations; this is done for each landscape parameter which will show whether individuals are avoiding a parameter or feature (Koper and Manseau 2012). Generalized linear mixed models (GLMMs) are used to analyse the absence/presence data set because such models can incorporate non-parametric data and include fixed and random independent variables (Koper and Manseau 2012). RSFs can be used to investigate whether elephants avoid features in their environment and thus determine whether these features are barriers to elephant space use.

Resource (or feature) selection is a hierarchal process and therefore it is scale dependent meaning that animals might select resources at different spatial scales (Johnson 1980; Senft *et al.*1987). The resource selection process defined by Johnson (1980) includes: first order selection which involves selection of a broad geographic/landscape range, second order selection which involves selection of a home range within the geographic range, third order selection which involves selection of habitat components within the home range, and fourth order selection which involves the selection of specific resources (e.g. food items) within habitat components.

The study of resource selection at multiple scales shows at which scale particular resources is important to an individual animal. Studies that include elephant resource selection at a multi-scale approach showed that reserve management and decision making must occur at an appropriate scale (Young *et al.* 2009; Marshal *et al.* 2011). For instance, if we use a hypothetical example: rivers might have an important influence on elephant space use at a large scale (establishing where a home range is within the landscape) but not at a smaller scale, and perhaps roads influence elephants space use at the small scale (establishing what areas elephants use within the home range). Therefore, if a study was done on the effects of elephant space use only at the broad scale, reserve managers would only focus on rivers without knowing that roads also affect elephant space use.

Research hypotheses and predictions

Home ranges:
I predicted that the total and core home range size would be smaller in the dry season than the wet season for both sexes because elephants stay closer to rivers and water holes in the dry season thus they use less space (Loarie *et al.* 2009; Vanak *et al*. 2010). I expected males would have larger home range (total and core) than females because males are more prepared than females to explore and roam into new areas or travel further distances (Shannon *et al*. 2006; Druce *et al* 2008; Harris *et al*. 2008).

Anthropogenic features:
I predicted that fences, railway lines and infrastructure act as barriers to elephants because the literature suggests that elephants avoid these structures (Shannon *et al*. 2006; Cushman *et al*. 2010; Vanak *et al*. 2010; Duffy *et al*. 2011). I expected a seasonal influence on the use of fences by elephants, with elephants occurring closer to fences in the wet season because elephants usually move away from rivers when the rains begin, thus increasing their home range size and resulting in an edge effect - meaning elephants encounter the fence line more often (Hofer and Mpanduji 2004; Loarie *et al.* 2009). I also expected males to occur closer to fences than females as most studies and evidence shows that it is mostly bulls (young males as well as older mature males in musth) that break through fences and therefore are located near the fence line more often (McCagh 2008; Slotow 2012).

I did not expect differences in use of railways between seasons because I assumed that trains are active all year round (Duffy *et al*. 2011). Literature suggests that females avoid crossing or occurring near railway lines more than males (Shannon *et al*. 2006) therefore I predicted males should occur closer to railway lines more than females.

I expected a difference in the use of infrastructure between seasons, elephants would be closer to villages in the dry season compared to the wet season because, even if people at these settlements have food (which might attract elephants) all year round (Foxcroft *et al*. 2008; Hema *et al*. 2010), the dry season is the period when natural resources might be limited. A study by Harris *et al*. (2008) showed that the elephants occurring near camps and villages were mostly males therefore I predicted that male elephants should occur closer to infrastructure more than females.

Natural features:

I predicted that all natural features (rivers, geological features, and vegetation) in the study site are barriers to elephant space use. I predicted that rivers act as barriers and that there would be a seasonal influence on the use of rivers by elephants; elephants would occur closer to rivers in the dry season when they use riverbeds as corridors, than in the wet season when water levels are high (Vanleeuwe and Lambrechts 1999; Hofer and Mpanduji 2004; Mpanduji *et al*. 2008).

I predicted that geological features and vegetation would act as barriers to elephant space use because elephants use particular vegetation types found on particular geological features (Grant and Scholes 2006; Vanleeuwe 2008; Loarie *et al.* 2009). Geological features and vegetation are both influenced by seasonality, with vegetation in the wet season being more nutritious compared to the dry season (Codron *et al*. 2006). Male and female elephants differ in habitat use and requirements (Stokke and Du Toit 2002) and in their behaviour (Poole 1996): males appear to be more prepared to roam in any area and travel long distances from known resources compared to females (Shannon *et al*. 2006; Druce *et al* 2008; Harris *et al*. 2008). Therefore I predicted there would be a difference in selection type of geological features and vegetation by the sexes because literature suggests sexual segregation in habitat use (Stokke and Du Toit 2002). Geological features influence vegetation type therefore selection of a specific vegetation type infers selection of a specific geological feature type (Grant and Scholes 2006).

I expected a seasonal difference in the use of rivers and vegetation between the sexes. In the dry season, resources are less abundant and limited therefore elephants usually stay near rivers and water sources; however, the large body size of male elephants enables them to travel further from rivers than females in search for resources where as females could be lactating or with their young, and therefore need to remain near water sources more than males (Gordon 1977; Stokke and Du Toit 2002) thus I predicted male elephants would occur further away from rivers and cover a wider diversity of vegetation types in the dry season, and female elephants in the wet season would have a higher nutritional requirement as a result of pregnancy and lactation where as bulls do not therefore it was predicted that females would utilize a wider diversity of vegetation types in the wet season to meet these requirements (Stokke and Du Toit 2002).

Materials and methods

Study area

The study site included the Kruger National Park (KNP) and four privately owned reserves that are members of the Associated Private Nature Reserve (APNR) which border central-west of KNP: Balule, Timbavati, Klaserie and Umbabat (Figure 1). This study area occurs in the savanna biome of South Africa (Venter *et al*. 2003). The Olifants River within KNP divides the park into north and south, which have different climatic zones (Codron *et al*. 2006). The south (lowveld) has a higher average annual rainfall than the north (arid bushveld) (Codron *et al*. 2006); for example, the average annual rainfall at Pretoriouskop (in the south of Kruger) is 746mm compared to the average annual rainfall in at Letaba (in the north of Kruger) which is 458mm (Zambatis 2003). The vegetation in the west of KNP on the granites is dominated by broad-leaved species such as *Combretum* and includes vegetation types of Granite Lowveld and Phalaborwa-Timbavati Mopaneveld, whereas fine-leaved species such as *Acacia* dominate on the basalts in the east and includes Thsokwane-Hlane Basalt Lowveld and Northern Lebombo Bushveld (Mucina and Rutherford 2006). The north is dominated by *Colophospermum mopane* shrubveld and includes Lowveld Rugged Mopaneveld, Tsende Mopaneveld and Mopane Basalt shrubland (Mucina and Rutherford 2006).

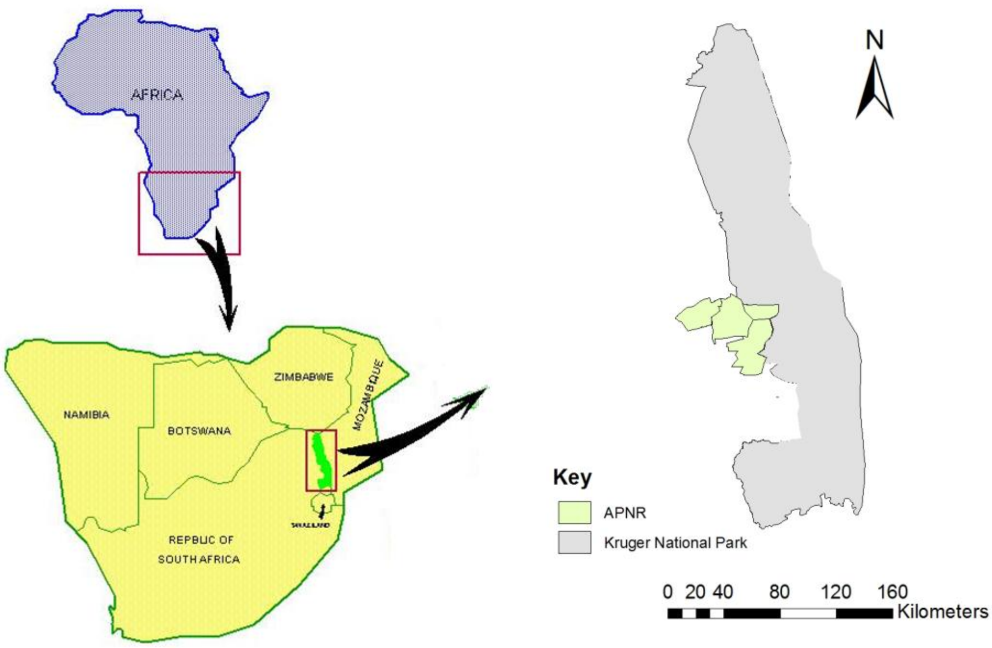


Figure 1: The study site - Kruger National Park and the APNR in the west.

Elephant locations

The data used in my study were collected and provided by Dr Michelle Henley from "Save the Elephants", a non-profit organisation founded in 1993 that serves to protect African elephants through research projects involving collaring and tracking. The elephants were fitted with AWT (African Wildlife Tracking) GSM-GPS collars by the organisation. The collars recorded the location of each individual and sent the information in real time though the cell phone network. In areas with no cell phone coverage, the collar stored the information and sent them though as soon as reception returned .The elephants were darted by experienced wildlife veterinarians from a helicopter (Dr Michelle Henley *pers.com*). The collars were set to record locations every hour, which they would then transmit in real time through the satellite. I only used locations recorded between June 2007 and May 2010, as this was the longest time period that included the most male and female elephants with continuous collaring data. These raw data were made available to me from Dr Michelle Henley. I sorted the data to select study subjects and extracted the appropriate data stream for analyses, using Microsoft Excel. I then analysed the data set as described later.

The data provided GPS locations of collared adult male and female elephants in KNP and APNR recorded over a three year period (June 2007- May 2010).There were 15 elephant bulls and 6 elephant cows with recorded GPS locations during June 2007 - May 2010 (Table 1). The collared time period of the elephants showed how long the elephants have had to adjust back to normal after the collaring procedure, any abnormal behaviour in space use could be as a result of being newly collared. Most of the elephants had been collared for a while before my study analysis, except for 3 of the males and 1 female (Table 1). On average, males were collared for 11 months and females were collared for 20 months.

Table 1: The elephants used in this study and the time period that they were collared prior to my study period (* represents males observed to be in musth during study period).

Sex	Name	Collaring start period	Time collared before my study (months)
Males	*Mac	2005/05/09	61
	*General	2005/05/16	25
	*Classic	2006/06/16	12
	*Striburus	2006/06/22	12
	*Caughley	2006/09/27	9
	*Tussle	2006/09/27	9
	*Gower	2006/10/24	8
	*Proud	2006/11/15	7
	*Wessa	2006/11/20	7
	Mbiri	2006/12/07	6
	Mune	2006/12/07	6
	Tsevo	2006/12/08	6
	Captain Hook	2007/04/13	2
	*Mellow	2007/04/13	2
	*Namaste	2007/06/22	0
Females	Diney	2004/05/24	37
	Joan	2004/11/02	31
	Mandy	2005/05/16	25
	Umbabat	2005/10/20	20
	Lapajuma	2006/10/24	8
	Yvonne	2007/07/21	0

I assumed that a collared female elephant represented a group of individuals (females and young) whereas a collared bull elephant was most likely solitary (Poole 1996). Therefore I was able to compare males and females because the 6 females selected represented an equal number to the 15 males selected. Data on musth of male elephants during the study period were available but was not included in analyses. It was necessary to analyse data for the two sexes separately and then compare male and female elephants because the literature shows that features have different effects on movement for males and females (Shannon *et al*. 2006; Druce *et al* 2008).

I analysed data separately for dry and wet seasons. The wet season was defined every year as the period when the mean NDVI (Normalised Difference Vegetation Index) was above the long term average for the area, and the dry season as the period when the NDVI was below the long term average (Table 2).

Table 2: The classification of season (wet or dry) for each month over the 3-year study period in KNP and APNR. Grey blocks show the months excluded from study period.

<table>
<tr><th rowspan="2">Year</th><th colspan="12">Month</th></tr>
<tr><th>J</th><th>F</th><th>M</th><th>A</th><th>M</th><th>J</th><th>J</th><th>A</th><th>S</th><th>O</th><th>N</th><th>D</th></tr>
<tr><td>2007</td><td></td><td></td><td></td><td></td><td></td><td colspan="4">Dry season 1</td><td colspan="3">Wet season1</td></tr>
<tr><td>2008</td><td colspan="2"></td><td colspan="8">Dry season 2</td><td colspan="2"></td></tr>
<tr><td>2009</td><td colspan="4">Wet season 2</td><td colspan="7">Dry season 3</td><td></td></tr>
<tr><td>2010</td><td colspan="5">Wet season 3</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Data analysis

ArcMap (version 9) was used to map the GPS locations for the 15 male and 6 female elephants. Seasonal home ranges were calculated with the Adaptive LoCoH in R, version 2.15.0 (http://www.r-project.com), using two locations per day (dawn and dusk), as suggested by Loarie *et al*. (2009) because this is the most active time of day for elephants. For each elephant and each season I calculated the 95% isopleth home range and 50% isopleth (core) home range (Shannon *et al*. 2006). To analyse sex and season differences in the total and core home range size, I ran a repeated measures ANOVA with sex as the independent variable and season (wet and dry) as the repeated measures variable. The data set was log transformed to approximate normality.

I used RSFs to estimate the probability of use of a feature (anthropogenic and natural) by the 15 male and 6 female elephants at two different spatial scales. If probability of occurrence at a feature (especially at the fine scale) is high, this will be interpreted as attraction to the feature thus there is a greater probability that the feature is not a possible barrier. The anthropogenic features in the study were fence lines, roads (sand and tar roads used by public and staff), railway lines (both active and non active), and infrastructure (including settlements, camp sites and staff villages). The natural features in the study were rivers (all major rivers), geological features (granite and basalt) and vegetation (22 different types occurred in the study site). These specific features were selected for study because these were the available shapefiles that allowed for analysis of barriers to elephant space use (Appendix 1).

The large scale analysis (2nd order) used elephant locations from the 95% isopleths. The small scale analysis (3rd order) used elephant locations from the 50% isopleths because core home ranges are used the most by elephants, and thus is important for fine scale analyses (Johnson 1980). The purpose of the analysis at a large scale (2nd order) was to establish whether any feature influenced where elephants select their home range in the landscape. Analyses at a smaller scale (3rd order) were to establish if features effect the elephant locations within the total home ranges.

For 2nd order analysis, I compared actual elephant location points from the 95% isopleth home ranges ("used" areas) to random points ("available" areas) in the entire available study site for each elephant in each season (Figure 2). Random points were generated in ArcMap using Hawth's Tools. In order to ensure that the available area was accurately represented, I applied a 1:10 ratio of actual: random (Marshal *et al.* 2011). For 3rd order analysis, I compared actual elephant location points in the 50% isopleth home ranges ("used") to random points in the 95% isopleth home range ("available") for each elephant for each season (Figure 2).

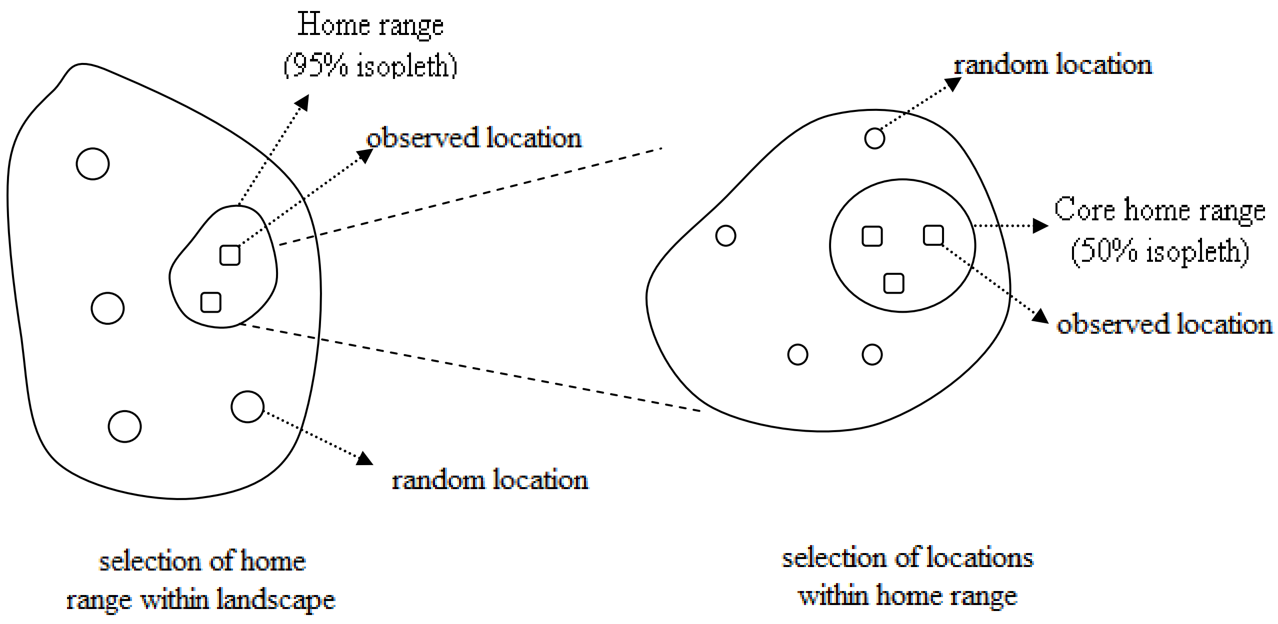


Figure 2: Diagram showing 2nd order selection on the left and 3rd order selection on the right.
I overlayed 7 different layers representing the 7 features (fences, roads, railway lines, villages, rivers, geological features and vegetation) on the elephant location shapefiles in ArcGIS to investigate which landscape features affected elephant space use. I calculated the distance-to-feature from each actual and random point using the “Euclidean Distance” and “Extract Values to Points” tools in ArcMap. An example to show the mapping distance from fences is provided in Figure 3.

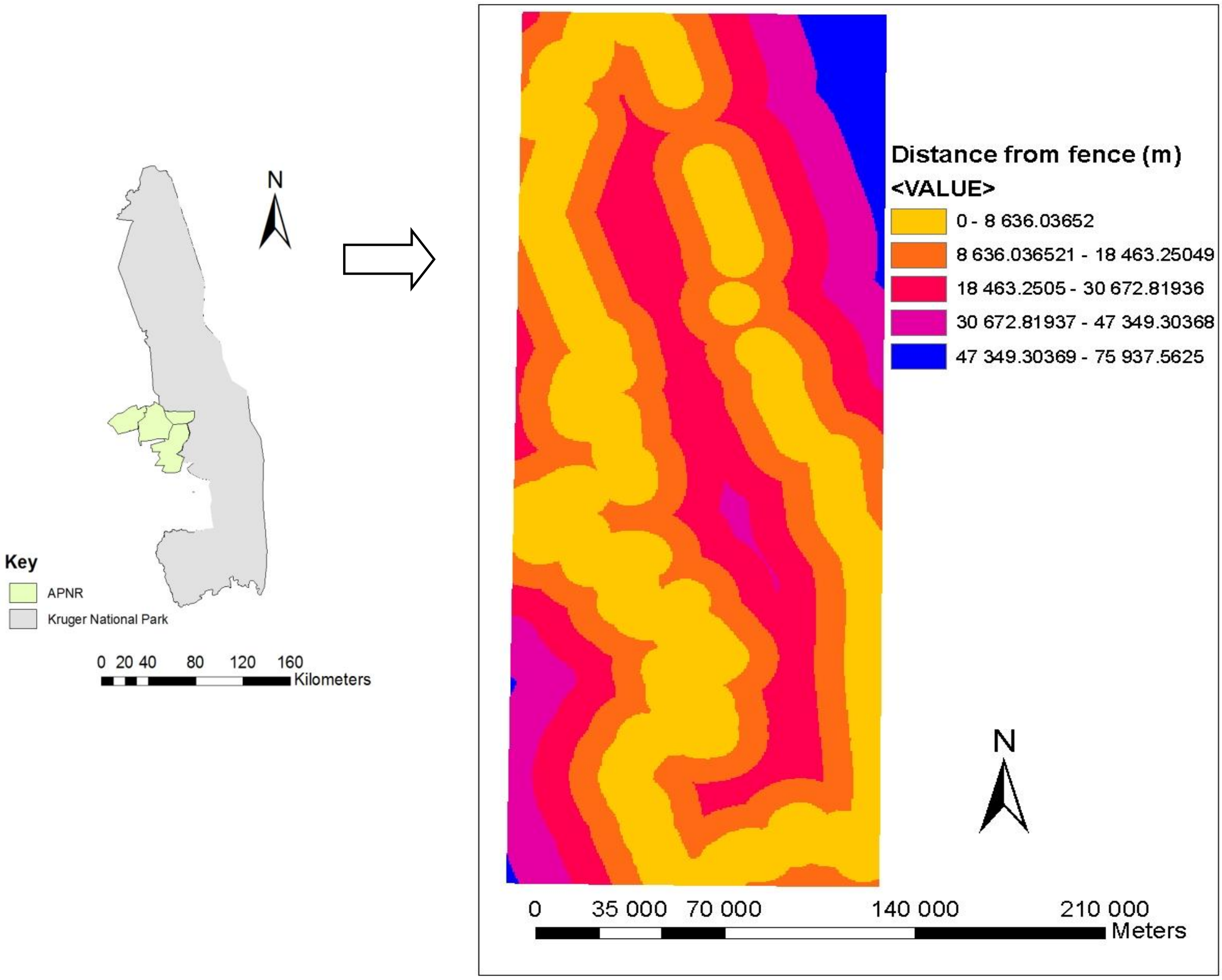


Figure 3: Distance (m) from fence line categories of the study site. The warmer colours such as yellow and orange are close distances to fences and colder colours such as pink and blue are further away from fences.

A series of logistic models were produced that represented equations describing the presence/absence of elephants in terms of the natural and anthropogenic features and their occurrence/abundance. The explanatory variables for each used/available point consisted of categorical variables which included fences, roads, railway lines, infrastructure, rivers, geological features and vegetation type. Generalized Linear Mixed Effects Models were compared using Akaike's Information Criterion (AICc) (Anderson 2008) using the 'lme4 package' in R, version 2.15.0 (Bates *et al.* 2008). The model with the lowest AIC value and the highest weight (ωi) was selected as the best model (Anderson 2008). The fixed effects were the explanatory variables, which included fences, roads, railway lines, infrastructure, rivers, geological features and vegetation, and the random effects included in the model were elephant ID and year (Crawley 2007; Koper and Manseau 2012). This was done for males and females in the wet and dry seasons.

A Logistic Regression was used on the best model selected using the 'lm' function in R which calculated the log-odd ratios (±95% confidence intervals) for each feature, thereby showing the likelihood of occurrence near a feature. Fences, roads, railway lines, infrastructure and rivers were divided into different distance categories (Appendix 2). Geological features were divided into two types, granite and basalt. Vegetation was divided into the 22 vegetation types. The statistical software used a reference cell coding for the categorical variables– meaning one category (e.g. one randomly selected vegetation type) of the categorical variable (e.g. vegetation types) is used as a reference and the effects of the other categories are relative to that reference category. All categories and their calculated 95% confidence intervals were compared to this reference category. Values above 0 implied that elephants were selecting for a category compared to the reference one and values below 0 indicated that elephants did not select for a category compared to the reference one. Any categories with confidence intervals overlapping meant there was no difference in selection of that category or any other category, as per the odd ratios procedure. Graphical representation of log-ratios for all features represented the odds of an elephant occurring at a location which thereby estimated whether elephants were avoiding a feature and thus if this feature could be a potential barrier to elephant space use (Van der Merwe and Marshal 2012). By establishing what the elephants were selecting, I could infer what the elephants were avoiding.

Results

Home ranges

The mean total home range size (km^2), at the 95% isopleth, for males and females for each season was calculated over the three year study period, June 2007-May 2010 (Figure 4). Males had a significantly larger home range than females ($F_{1, 19}$ = 4.586, p =0.045). Season (wet and dry) ($F_{1, 19}$ = 1.101, p =0.307) and sex * season ($F_{1, 19}$ =0.192, p =0.666) were not significant predictors of home range size

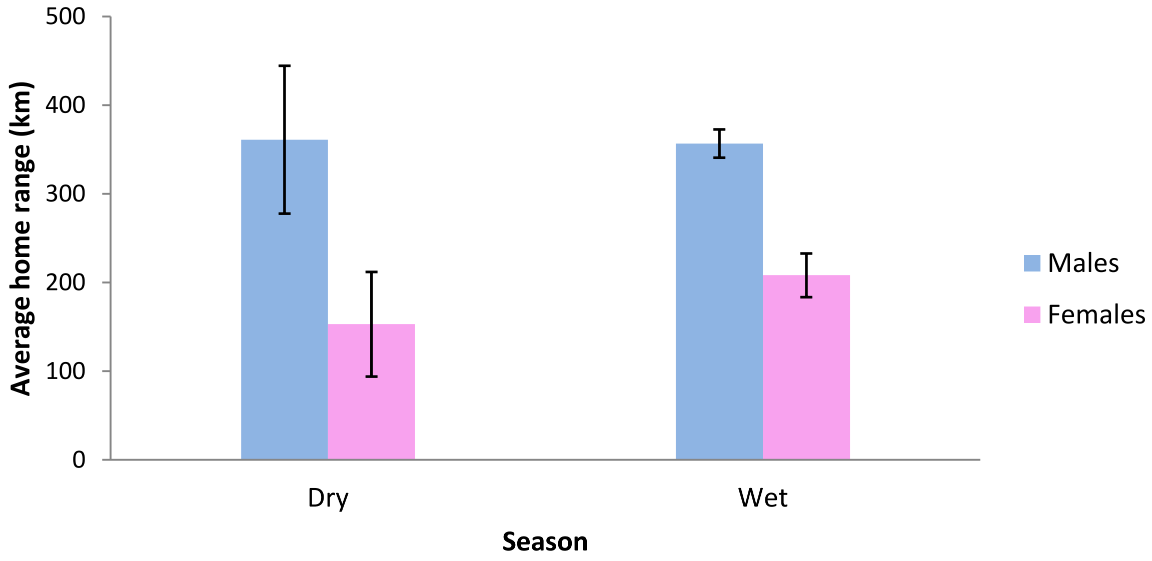


Figure 4: Mean (±SE) total home range size (km^2) for male and female elephants in the dry and wet season.

For the mean core home range size (km^2), at the 50% isopleth (Figure 5), there was no significant difference between sex (F1, 19 = 0.62, p =0.440). Season (F1, 19 = 0.17, p =0.682) and sex * season (F1, 19 =0.29, p =0.595) also did not significantly affect core home range size.

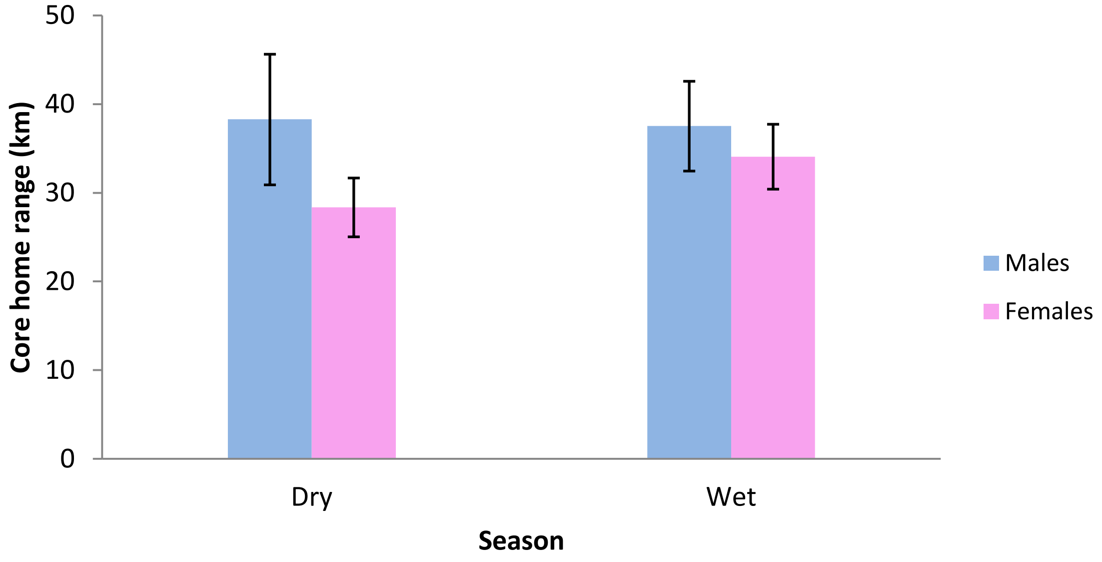


Figure 5: Mean (+SE) core home range size (km^2) for male and female elephants in the dry and wet season.

Barriers

Multiscale analysis on the influence of features (fences, roads, railway lines, infrastructure, rivers, geological features and vegetation) on elephant space use was used to determine which features were considered barriers to elephants. The 2nd order analysis involved determining whether all 7 features occurring throughout the entire study site affected elephant space use. The 3rd order analysis involved determining which features occurring in the 50% isopleth (core) home range of elephants affected elephant space use.

<u>2nd order selection</u>

Results from the model selection showed that the best model was: "lmer(Observed~fence+road+rail+infra+river+Geol+Veg+(1|Ellieid/Year),family=binomial, REML=F)" equally for males and females in the wet and dry seasons (Table 3). The variables included in the best model were considered the most important features that affect elephant space use at the landscape level (the entire study site). This model included all 7 features (fences, roads, railway lines, infrastructure, rivers, geological features and vegetation), meaning that all features affected elephant space use at the large scale (Table 3).

Table 3: Models generated in R software with the lowest AIC values that were considered the best to be selected at 2nd order level

Model	**AIC**	**Δ AICc**	**k**	**ω_i**
Dry Season (females):				
lmer(Observed~fence+road+rail+infra+river+Geol+ Veg+(1|Ellieid/Year),family=binomial,REML=F)	16865	0	29	0.95
Dry Season (males):				
lmer(Observed~fence+road+rail+infra+river+Geol+ Veg+(1|Ellieid/Year),family=binomial,REML=F)	62399	0	29	0.99
Wet Season (females):				
lmer(Observed~fence+road+rail+infra+river+Geol+ Veg+(1|Ellieid/Year),family=binomial,REML=F)	11175	0	29	0.96
Wet Season (males):				
lmer(Observed~fence+road+rail+infra+river+Geol+ Veg+(1|Ellieid/Year),family=binomial,REML=F)	57514	0	29	1

Fences

The mean actual distance from fences (GPS locations) versus the available area from any fence line in the study site were shown for both seasons for males and female elephants in Figure 6. Elephants occurred at intermediate distances from the fence and females occurred closer to fences than males (Figure 6).

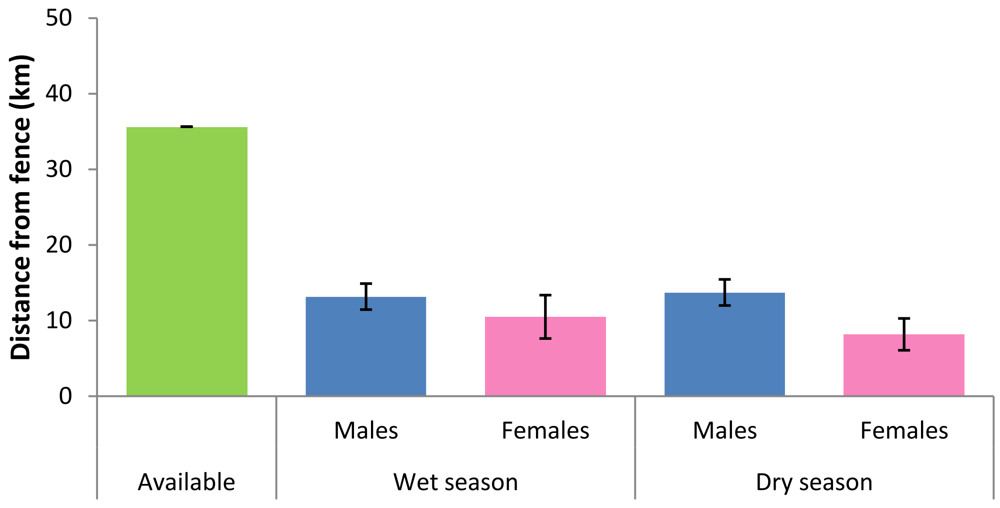


Figure 6: Mean (±SE) distance (km) of male and female elephants from fences in relation to the furthest available distance for fences in the study site (shown in green) in the wet and dry seasons.

The reference category (= 0) for the log odds, represented with an A in Figure 7, was the closest distance from fence, 0-7.05 km. For male elephants, the odds of occurrence at close to intermediate distances (location B) was highest in both the dry (log-odds = 0.030± 0.004) and wet season (log-odds = 0.028±0.004) (Figure 7) thus there was no seasonal difference in the occurrence of males close to fences because confidence intervals overlapped with each other. For females, the odds of occurrence at close to intermediate distances (location A and B) was highest, especially in the dry season (log-odds = 0.006±0.007) (Figure 7) suggesting that there was a greater chance that females occurred closer to fences in the dry season.

By looking at the close to intermediate distance (location B), where both sexes mostly occurred, the odds of female occurrence was lower than males suggesting that males had a more likely chance of occurring at locations close to fences compared to females (Figure 7).

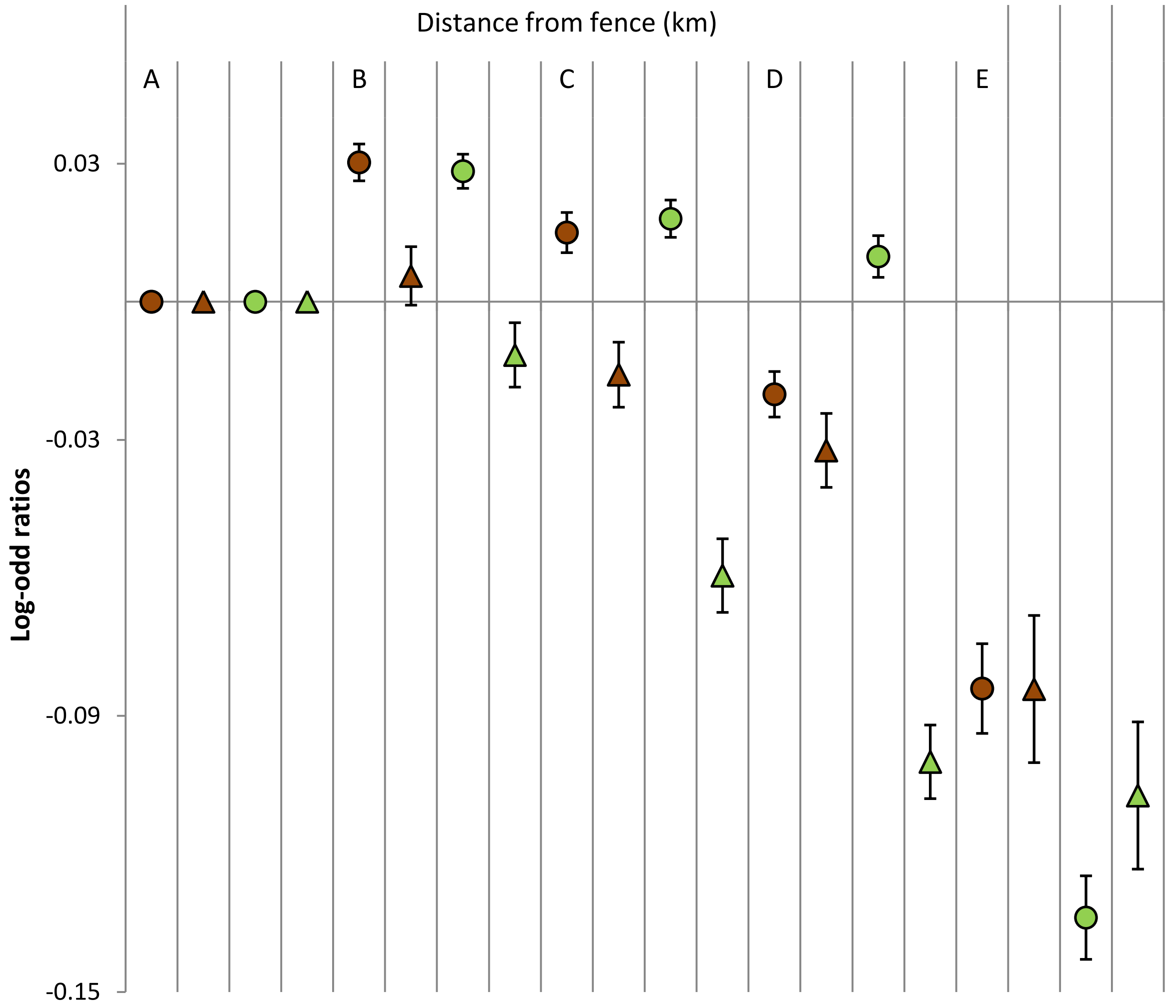


Figure 7: Distance from fence estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. A= 0-7.05 km, B= 7.06-14.10 km, C= 14.11-21.14 km, D= 21.15-28.19 km, and E= 28.20-35.24 km. Males occurred closer to fences than females.

Roads

The mean actual distances of elephant locations from roads versus the available area from any road in the study site are shown for both seasons for males and female elephants in Figure 8. Elephants occurred very close to the roads, but there were many roads in the study site, the furthest distance of any area from a road was just 34.04 km (Figure 8).

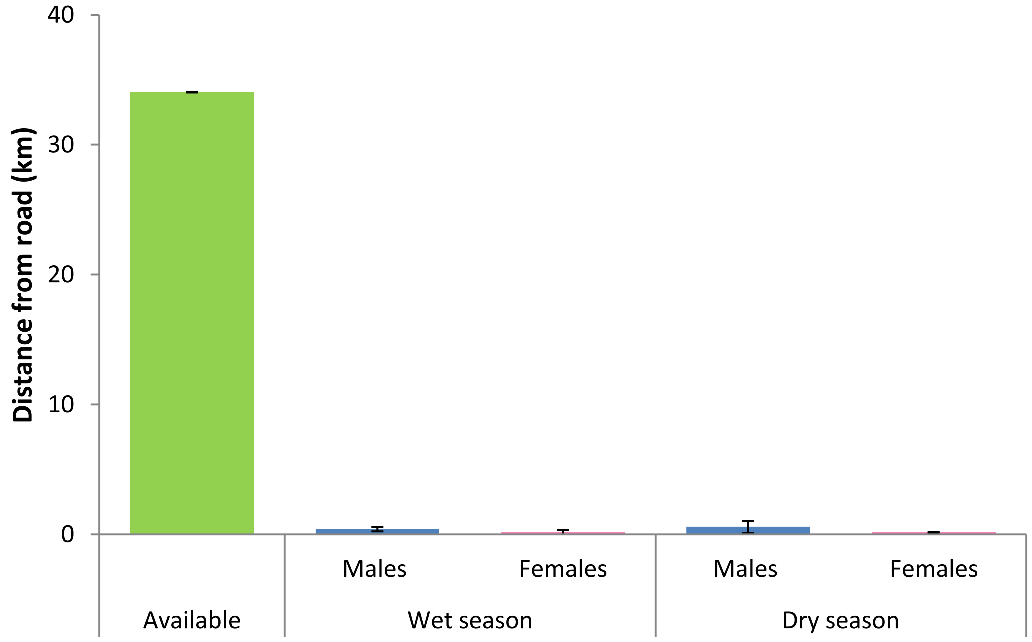


Figure 8: Mean (+SE) distance (km) of male and female elephants from roads in relation to the furthest available distance for roads in the study site (shown in green) in the wet and dry seasons.

The reference category (=0) was designated as A which included the closest distance, < 0.6km. B and C included 0.6-1.2 km and >1.2km, respectively. For both male and female elephants, occurrence was mostly at close distances to roads (A) in both seasons (Figure 9).

In both seasons, the odds of females occurring at further distances (B and C) were lower than males, suggesting that males had a more likely chance of occurring at far locations from roads compared to females (Figure 9).

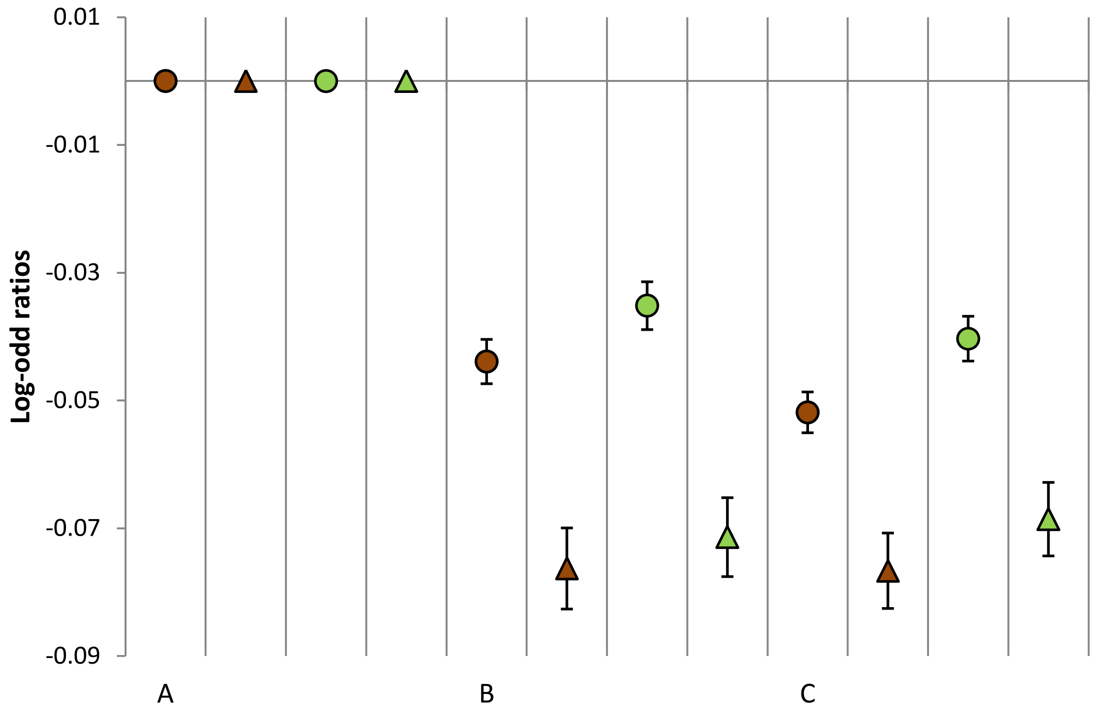


Figure 9: Distance from road estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. A= near. B= intermediate and C=far. Males occurred at far locations from roads more than females.

Railways

The mean actual distance of elephant locations from railway lines versus the available area from any railway line in the study site are shown for both seasons for males and female elephants in Figure 10. Elephants occurred relatively close to railway lines, especially females in both seasons (Figure 10).

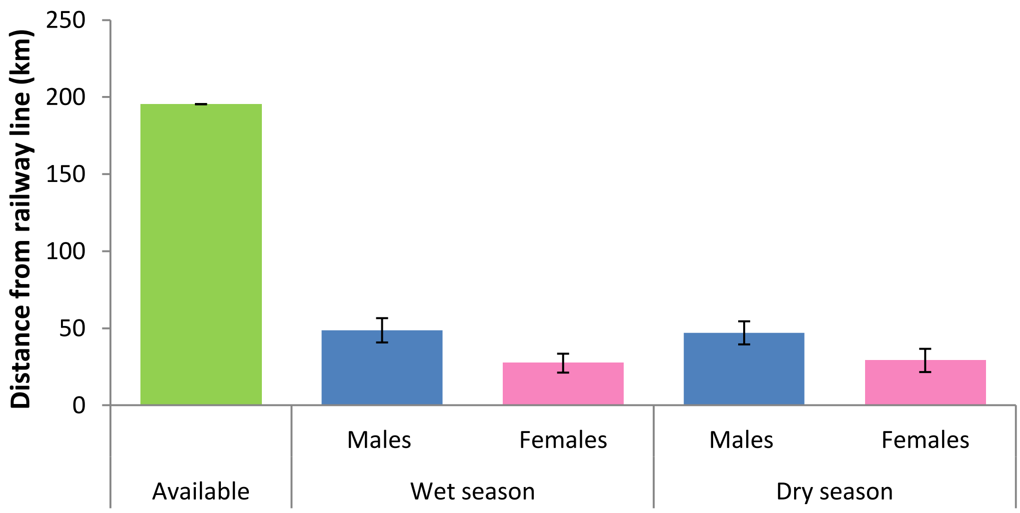


Figure 10: Mean (±SE) distance (km) of male and female elephants from railways in relation to the furthest available distance for railway lines in the study site (shown in green) in the wet and dry seasons.

The reference category (=0) was A which was the closest distance, 0-39.08 km. For both male and female elephants, the likelihood of occurrence close to railway lines, location A, was highest in both seasons (Figure 11).

There was no pattern in the use of railway lines between sexes (Figure 11).

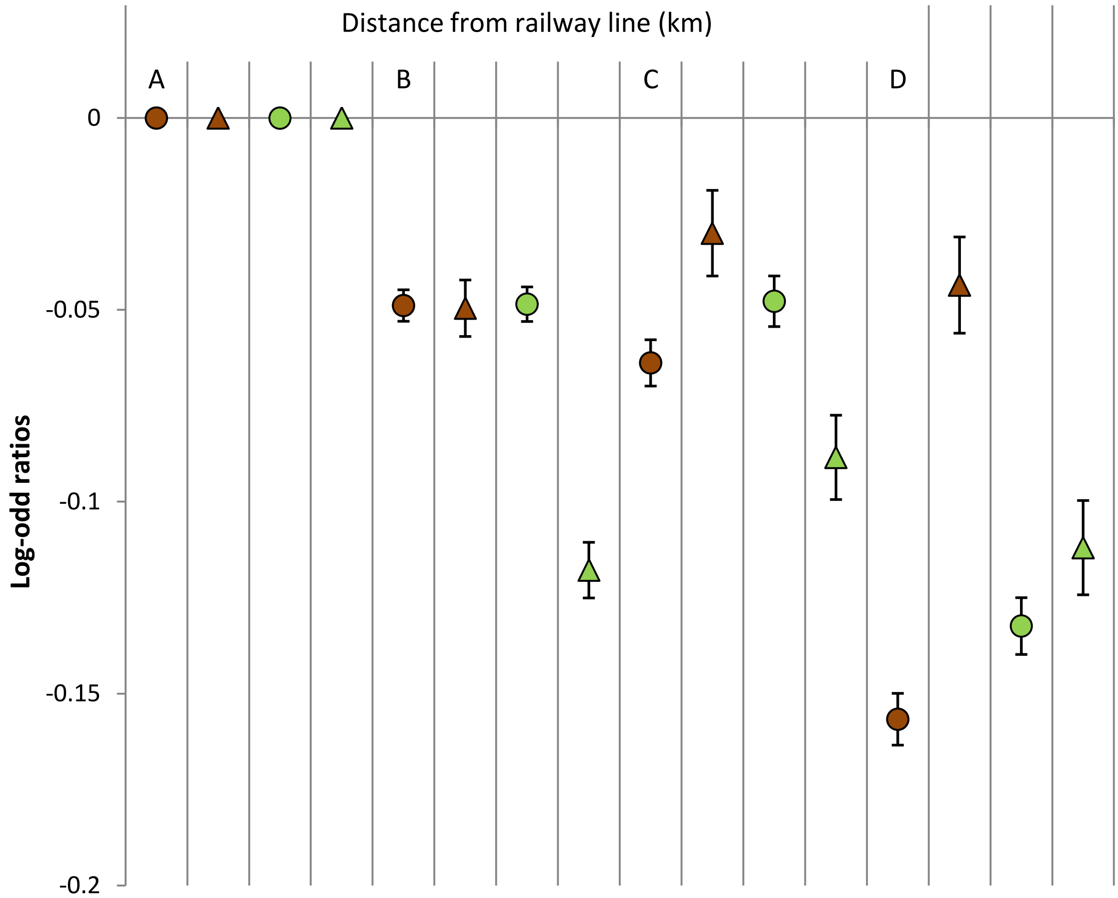


Figure 11: Distance from railway line selection estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. A= 0-39.08 km, B= 39.09 - 78.16 km, C= 78.17-117.24 km, and D= 117.25-195.46 km. Both sexes selected for the closest distance to railway lines.

Infrastructure

The mean actual distances of elephant locations from infrastructure versus the available area from any infrastructure in the study site are shown for both seasons for males and female elephants in Figure 12. Elephants occurred very close to infrastructure, especially females in both seasons (Figure 12).

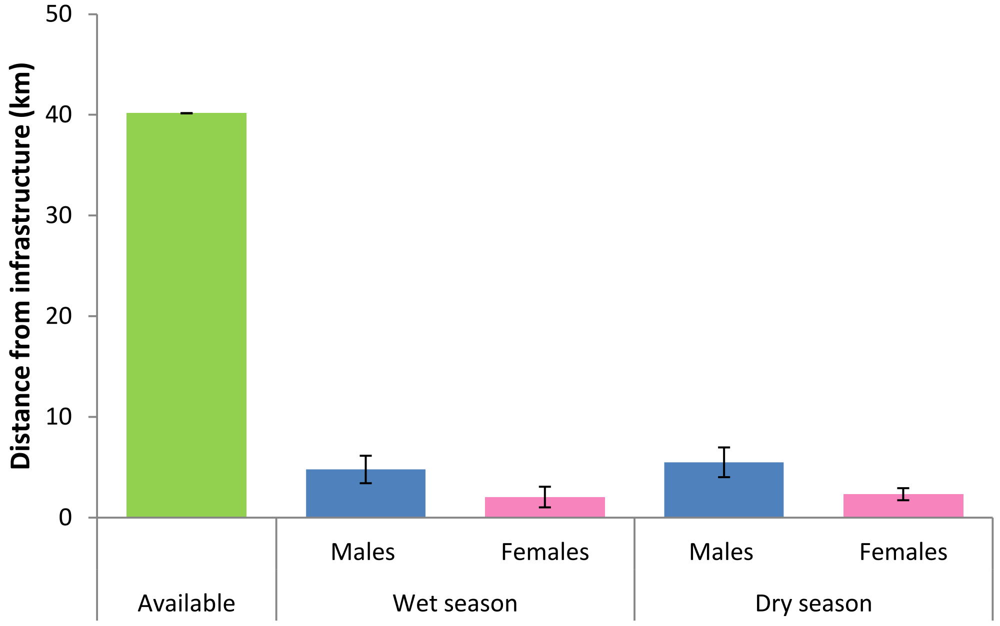


Figure 12: Mean (+SE) distance (km) of male and female elephants from infrastructure in relation to the furthest available distance for infrastructure in the study site (shown in green) in the wet and dry seasons.

The reference category (=0) was A which was the closest distance, 0-5.00 km. For both male and female elephants, the odds of occurrence at the nearest location to infrastructure (location A) were highest in both seasons (Figure 13).

In both seasons, the odds of females occurring at further distances (B, C and D) were lower than males (Figure 13), suggesting that there was a greater likelihood of males occurring at far locations from infrastructure compared to females.

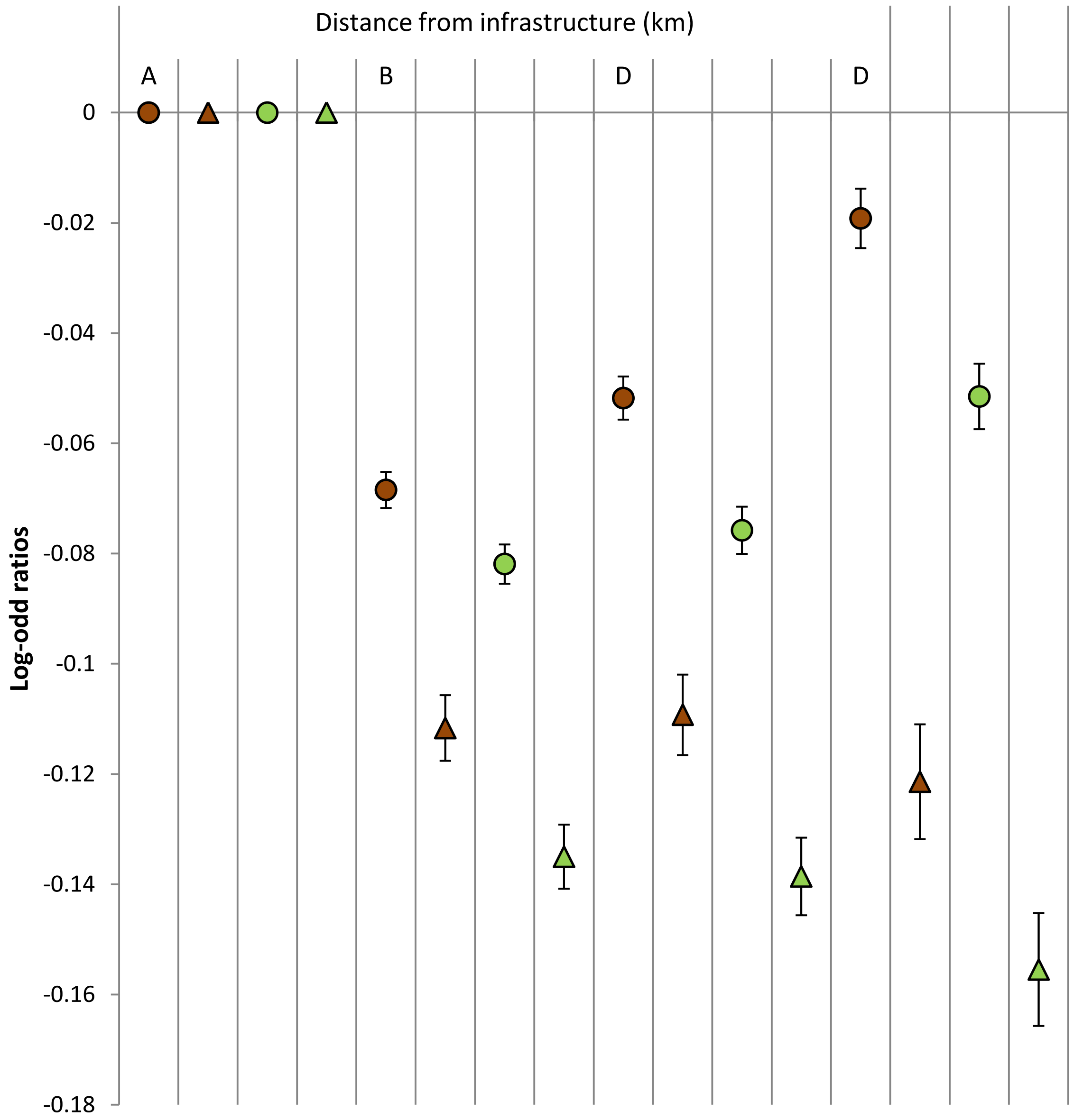


Figure 13: Distance from infrastructure estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. A= 0-5.00 km, B= 5.01-10.00 km, C= 10.01-15.00 km, and D= 15.01-40.16 km. Males occurred at far locations from infrastructure more than females.

Rivers

The mean actual distances of elephant locations from rivers versus the available area from any rivers in the study site are shown for both seasons for males and female elephants in Figure 14. Elephants occurred very close to rivers and there was no difference between sexes in both seasons (Figure 14).

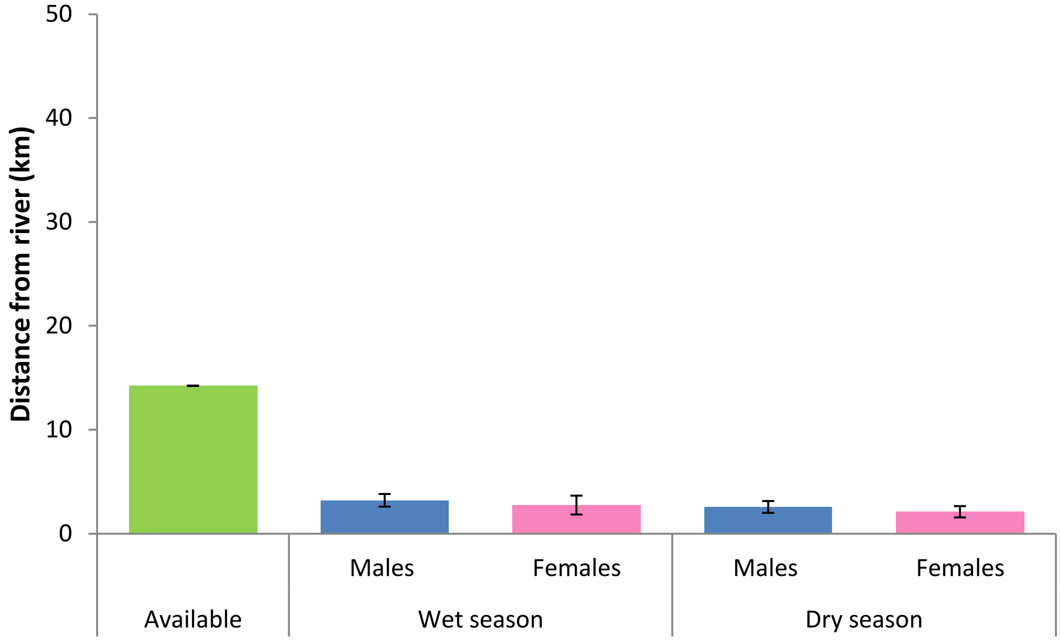


Figure 14: Mean (±SE) distance (km) of male and female elephants from rivers in relation to the furthest available distance for rivers in the study site (shown in green) in the wet and dry seasons.

The reference category (=0) was A which included the closest distance, < 2km. B and C included 2-5 km and > 5km, respectively. Males and females both occurred at closer distances to rivers in the dry season (Figure 15). In the wet season, both males and females mostly occurred at further distances, B and C (Figure 15). In both seasons, there was no difference in the use of rivers between sexes because confidence intervals overlapped (Figure 15).

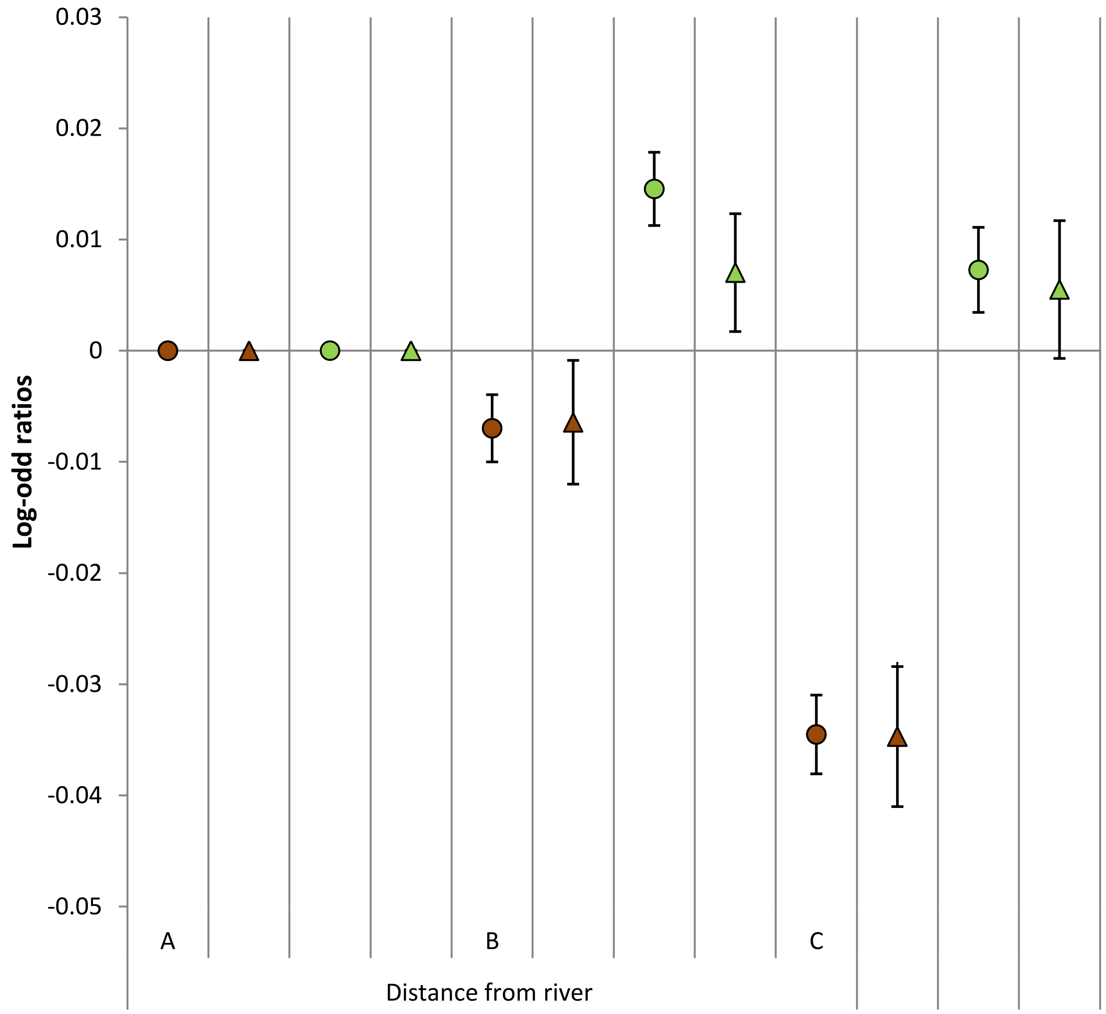


Figure 15: Distance from river selection estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. A= near, B= intermediate and C= far. No difference in use of rivers between sexes.

Geological features

The type of geological features (granite or basalt) used by elephants were provided in Figure 16. For males, the use of granite and basalt was similar to the ratio of geological features available in the study site in both seasons (Figure 16). For females, fewer granite areas were used and more basalt areas were used in both seasons (Figure 16).

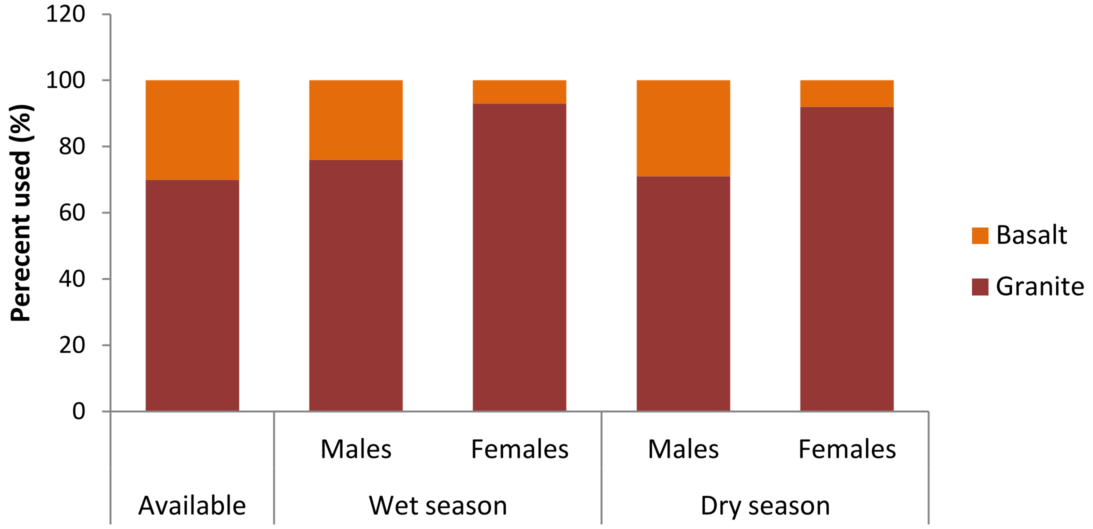


Figure 16: The percentage usage of geological features (granite and basalt), by male and female elephants compared to what is available in the study site in the dry and wet seasons.

Geological feature estimates of occurrence by elephants were calculated for basalt and granite (Figure 17). The reference category (=0) was basalt which was compared to granite. In both seasons, males selected basalt over granite and females selected granite over basalt (Figure 17).

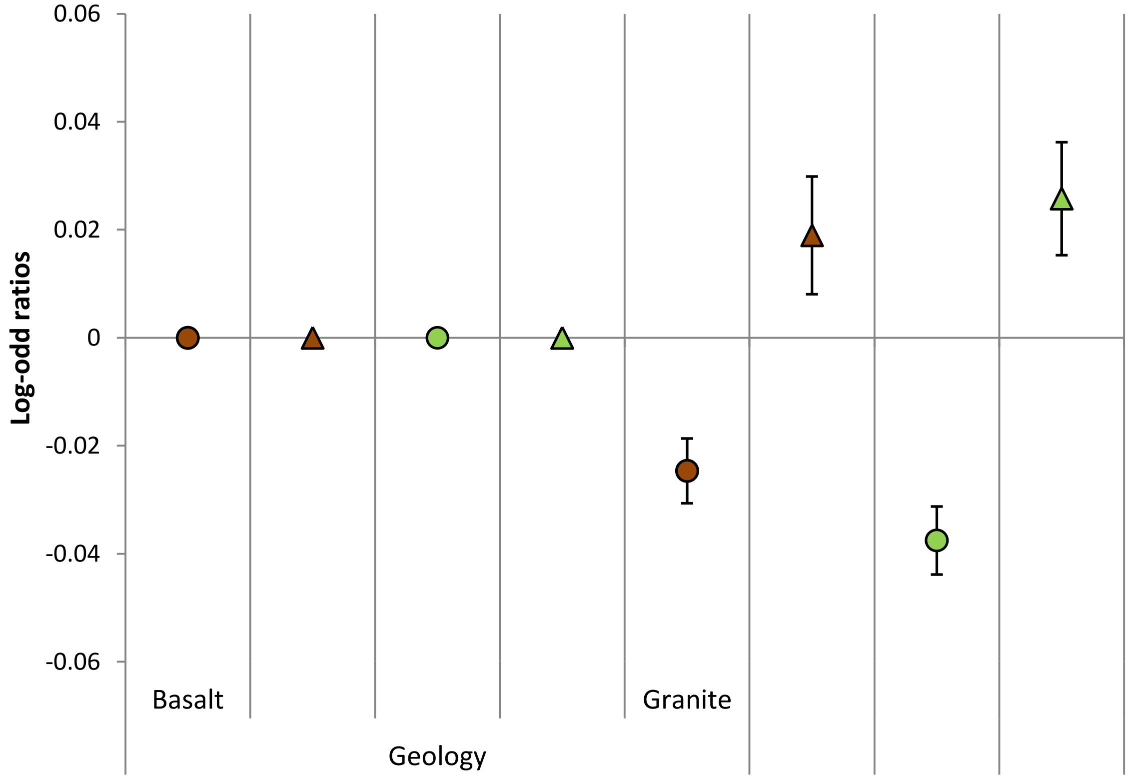


Figure 17: Geological feature selection estimates (±95% confidence intervals) by male (○) and female (Δ) elephants for the dry (brown) and wet (green) season. Sexes select for different geological features.

Vegetation

The type of vegetation used by elephants was provided in Figure 18. For males, similar vegetation was used in both seasons but there was some vegetation types used differently between seasons (Figure 18). For females, the use of vegetation between seasons was similar but the percentage used differed (Figure 18). The vegetation types mostly used by both sexes included Granite Lowveld and Phalaborwa-Timbavati Mopaneveld; however, vegetation use also differed between the sexes (Figure 18).

Males and females selected for specific vegetation types in the dry season (Figure 19). The reference category (=0) was Cathedral Mopane. Males mostly selected for Phalaborwa-Timbavati Mopaneveld (log-odds = 0.247±0.0144), Sand Forest (log-odds = 0.093± 0.0454), and Subtropical Alluvial Vegetation (log-odds = 0.232± 0.0174) (Figure 19a). All vegetation types below the reference category were avoided by males (Figure 19a). Females mostly selected for Gabbro Grassy Bushveld (log-odds = 0.033± 0.028), Granite Lowveld (log-odds = 0.080± 0.026), Lowveld Rugged Mopaneveld (log-odds = 0.180± 0.027), Mopane Gabbro Shrubland (log-odds = 0.046± 0.032), Phalaborwa-Timbavati Mopaneveld (log-odds = 0.174± 0.027) and Tshokwane-Hlane Basalt Lowveld (log-odds = 0.077± 0.028) (Figure 19b).

Males and females selected for specific vegetation types in the wet season (Figure 20). Males mostly selected for Phalaborwa-Timbavati Mopaneveld (log-odds = 0.274± 0.0156) and Subtropical Alluvial Vegetation (log-odds = 0.138 0.0195) (Figure 20a). Females mostly selected for Lowveld Rugged Mopaneveld (log-odds = 0.167 0.0258), Mopane Gabbro Shrubland (log-odds 0.035± 0.0308), and Phalaborwa-Timbavati Mopaneveld (log-odds = 0.259 0.0258) (Figure 20b).

The use of vegetation by males differed between seasons; a wider variety of vegetation types was selected in the dry season (Figure 19 and Figure 20). Females also differed in vegetation use between seasons; there was a wider variety in use of vegetation type in the dry season (Figure 19 and Figure 20). There was a difference in vegetation type selection between the sexes, with the exception of Phalaborwa-Timbavati Mopaneveld which was commonly selected by males and females in both seasons (Figure 19 and Figure 20).

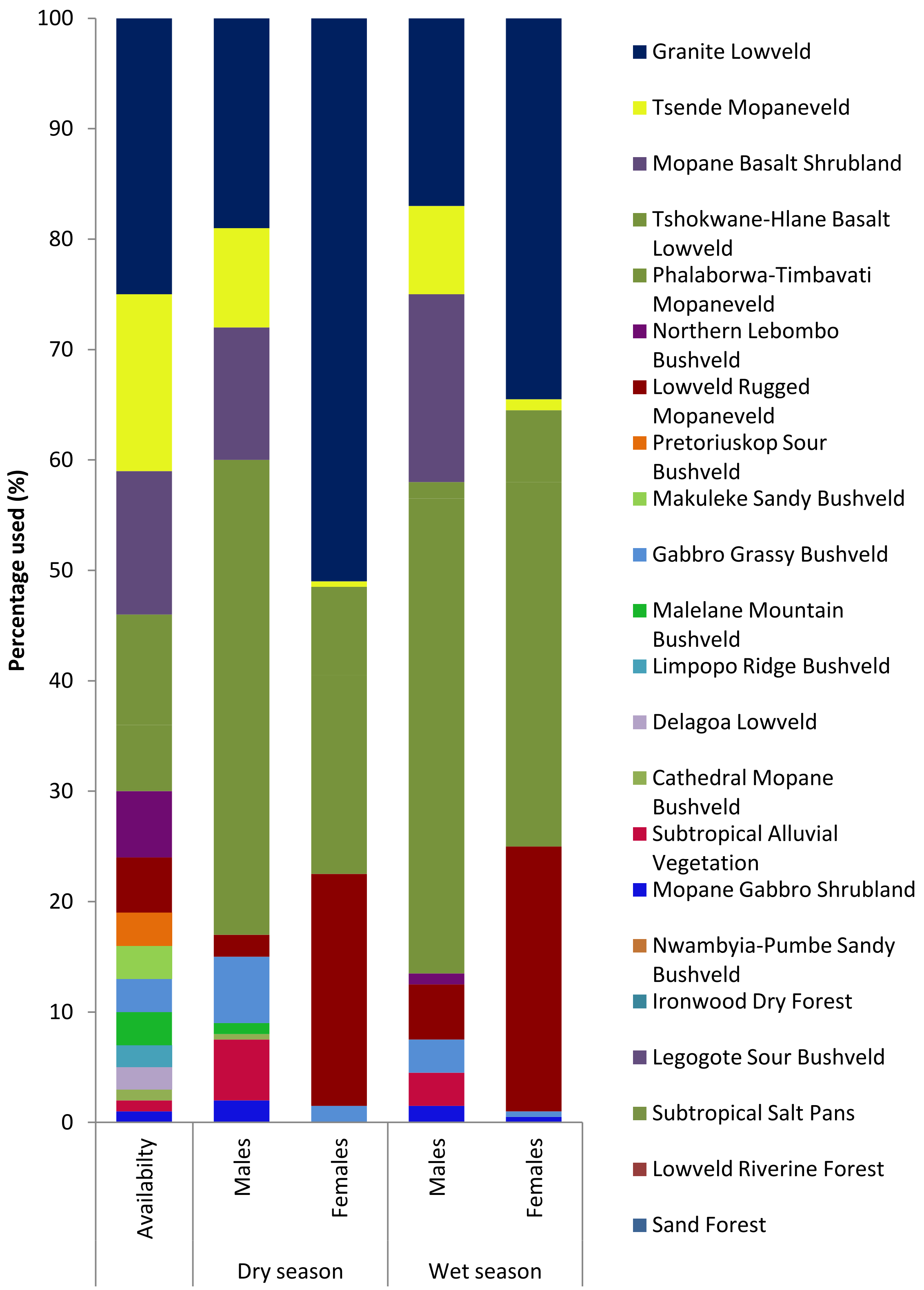
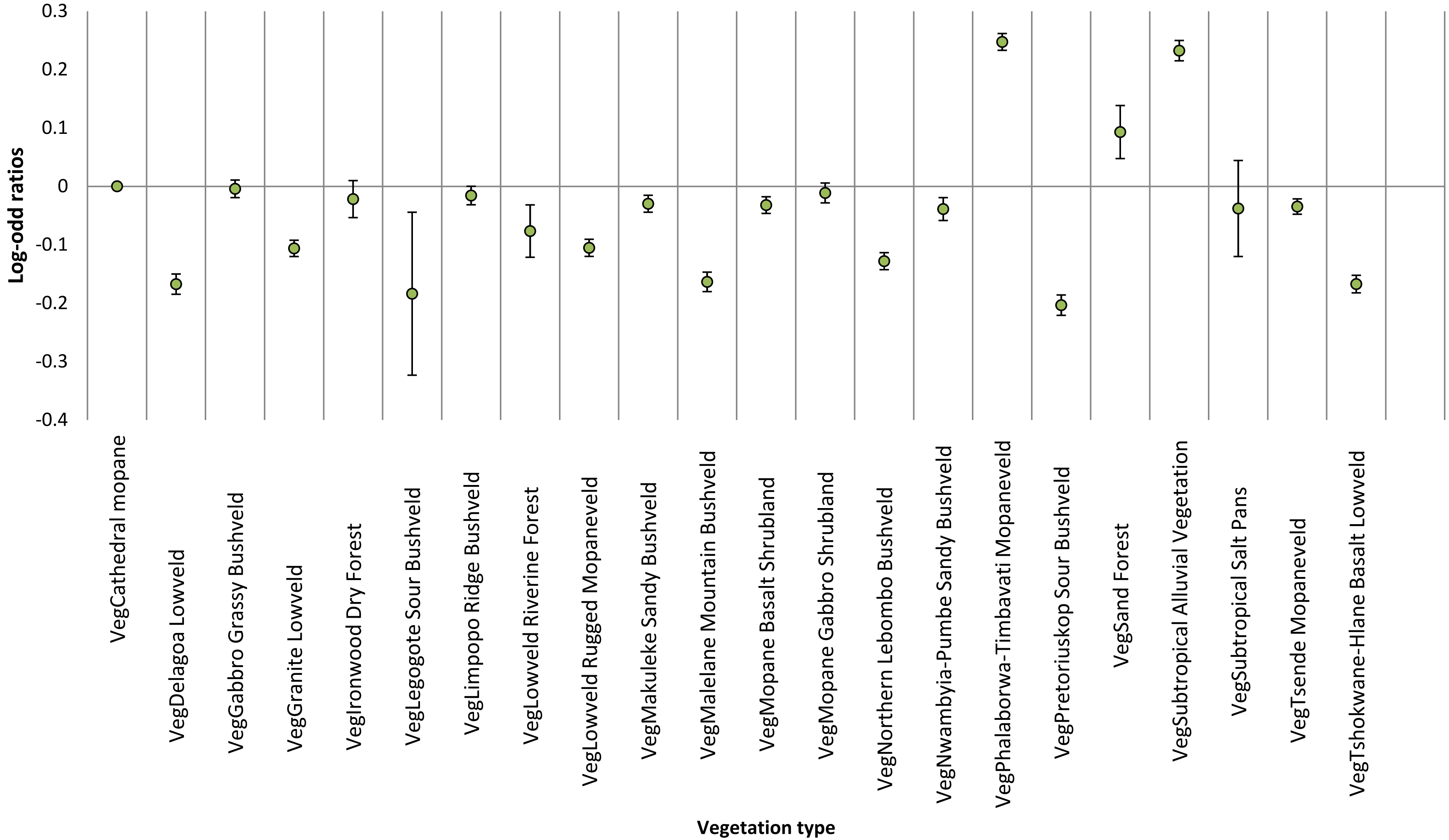


Figure 18: The percentage usage of different vegetation types, by male and female elephants compared to what is available in the study site in the dry and wet seasons.

a)


Log-odd ratios
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
VegCathedral mopane
VegDelagoa Lowveld
VegGabbro Grassy Bushveld
VegGranite Lowveld
VegIronwood Dry Forest
VegLegogote Sour Bushveld
VegLimpopo Ridge Bushveld
VegLowveld Riverine Forest
VegLowveld Rugged Mopaneveld
VegMakuleke Sandy Bushveld
VegMalelane Mountain Bushveld
VegMopane Basalt Shrubland
VegMopane Gabbro Shrubland
VegNorthern Lebombo Bushveld
VegNwambyia-Pumbe Sandy Bushveld
VegPhalaborwa-Timbavati Mopaneveld
VegPretoriuskop Sour Bushveld
VegSand Forest
VegSubtropical Alluvial Vegetation
VegSubtropical Salt Pans
VegTsende Mopaneveld
VegTshokwane-Hlane Basalt Lowveld
Vegetation type

b)

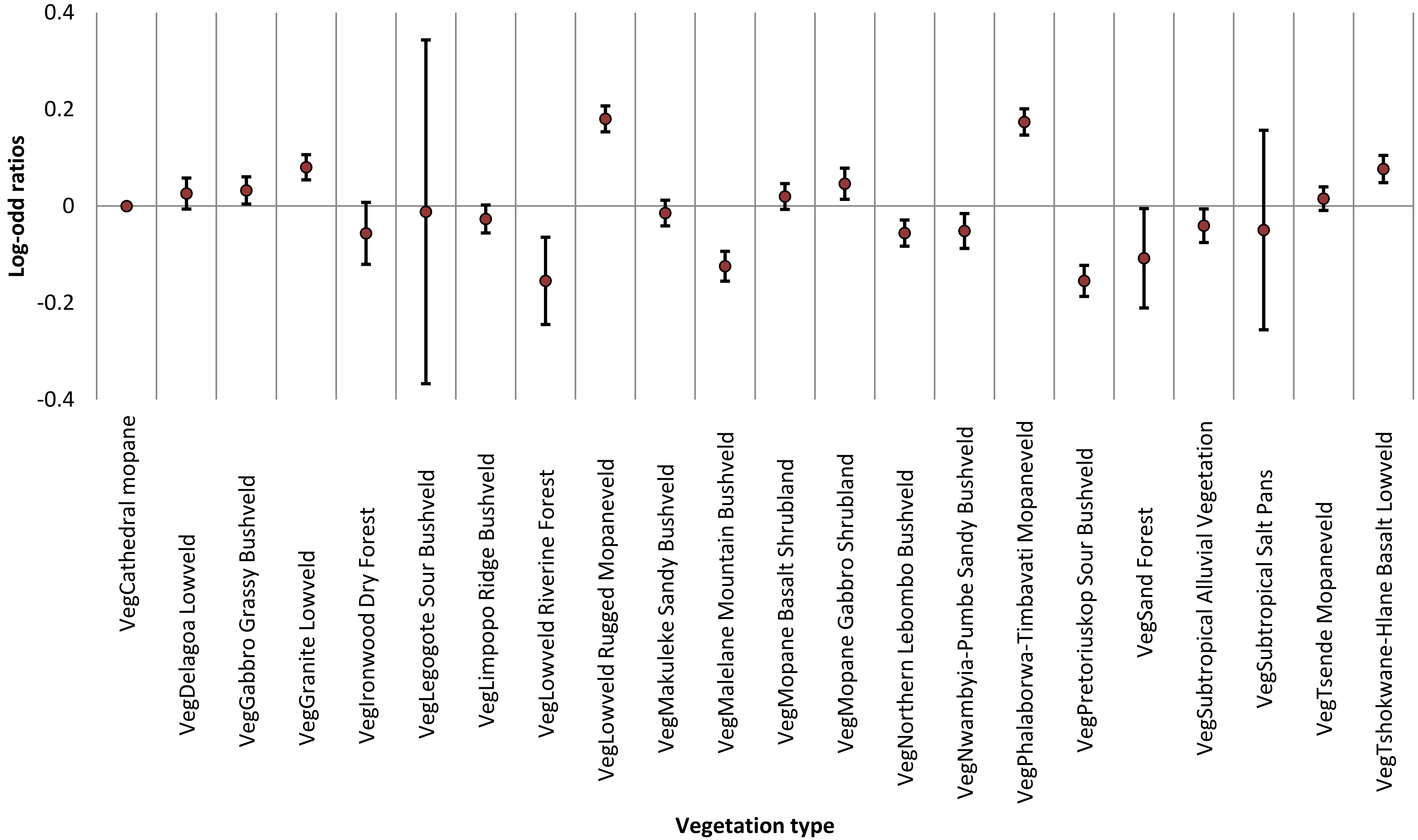
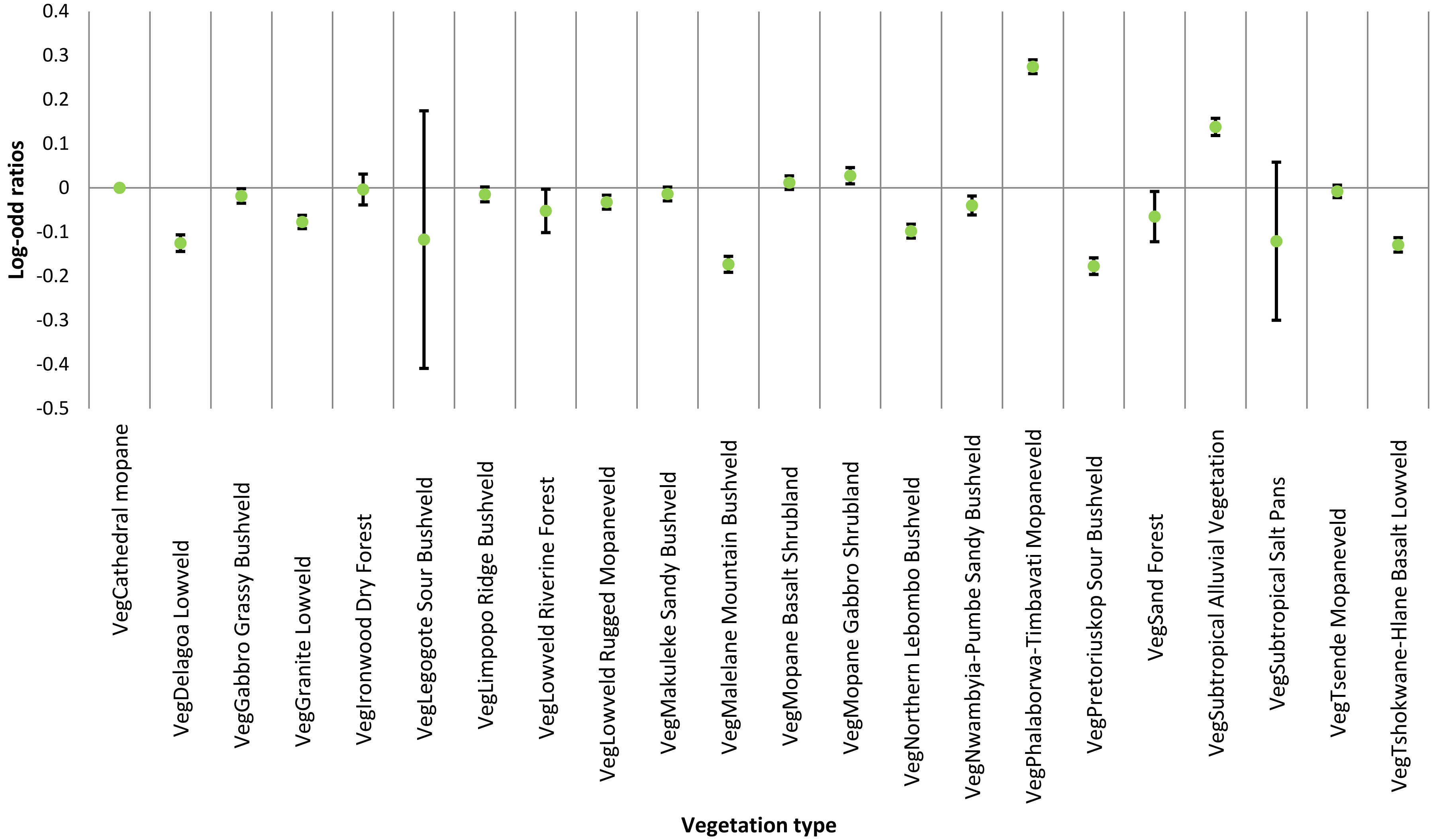


Figure 19: Vegetation selection estimates (±95% confidence intervals) by a) male and b) female elephants in the dry season.

a)


0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
Log-odd ratios
VegCathedral mopane
VegDelagoa Lowveld
VegGabbro Grassy Bushveld
VegGranite Lowveld
VegIronwood Dry Forest
VegLegogote Sour Bushveld
VegLimpopo Ridge Bushveld
VegLowveld Riverine Forest
VegLowveld Rugged Mopaneveld
VegMakuleke Sandy Bushveld
VegMalelane Mountain Bushveld
VegMopane Basalt Shrubland
VegMopane Gabbro Shrubland
VegNorthern Lebombo Bushveld
VegNwambyia-Pumbe Sandy Bushveld
VegPhalaborwa-Timbavati Mopaneveld
VegPretoriuskop Sour Bushveld
VegSand Forest
VegSubtropical Alluvial Vegetation
VegSubtropical Salt Pans
VegTsende Mopaneveld
VegTshokwane-Hlane Basalt Lowveld
Vegetation type

b)

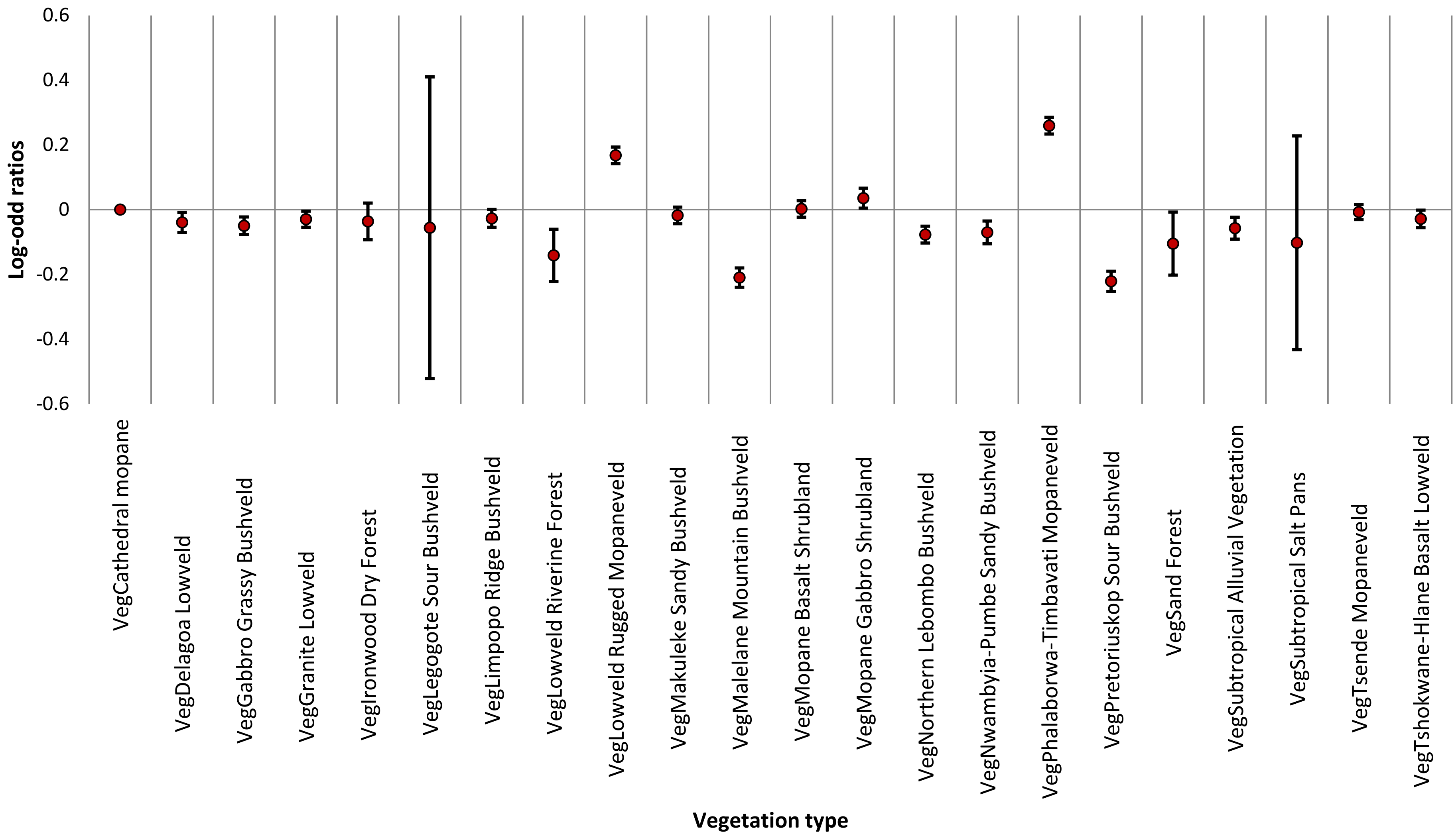


Figure 20: Vegetation selection estimates (±95% confidence intervals) by a) male and b) female elephants in the wet season.

3rd order selection

Analysis at the finer scale used 50% isopleth home ranges of elephants which is the core home range of the elephants and shows where most of their time is spent. Results from the model selection using R software showed that the best model was different for each sex in each season which can be seen below in Table 4. The variables included in the best model were considered the most important features that affected elephant space use within the home range.

Table 4: Models generated in R software with the lowest AIC values that were considered the best to be selected at 3rd order level

Model	**AIC**	**Δ AICc**	**k**	**ω_i**
Dry Season: Females				
lmer(Observed~road+(1|Ellieid/Year),family=binomial,REML=F)	16865	0	29	0.95
Dry Season: Males				
lmer(Observed~fence+river+Geol+Veg+(1|Ellieid/Year),family=binomial,REML=F)	62399	0	29	0.99
Wet Season: Females				
lmer(Observed~rail+(1|Ellieid/Year),family=binomial,REML=F)	11175	0	29	0.96
Wet Season: Males				
lmer(Observed~fence+road+rail+infra+river+Veg+(1|Ellieid/Year),family=binomial,REML=F)	57514	0	29	1

The most important features for male elephants at the 3rd order analysis were fences, roads, railway lines, infrastructure, rivers, geological features and vegetation (Table 4). For females, the most important features at the 3rd order analysis were roads and railway lines (Table 4). Therefore, female elephants had much fewer features that influence their space use at the 3rd order analysis compared to males. The log-odd ratios were calculated to estimate what the elephants were selecting or avoiding.

Fences

The odds of males occurring closer to fences was higher in the dry season than the wet season (Figure 21) therefore males were located closer to fences in the dry season. Fences had no effect on females at the core home range level.

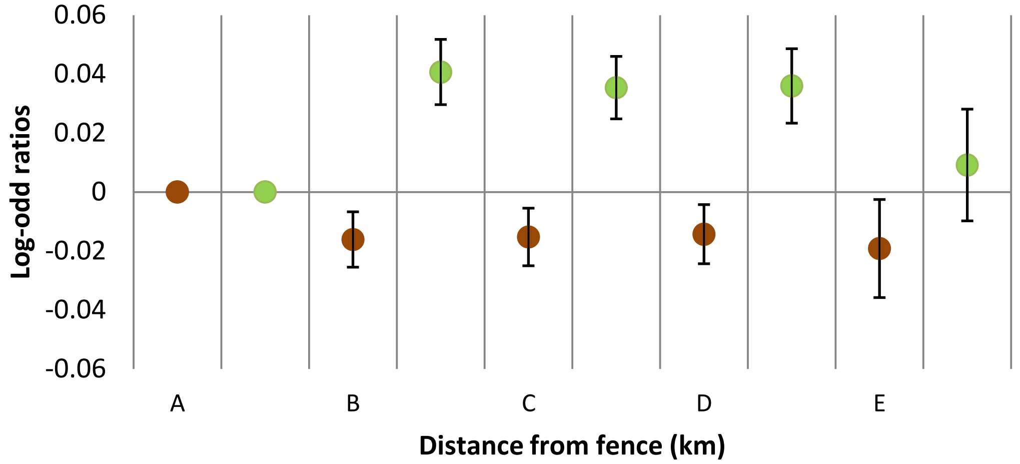


Figure 21: Distance from fence estimates (±95% confidence intervals) of male elephants for the dry (brown) and wet (green) season. A= 0 -6.26 km, B = 6.27-12.52 km, C= 12.53-18.78 km, D= 18.79-25.05 km, and E= 25.061-31.32 km. Males were located closer to fences in the dry season.

Roads

Males occurred mostly at the furthest distance from roads (C) compared to the nearest distance (A) in the wet season (Figure 22). There was no effect of roads on males at the core home range level in the dry season. Females tended to occur more at the closest location (A) than at intermediate distances from roads in the dry season (Figure 23). There was no effect of roads on females at the core home range level in the wet season.

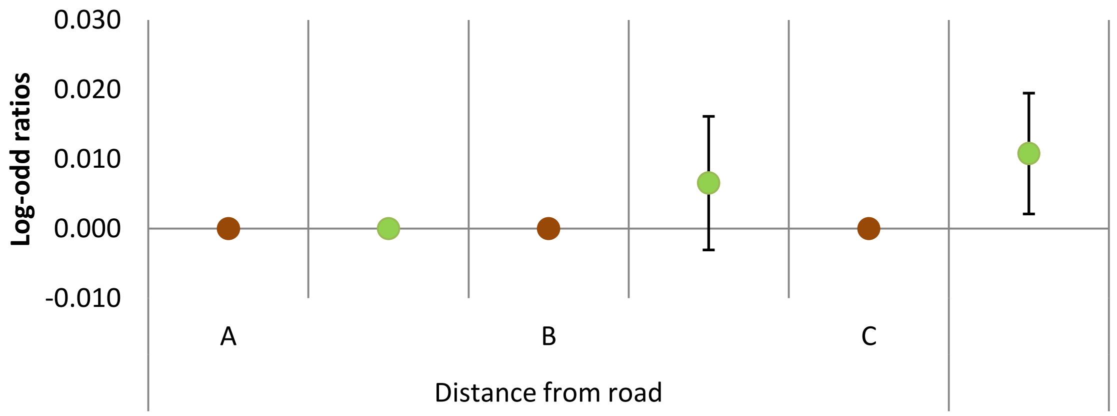


Figure 22: Distance from road estimates (±95% confidence intervals) by male elephants for the dry (brown) and wet (green) season. A= near, B= intermediate and C= far. Males were mostly located at the furthest distance from roads in the wet season.

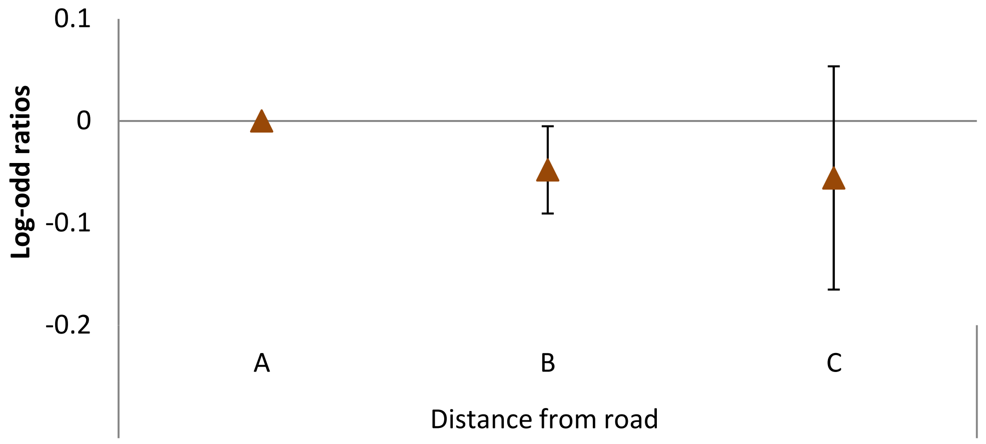


Figure 23: Distance from road estimates (±95% confidence intervals) by female elephants for the dry season. A= near, B= intermediate and C= far. Females were located mostly at near and far distances.

Railway lines

Males were mostly located at intermediate to far distances (B and D) in the wet season, while in the dry season railway lines did not appear to influence space use within the home range (Figure 24). Females did not occur as far away from railway lines compared to males and occurred mostly at location B in the wet season (Figure 25).

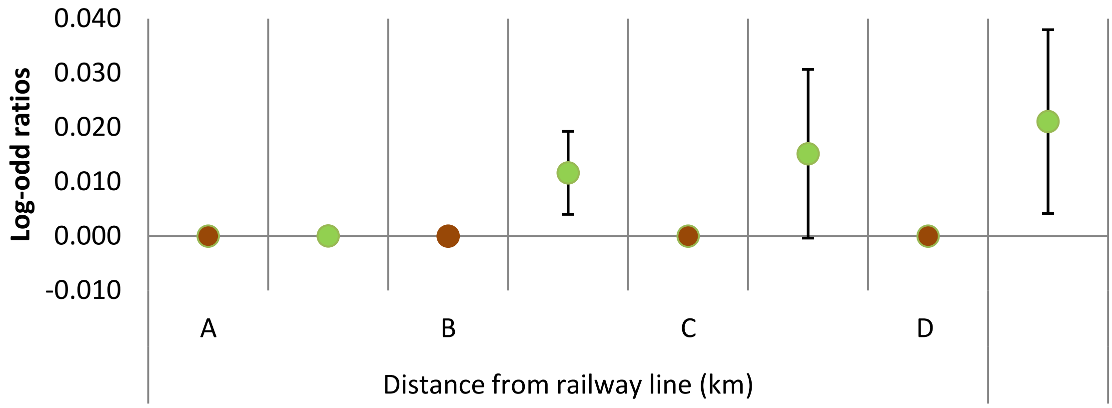


Figure 24: Distance from railway line estimates (±95% confidence intervals) by male elephants for the dry (brown) and wet (green) season. A= 0-31.40 km, B = 31.41-62.80 km, C= 62.81-94.20 km, and D= 94.21-125.60 km. Males were located at further distances from railway lines.

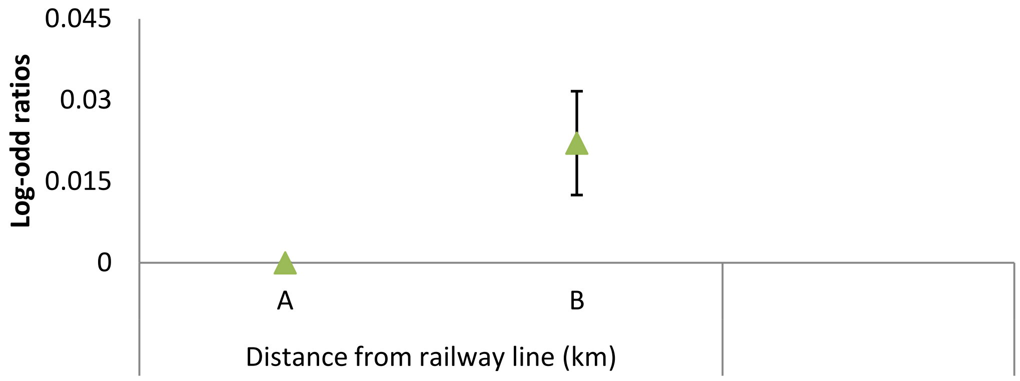


Figure 25: Distance from railway line estimates (±95% confidence intervals) by female elephants for the wet season. A= 0-31.40 km and B = 31.41-62.80 km. Females occurred mostly at the distance furthest from railway lines.

Infrastructure

Males occurred mostly at close distances to infrastructure (A and B) in the wet season while in the dry season infrastructure did not appear to influence space use within the home range (Figure 26). Infrastructure had no effect on females at the core home range level.

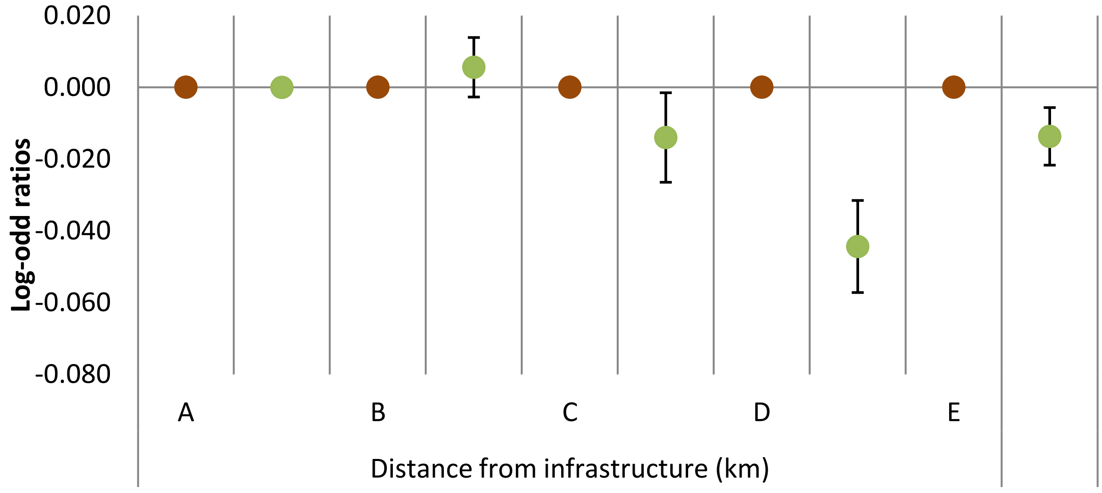


Figure 26: Distance from infrastructure estimates (±95% confidence intervals) by male elephants for the dry (brown) and wet (green) season. A= 0-2.00 km, B = 2.01-4.00 km, C= 4.01-6.00 km, D= 6.01-8.00 km, and E= 8.01-19.89 km. Males were mostly located close-intermediate distances from infrastructure in the wet season.

Rivers

Males mostly occurred at close and intermediate distances (A and B) in the dry season but were mostly located at further distances (B and C) in the wet season (Figure 27). Rivers had no effect on females at the core home range level.

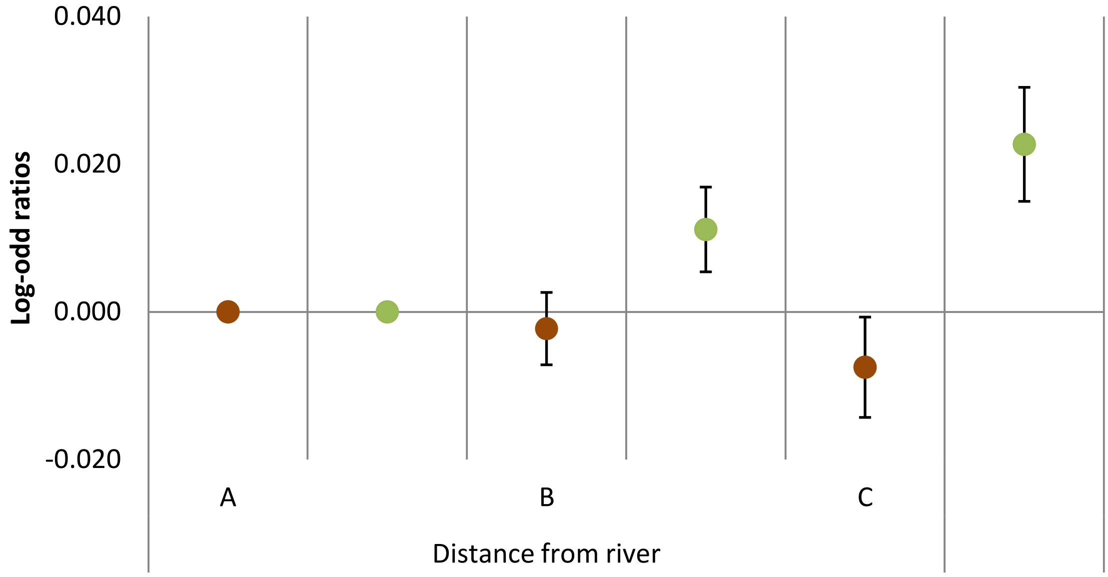


Figure 27: Distance from river estimates (±95% confidence intervals) of male elephants for the dry (brown) and wet (green) season. A= near, B= intermediate and C= far. Males occurred closer to rivers in the dry season.

Geological features

Males showed no preference for basalt over granite areas in the dry season while in the wet season geological features did not appear to influence space use within the home range (Figure 28). Geological features had no effect on females at the core home range level.

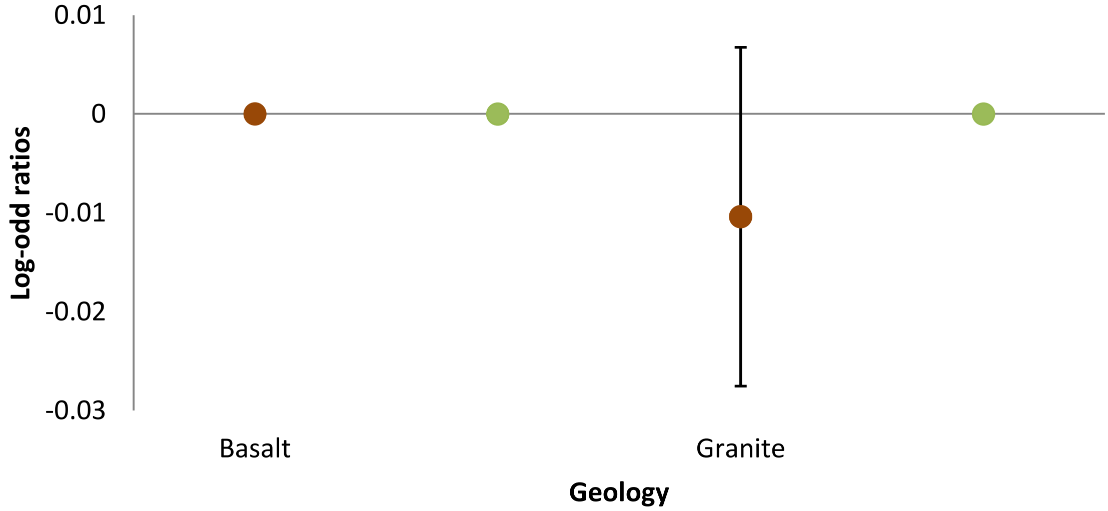


Figure 28: Geological feature estimates (±95% confidence intervals) of male elephants for the dry (brown) and wet (green) season. There was no difference in the use of basalt and granite in the dry season because the confidence intervals overlapped with the basalt reference line.

Vegetation

Male elephants selected most for Lowveld Rugged Mopaneveld (log-odds = 0.037±0.021) and least selected for Malelane Mountain Bushveld (log-odds = -0.105±0.027) in the dry season (Figure 29). There was no specific vegetation type selected by males in the wet season therefore a wider diversity of vegetation types were selected in the dry season (Figure 30). Vegetation had no effect on females at the core home range level.

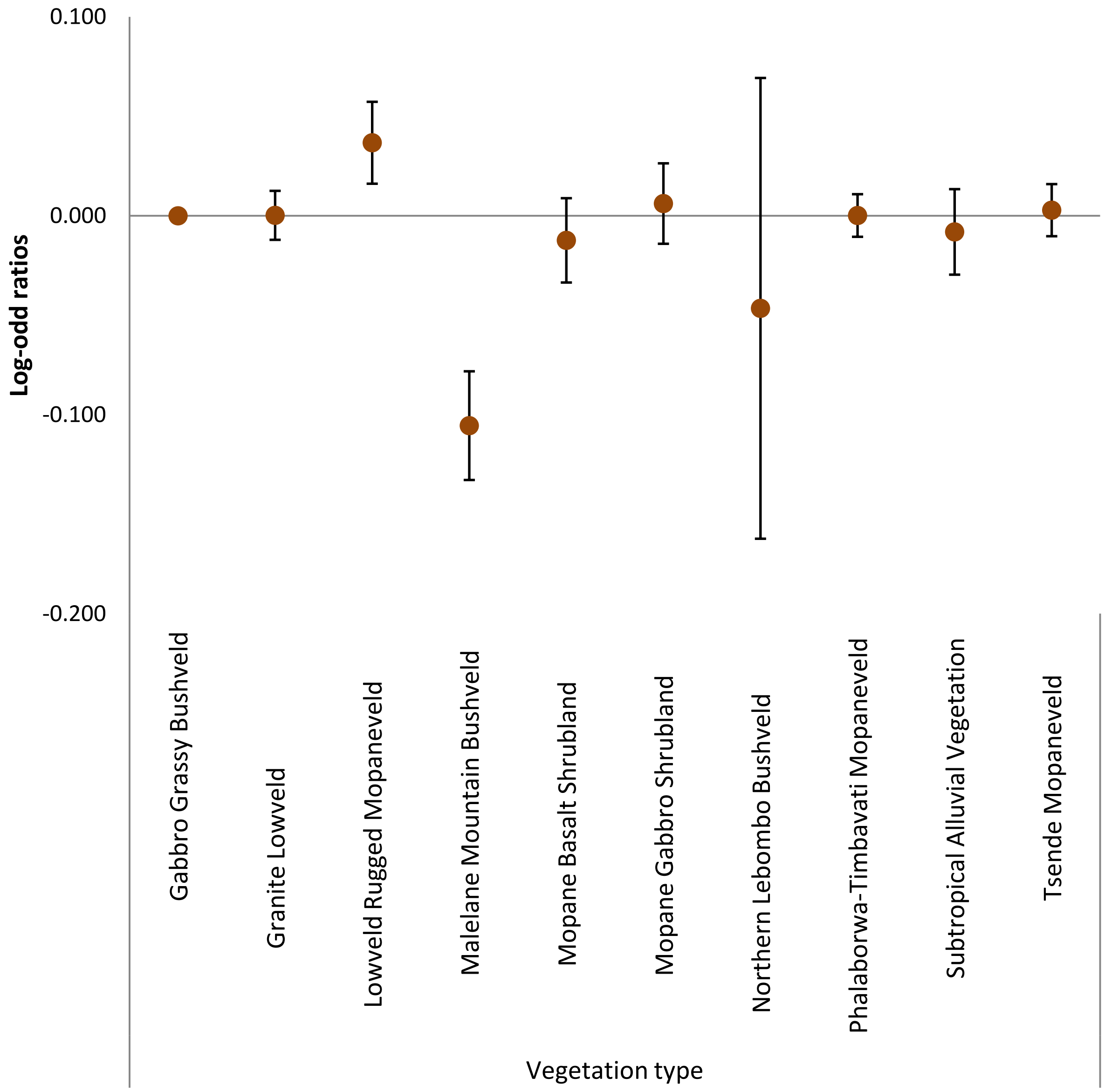


Figure 29: Vegetation selection estimates (±95% confidence intervals) of male elephants for the dry season. Males selected most for Lowveld Rugged Mopaneveld and least selected for Malelane Mountain Bushveld.

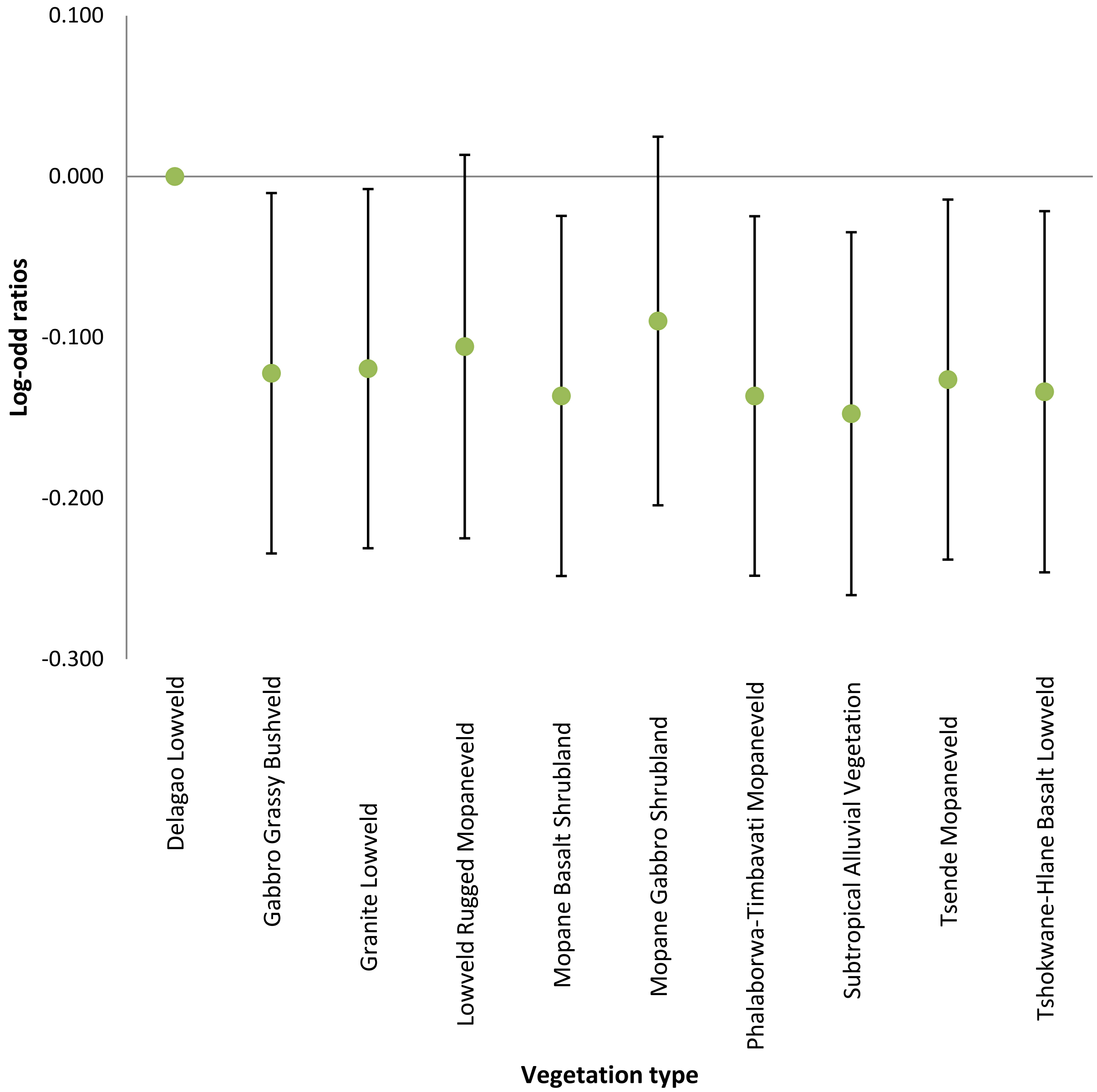


Figure 30: Vegetation selection estimates (±95% confidence intervals) by male elephants for the wet season. There was no specific vegetation type that was selected by males

A summary of the results was done to compare the influence of features on elephants at both the 2nd and 3rd order to investigate which features were considered barriers to elephant space use (Table 5).

Table 5: A summary of the predictions and results on the influence features (anthropogenic and natural) on male and female elephants at the 2nd and 3rd order analyses. The blocks in green represent the expected predictions.

Feature	**Predictions**		**Results**					
			2nd Order			**3rd Order**		
	Seasonal	**Sex**	**Seasonal**		**Sex**	**Seasonal**		**Sex**
			Males	**Females**		**Males**	**Females**	
Fences	Closer in wet season	Males occur closer	Closer in both seasons	Closer in dry season	Males were closer	Further in wet season	-	-
Roads	Close in both seasons	Both sexes occur closer	Closer in both seasons	Closer in both seasons	Males were further	Further in wet season	Closer in dry season	-
Railways	Same for both seasons	Males occur closer	Closer in both seasons	Closer in both seasons	No pattern in use by sex	Further in wet season	Closer in wet season	Females were closer
Infrastructure	Closer in dry season	Males occur closer	Closer in both seasons	Closer in both seasons	Males were further	Closer in wet season	-	-
Rivers	Closer in dry season	Females occur closer	Closer in dry season	Closer in dry season	No difference in use by sex	Closer in dry season	-	-
Geological features	Difference in use	Difference in use	Selected basalt in both season	Selected granite in both seasons	Yes	No specific geological features selected	-	-
Vegetation	Difference in use	Difference in use	Used wider variety in dry season	Used wider variety in dry season	Yes	Used wider variety in dry season	-	-

Discussion

Behavioural studies on animal movement can indicate how animals are responding to their environment (Whyte 1996; Cushman *et al*. 2010). This is especially useful to establish whether certain features in their environment are acting as barriers to their space use (Boyce and McDonald 1999). In my study, barriers were defined as features, artificial or natural, that elephants avoid or use rarely in terms of their occurrence in space (Graham *et al*. 2009). Elephants are known to travel over long distances (Poole 1996) and therefore the chance of encountering a feature (anthropogenic and natural) in the study site (Kruger and the APNR) was high. Males and females do not travel together; females form family units or herds while mature males are usually solitary (Poole 1996), which results in sex differences in habitat requirements and use (Stokke and Du Toit 2002). Therefore, males and females should encounter features in their landscape differently. In addition, there should be an expected seasonal influence on encounter rates because of the seasonal variation in elephant home range size and use (Shannon *et al*. 2006).

The aim of my study was to investigate the effects of anthropogenic and natural features on the space use of adult male and female elephants in the Kruger National Park and surrounding reserves in the APNR. This was achieved by analysing GPS location points of the elephants and their surrounding features in the landscape, including fences, roads, railway lines, infrastructure, rivers, geological features and vegetation. I analysed the potential barriers to elephant space use at two different scales: a large-scale level considers how barriers influence the establishment of the home range within the landscape, and a small-scale level considers the influence of barriers on the establishment and use of core areas within the home ranges.

Home ranges

I first compared the size of the total and core home ranges for male and female elephants in the dry and wet seasons. Males had a larger total home range size (361 km^2 in the dry season and 357 km^2 in the wet season) than females (153 km^2 in the dry season and 208 km^2 in the wet season) in both seasons. Similarly, a study in the Pongola Game Reserve in South Africa showed that the total home range size (95% kernel) of elephant bulls was approximately double that of female herd home ranges in both the dry and wet seasons (Shannon *et al*.

2006). The larger total home range size of males may be explained by the neophilic and roaming behaviour of males. Druce *et al*. (2008) found that older mature bulls are more prepared to explore new areas compared to family groups that prefer to stay in areas of known resources. Sexually mature bulls are known to roam large areas in search of oestrus cows (Grainger *et al*. 2005).

The main determinant of large-scale distribution patterns of large herbivores is abiotic factors, such as water availability, whereas biotic factors, such as resource quality and quantity influence distribution at a smaller scale (Bailey *et al.* 1996). Interestingly, I found no seasonal variation in home range size, contrary to other studies that showed how home range size, shape and location are influenced by season as a result of the distribution and abundance of resources (Shannon *et al*. 2006; Vanak *et al*. 2010). For example, Vanak *et al*. (2010) showed that elephant home range size in the Pilanesberg National Park within the Northwest Province, South Africa, is usually larger in the wet season than the dry season; however, Shannon *et al*. (2006) showed the opposite in their study in the Pongola Game Reserve in South Africa in that home range size was larger in the dry season than the wet season. Ntumi *et al*. (2005) showed that male elephants in the Maputo Elephant Reserve in Mozambique had larger total home range areas (95% kernel) than females but no seasonal influence on home range size was detected, because the elephants selected their home ranges within areas of the landscape that were near rivers and thus water availability was not an issue. Similarly, in my study the elephants selected home ranges near rivers in both seasons, which could explain the lack of seasonal variation in home range size.

Water is not the only determinant of seasonal variation in home range size (Grainger *et al*. 2005). Landscape heterogeneity also influences elephant home range size because different vegetation types impose different nutritional constraints and thus vegetation availability determines elephant home range size (De Beer and van Aarde 2008). The trade-off between forage quality and quantity depends on vegetation availability (Bailey *et al.* 1996). The lack of seasonal variation in elephant home range size suggests that resource availability is similar between seasons (De Beer and van Aarde 2008). Elephants do not seem to follow the pattern of seasonal variation in home range size that is found in most large herbivores. For example, elk (*Cervus elaphus*), a large North American herbivore, have smaller home ranges in summer because resources are abundant and have larger home ranges in winter because they travel further distances in search for scarce resources (Anderson *et al.* 2005).

Despite males having larger total home ranges than females, there was no difference in core home range size between sexes, as well as no seasonal variation. Shannon *et al*. (2006) also found no difference in core home range size of elephants between sex and season. Similar findings by De Villiers and Kok (1997) and Grainger *et al*. (2005) showed that there was no difference in home range size between male and female elephants. The core home range is the area of the home that is used mostly. If, as I discussed earlier that elephants established their home ranges near water sources, core home range size might be similar in size because water does not limit the movement of breeding herds (Viljoen 1989). There is no need for elephants to travel further distances in the dry or wet season for water because the maps of the APNR show that their core home ranges were established near rivers already.

Space use and barriers to movement

Resource selection is scale dependent, meaning that animals might select resources at different spatial scales (Johnson 1980) which is why I analysed the use of features at 2nd order selection (selection within the geographic range) and 3rd order selection (selection within the home range). Multi-scale analysis shows at which scale a particular feature is important or a barrier to elephant space use. I investigated whether anthropogenic features and natural features influence elephant space use between the sexes and seasonally at both spatial scales. Each feature will be discussed separately, below.

Fences

Elephants occurred close to fences at the large scale analysis. Males showed no seasonal differences in their proximity to fences, occurring closer to fences in both seasons. In contrast, females occurred at closer distances to fences in the dry season. Thus, my prediction that elephants would have a greater probability of occurring close to fences in the wet season (Loarie *et al*. 2009) was not supported. At the finer scale analysis (3rd order), there was no influence of fences on females but males occurred further away from fences in the wet season more than the dry season.

A reason that elephants were occurring close to fences at the large scale could be as a result of resources, such as specific plants that contain necessary nutrients. Elephants are known to break through fences (even fenced camps) or travel through a broken fence into another reserve in search for these resources (Shannon *et al*. 2006; McCagh 2008). This could explain why females occurred closer to fences in the dry season because this is when resources are scarce meaning females had a greater need to search for resources, especially since females had a smaller home range size than males. At the fine scale, males occurred further from fences in the wet season probably because resources were not scarce and therefore males did not have to travel greater distances to find these resources (Shannon *et al*. 2006). The reason that fences do not influence female core area selection within the home range could be because the area they mostly utilized consisted of resources that were not restricted at this scale to female elephants. Therefore, elephants travel further distances in search for resources when they are scarce which possibly results in them incurring a higher rate of fence line encounters, known as the edge-effect (Loarie *et al*. 2009).

There have been reports of elephant break-ins into camps through fences; for example, several elephants (male and female) have broken through the fence at Ingwelala camp in Umbabat of the APNR (McCagh 2008), and I have observed elephants break through fences between reserves in the APNR. A feature was defined as a barrier in my study if the structure was completely avoided by the elephants; however, my study suggests that elephants are attracted to certain vegetation types or villages, access to which are restricted by fences. Therefore, I believe that fences could be possible barriers to elephants if it impedes their movement and use of space.

Male elephants occurred at closer locations to fences more than females, as was expected because bulls reportedly mostly break through fences in my study area (McCagh 2008; Slotow 2012) and therefore males should be found closer to fence lines. A possible explanation for why female elephants occurred further away from fences than males could be because they experienced a stressful incident historically, resulting in fences being a psychological barrier (Kioko *et al*. 2008; Jachowski *et al*. 2012). There have been incidents where elephants that have broken through fences into camp sites have been shot at (McCagh 2008). Therefore, perhaps females have learnt from others or personal experience to stay away from fences (Eerkens and Lipo 2007).

Roads

I expected that roads do not act as barriers to elephant space use, and in fact both males and females tended to use locations close to roads (< 0.6km) in both seasons at the large scale, with the selection for distances close to roads being stronger in females. Therefore, because elephants were not avoiding the roads, this feature is considered not to be a barrier to elephants space use. The little research available on the influence of roads on elephant space use suggests that protected roads in reserves do not influence elephant movement (Blake *et al*. 2008). It must be noted that there are many roads in my study site (Appendix 1), which explains why the encounter rate with roads at the large scale was greater. Most of the roads in the study site are sand roads. Protected roads are easier for elephants to move along instead of travelling through savanna bush (Vanak *et al*. 2010). In contrast to the large scale, at the 3rd order analysis, males occurred the furthest distance away from roads in the wet season and females occurred close to roads in the dry season. This could be because males and females might be selecting for different resources (Stokke and Du Toit 2002). Alternatively, males and females were possibly selecting different vegetation types that differ in spatial relation to roads (Stokke and Du Toit 2002).

Railway lines

Elephants occurred close to railway lines at the large scale. I had predicted no difference in the use of railway lines between seasons by elephants, which was supported by my results at the 2nd order because both sexes were more likely to occur close to the railway lines in both seasons. However, in the 3rd order analysis, males occurred far from railway lines and females occurred close to railway lines in the wet season. The results show that elephants select their home ranges near or over railway lines at a large scale but core area selection within the home range in relation to railway lines vary by sex and season.

Some elephants have been killed by trains along the active railway line that runs through Balule in the APNR (Dr Michelle Henley pers.com; Appendix 1). Despite this, railways do not seem to be a psychological barrier triggered by historic experiences at the site of a railway line (Kioko *et al*. 2008; Jachowski *et al*. 2012) and this railway line and the two inactive railway lines in Kruger National Park clearly do not deter elephants. In some areas such as the Tsavo East National Park in Kenya, there is evidence that elephants do cross over railway lines in which they do not act as a space use restricting feature for elephants (McKnight 2004).

Females occurred closer to railway lines than males at the fine scale. Females might find the railway line is easier to travel on, similar to that of roads (Vanak *et al*. 2010). Alternatively, there could possibly be some other features that coincidentally occurred near railway lines that attracted female elephants at the fine scale; for example, rivers occur near the three different railway lines in the study site (Appendix 1) or perhaps there were specific vegetation types that females were attracted to that were in the vicinity of the railway line. I did notice, however, that the female home ranges were mostly in the APNR area of the study site, which is where the active railway line occurs. Females might select their home ranges near railway lines as a result of them having regular movement patterns that occur in these areas and they could have acquired these behaviours through social learning (e.g. cultural transmission) from others in their social group (Eerkens and Lipo 2007). Thus, because their ancestors had always lived there, they continue to use that area.

Another explanation for why female elephants occur close to the railway lines could be that females occasionally approached the line and then turned away, as reported by Shannon *et al*. (2006). This creates an appearance of attraction; however, the female elephants might be clearly avoiding crossing the structure. If the railway affected the female elephants negatively, they would potentially move their home range; however, because of the above explanations, I think the elephants are occurring near the railways but might not specifically be crossing them and therefore I believe that railway lines are a possible barrier to the elephants in my study.

Infrastructure

Both sexes occurred close to infrastructure in both seasons at the large scale contrary to my predictions. I expected that infrastructure, including settlements, staff villages and camp sites, is a barrier to elephant space use because these structures are impermeable and restrict the space use of elephants (Vanak *et al*. 2010). I expected elephants to occur closer to villages in the dry season because resources, such as food and water, are scarce during this period but would presumably be available at settlements (Foxcroft *et al*. 2008; Hema *et al*. 2010). However, both sexes occurred close to infrastructure in both seasons at the large scale analysis. Fine scale analysis showed that contrary to my prediction, males occurred closer to infrastructure in the wet season. Perhaps there was a specific plant/crop available around settlements that attracted males in the wet season (McCagh 2008). Males and females therefore did not avoid infrastructure at the home range level, nor did males within the home range in the wet season, suggesting that infrastructure is not a barrier. Infrastructure was not found to influence the space use of female elephants at the fine scale, indicating that infrastructure does not seem to influence where females establish their core area within the home range.

A reason that elephants occurred close to infrastructure could be that the elephants were searching for food (e.g. agricultural crops) at villages/camps (Foxcroft *et al*. 2008; Hema *et al*. 2010). A report on elephant break-ins into the Ingwelala camp in the Umbabat private reserve stated that elephants break through the electric fence to access highly nutritious food inside camps (McCagh 2008). Reports have stated that it is mostly bulls that break into camp sites (McCagh 2008) and the literature suggests that female elephants stay further away from human settlements compared to male elephants (Harris *et al*. 2008) whereas my results showed that females selected for close distances more strongly than males. Female elephants have a greater nutritional requirement as a result of pregnancy and lactation which could possibly explain why females occurred closer to infrastructure which would provide high energy food resources (Stokke and Du Toit 2002). Another explanation for why females occur closer to villages for food could be because these regular movement patterns are culturally re-enforced over generations (Eerkens and Lipo 2007).

Rivers

Both males and females occurred closer to rivers in the dry season than the wet season at the large scale which supported my prediction that rivers act as barriers to elephant space use only in the wet season when water levels were high (Vanleeuwe and Lambrechts 1999; Hofer and Mpanduji 2004; Mpanduji *et al*. 2008). Fine scale analyses supported my prediction in that males occurred close to rivers in the dry season, and occurred at the furthest distance from rivers in the wet season. Therefore, males did not avoid rivers in the dry season at the home range level as well as within the home range, suggesting that rivers seem to influence where males establish their home range and the area of the home range the males use in the dry season, but they occur further away from rivers in the wet season. Rivers did not influence the occurrence of female elephants at the fine scale.

Male and female elephants used rivers similarly, thus not supporting my prediction that females would occur closer to rivers than males in the dry season because they remain near water sources more than males (Gordon 1977; Stokke and Du Toit 2002). Thus, male and female elephants possibly located their home ranges near rivers and this explains why there was no seasonal difference in total home range size because water was available in both seasons and elephants did not need to travel further distances to find water (Ntumi *et al*. 2005).

Geological features and Vegetation

I predicted that geological features and vegetation do influence elephant space use because elephants use particular vegetation types which are found on particular geological features (Grant and Scholes 2006; Vanleeuwe 2008; Loarie *et al*. 2009). An important finding in my study was that males selected basalt over granite and females selected granite over basalt for both the dry and wet seasons at 2nd order analysis. As a consequence, there was a difference in vegetation use by sex because different vegetation types are found on basalt and granite, although some vegetation types sometimes occur on both geological feature types.

Since geological features characterise vegetation type (Grant and Scholes 2006; Vanleeuwe 2008; Loarie *et al*. 2009), the use of particular geological features are likely to vary seasonally (Codron *et al*. 2006). A variety of factors influence vegetation selection by elephants, including temperature, rainfall, food, water, and shelter (Ntumi *et al*. (2005). In the dry season, males and females were associated with different vegetation types except for Phalaborwa-Timbavati Mopaneveld, which was common to both sexes. Such a wide selection of vegetation types in the dry period could indicate a need to exploit many plant types to meet nutritional requirements since this is the period when resources that are rich in protein and energy are scarce and thus the elephants rely on resource quantity and not quality (De Villiers and Kok 1997; Shannon *et al*. 2006). In the wet season, males and females were associated with different vegetation types except for Mopane Gabbro Shrubland and Phalaborwa-Timbavati Mopaneveld, which was common to both sexes.

At the fine scale analysis (3rd order), males preferred no specific geological feature type in the dry season. Geological features did not influence male elephants in the wet season and female elephants in both seasons at the fine scale. Therefore, geological features are important predictors of elephant space use at the large scale and influences where elephants establish their home ranges in the landscape, but do not seem to influence elephant core area selection at the fine scale. The most preferred vegetation type at the fine scale for males in the dry season was Lowveld Rugged Mopaneveld but there was no specific vegetation type preferred by males in the wet season. Vegetation did not influence female elephants at the fine scale. Therefore, vegetation influences male elephant space use in the dry season at the fine scale as well as the large scale. Vegetation only influenced the occurrence of males in the wet season and females in both seasons at the large scale but not within the home range, similar to the effect of geological features.

I predicted that male elephants would select a wider diversity of vegetation types in the dry season than the wet season (as per Gordon 1977; Stokke and Du Toit 2002), which was supported by my results at both scales. Elephant bulls possibly selected for a more diverse variety of vegetation types in the dry season because their larger body size enables them to travel further distances from water sources than females (Gordon 1977). I also predicted that females would select a wider diversity of vegetation types in the wet season than the dry season (Gordon 1977; Stokke and Du Toit 2002), but this was not supported by my results. Male and female elephants were both associated with diverse vegetation types in the dry season at the larger scale. Some studies have shown that elephant home range size is larger in the dry season compared to the wet season because food availability is limited in the dry season, causing elephants to cover larger areas in search for food as well as in search for plants with greater nutritional quality (Shannon *et al*. 2006). This pattern is also found in other large herbivores such as Cape buffalo (*Syncerus caffer*), which show seasonal variation in home range size and home range selection, depending on the proximity of water (Funston *et al.* 1994). In contrast to the literature, there was no significant difference in home range size between seasons in my study. Grainger *et al*. (2005) showed similar results to my study and suggested that the results were possibly due to the high availability of artificial water sources distributed in the Kruger National Park. The elephants in my study are not restricted by water availability, and the vegetation types they selected were associated near rivers. Thus, instead of elephant home ranges differing in size between seasons, their home ranges differ in size in areas of high water point richness density (where they have smaller home ranges) and in areas with low water point richness density (where they have larger home ranges), irrespective of season (Grainger *et al*. 2005). These resulting impacts have important implications for conservation managers because the reduced home ranges in areas of increased density of water sources could increase the intensity of patch use within a home range (Grainger *et al*. 2005).

Patterns of large and fine scale space use

The features investigated in my study influenced elephant space use (either avoiding them or not) at the large scale (2nd order analysis). At the large scale (2nd order), elephants occurred closer to all anthropogenic structures as well as rivers and in various geological and vegetation types than chance. This suggests that these features occurred in all the elephants' home range and that these features did not have a negative influence on where elephants establish their home range. However, because the elephants were not avoiding these features does not mean that all of them are not barriers to elephant space use. For example, fences and railways appear to attract elephants; however, I have suggested that the elephants are possibly avoiding these structures. At the fine scale (3^{rd} order analysis), elephants utilized these features differently. Male elephants tended to avoid specific features seasonally, occurring further way from all anthropogenic features and rivers in the wet season, except for infrastructure. This is very important for conservation and management to consider at which scale actions needs to take place in eliminating restricting features to elephant space use. Therefore, it is essential to analyse the behavioural response of a species at the correct scale as it has a major impact on conservation. Some features possibly interact together to affect space use, such as fences and infrastructure or vegetation and infrastructure. Managers need to be aware of these features that limit elephant space use because they affect how elephants utilise their environment (Poole 1996) and managers need to apply action where possible to allow successful conservation of elephants in reserves (Whyte 1996; Margules and Pressey 2000; Boettiger *et al*. 2011).

Males and females differed in the use of features mostly at the large scale because there was no influence on sex at the fine scale except for railways, in which males especially avoided. This was probably because female home ranges included railway lines compared to male home ranges. A similar study in the Kruger National Park suggested that there was no sex difference in home range size because the complete fencing of the park possibly prevents bulls from travelling the large distances that are seen in unfenced elephant populations (Grainger *et al*. 2005). Water sources are also distributed less than 10 km apart within the park and therefore water is probably not a restricting feature of female herd movements (Grainger *et al*. 2005) and both males and females result in similar sized core home ranges. At the fine scale (3^{rd} order), preference or avoidance of features is better illustrated. Most of the features did not influence female elephants at this scale, except for roads and railways. Male elephants are more prepared to travel far from known resources into unknown areas compared to females (Shannon *et al*. 2006; Druce *et al*. 2008; Harris *et al.* 2008) and they also travel further distances when in musth which could explain why they travelled further from roads and villages and possibly encountered fences more often than females (Poole 1996; Hollister-Smith *et al*. 2008). Females had smaller home ranges than males which probably decreased their encounter with fences. Another possible reason why females occurred further away from fences or closer to railway lines could be as a result of their repeated use of set paths or areas over several generations and thus their home ranges remain in these areas where these features do or do not occur. The differences of the proximity to features could be due to variation in space use because of changes in resource availability (Foxcroft *et al*. 2008; Hema *et al*. 2010). Juvenile elephants constrain the movement of breeding herds to travel far from water sources, especially in the dry season, because this risks of mortality of the young (Grainger *et al*. 2005). Female elephants have a greater nutritional requirement than males because of their greater relative investment in reproduction (Stokke and Du Toit 2002) and this might explain why females occurred closer to infrastructure which almost guarantees resources.

Applying space use data to wildlife management

Ferguson *et al*. (2011) studied the effects on elephant behaviour of the western boundary fence in the Kruger National Park, the same area of my study, in which the elephants also occurred close to the fence. Elephant (mostly bulls) home ranges in this area were suggested to be constrained by musth and the decline in forage quality causing elephants to search for food grown outside the protected area over the fence (Ferguson *et al*. 2011). Fences possibly act as barriers to elephants because they restrict elephant space use. I would assume that elephants are attracted to the fence line in search for desired vegetation on the other side or simply because they travel greater distances and encounter the fence line (Poole 1996; McCagh 2008). Perhaps musth also influenced elephant bulls to travel longer distances (Poole 1996). Removal of all fences is unlikely because any protected reserve with such large mammals needs to be controlled through fencing. Elephants, however, need a large amount of space to obtain sufficient food to meet their metabolic needs (Harris *et al*. 2008). Strategic conservation planning should consider having several protected areas built around or near one another, similar to Kruger and the APNR, allowing fences to be dropped and a corridor for elephant use (Margules and Pressey 2000), thereby reducing the edge-effects.

I discussed earlier that elephants are occurring close to the railway lines but they might not have been crossing them, as reported by Shannon *et al*. (2006); however, my study cannot conclude this for certain. Railway lines could possibly act as barriers to elephant space use, as exemplified by the deaths of elephants by trains. Therefore, the location of new reserves should be in areas where there are no railway lines that will pass through the reserve, or, alternatively, the railways should be inactive as is the case in Kruger National Park.

Roads, infrastructure and rivers, on the other hand, do not seem to act as barriers to elephants because these features were located in the home ranges of elephants and they occurred close to these features. Human settlements/camps do not seem to be barriers to elephants in my study but they are points of attraction, increasing the risk of human-elephant conflicts. However, management strategies need to be implemented to address the risk that these elephants pose to people in camps as well as the financial costs of damage (McCagh 2008). If elephants are breaking into campsites and villages, as assumed here by their close distances to infrastructure, the possible damage caused by these elephants necessitates barriers (e.g. fences) to prevent them accessing camps/settlements. Rivers were barriers in the wet season, as expected, when possibly high water levels restricted elephant space use (Hofer and Mpanduji 2004). Elephants are able swimmers but they cannot cross rivers when water levels are too high (West 2001). Rivers are natural features in the landscape and can act as barriers to crossing, especially in the wet season.

Geological features and vegetation also influenced where male and female elephants located their home range in the landscape. Males clearly selected for basalt areas and the associated vegetation and females selected for granite areas and the associated vegetation. The sexes possibly selected for different geological features because they selected for different vegetation types as a result of their nutritional requirements and space use (Stokke and Du Toit 2002; Grant and Scholes 2006) therefore they happened to occur on different geological features. Phalaborwa-Timbavati Mopaneveld was selected by both sexes in both seasons and is therefore an important vegetation type that influences home range selection by elephants within the study site. Mopane trees are favoured by elephants, supporting their association with these trees in my study (Mucina and Rutherford 2006). Therefore, these vegetation types should be conserved in areas where elephants occur, particularly in the lowveld of South Africa.

Conclusion

The study of elephant movements can be of value for creating future corridors in reserve design (Mpanduji *et al*. 2008; Cushman *et al*. 2010). By mapping space use of elephants using satellite tracking and overlaying maps of potential barriers, studies can identify the landscape features that elephants might be avoiding (Cushman *et al*. 2010) and design reserves or corridors accordingly. This can also produce spatially explicit maps of elephant resource/feature use (Harju *et al*. 2011). This type of satellite mapping analysis can also show regular movements and the important routes for travelling and crossing of elephants (Mpanduji *et al*. 2008). Therefore, future reserve design and corridor formation between reserves can be created by identifying which features restrict elephant space use and need to be removed to allow increased space use (Harris *et al*. 2008; Mpanduji *et al*. 2008), but most importantly, reserve design must be considered at both 2^{nd} order or 3^{rd} order analyses.

My study provided a broad perspective on elephant space use and features that influence their movement. The approach used was dictated by the type and quality of the data provided by the Save the Elephants. However, future studies should establish the actual movement patterns of elephants and whether the features considered in my study are in fact barriers to movement. This will involve generating and analysing movement paths of elephants to assess features rarely used which can be defined in terms of residence (how long elephants stay in or on the feature), timing (present at day or night), and speed of movement (Graham *et al*. 2009). This type of detailed information on each individual at a finer scale than in my study can actually show what the elephants are doing near these features, and whether they are crossing them or specifically avoiding them. For example, the elephants could be occurring at close locations to railway lines, because they are attracted these features or other features in close proximity, but they might not be crossing the tracks.

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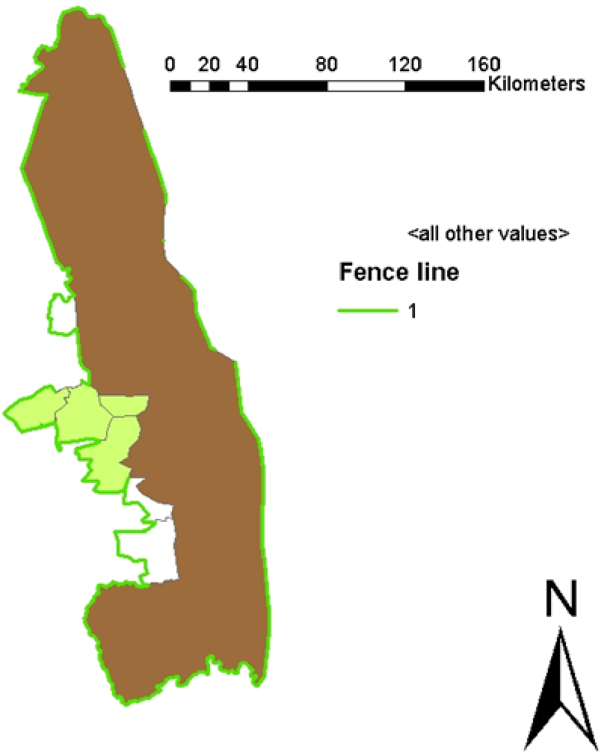
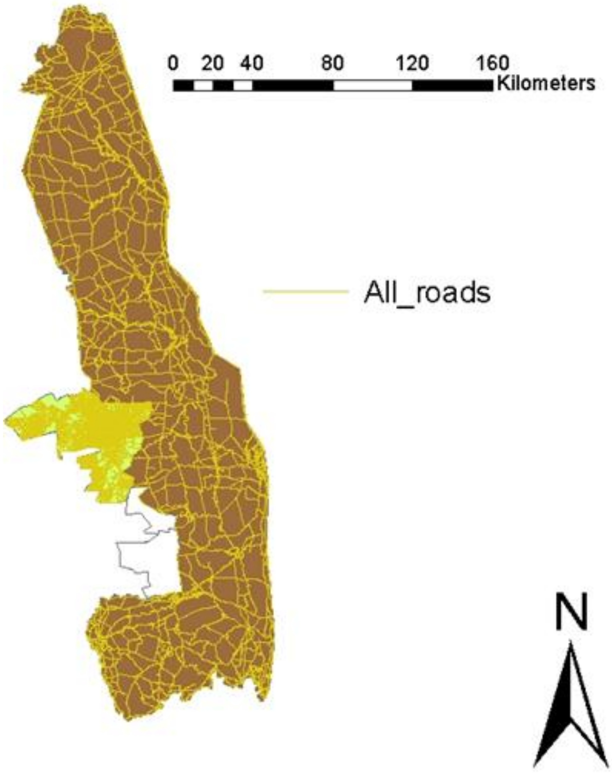
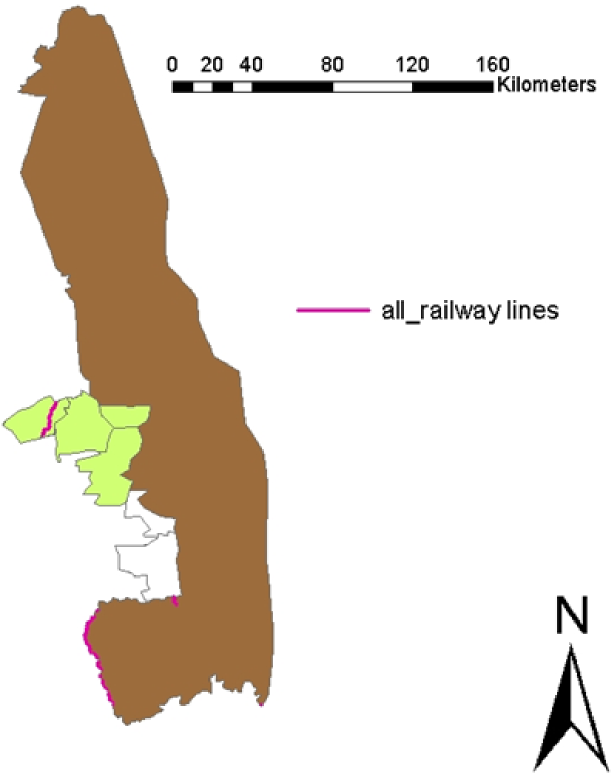
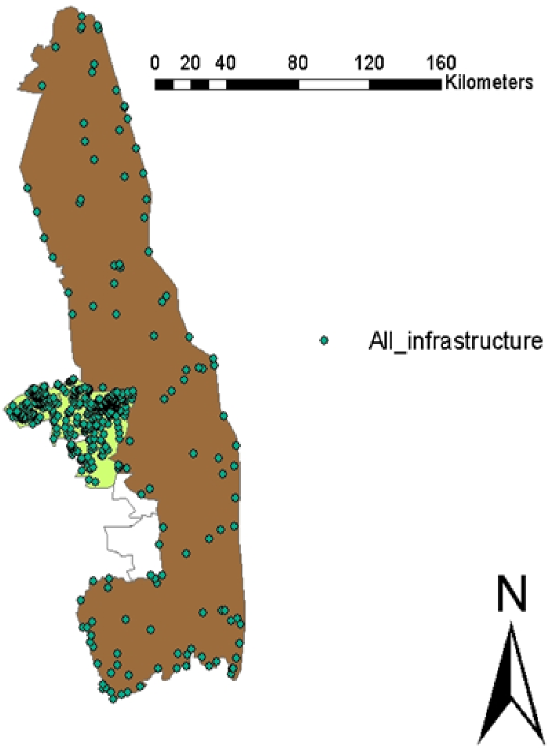
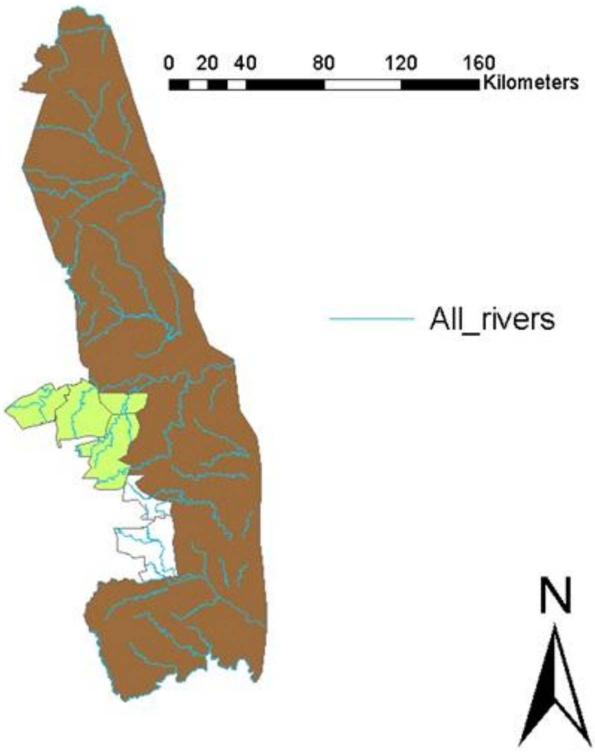
Appendix 1: Maps of the 7 different features in my study site







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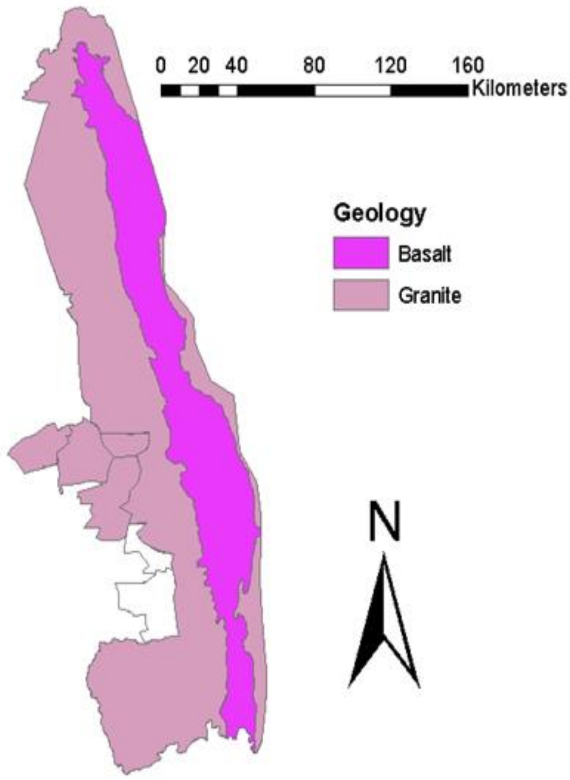
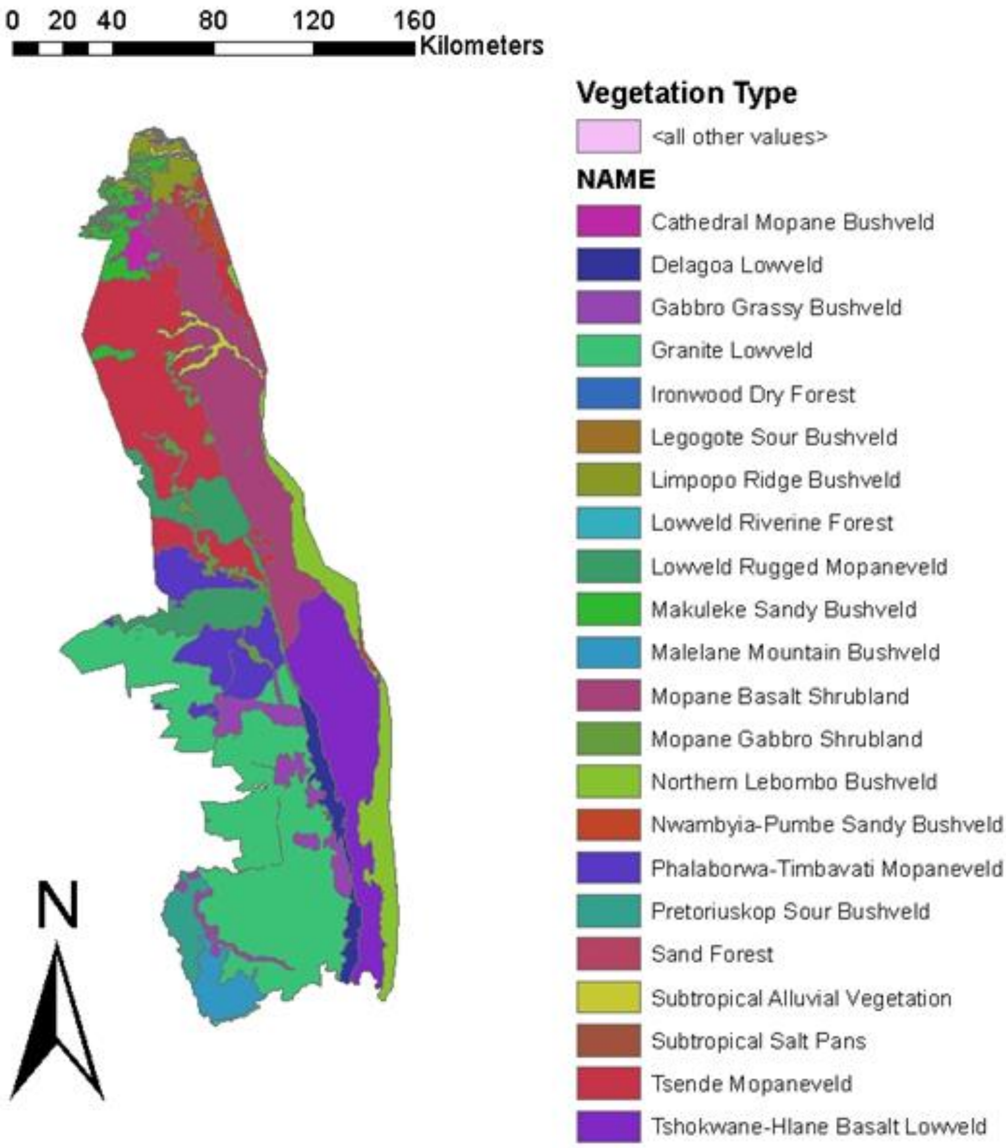
All_rivers
N


0 20 40 80 120 160
Kilometers
Geology
Basalt
Granite
N


0 20 40 80 120 160
Kilometers
Vegetation Type
<all other values>
NAME
Cathedral Mopane Bushveld
Delagoa Lowveld
Gabbro Grassy Bushveld
Granite Lowveld
Ironwood Dry Forest
Legogote Sour Bushveld
Limpopo Ridge Bushveld
Lowveld Riverine Forest
Lowveld Rugged Mopaneveld
Makuleke Sandy Bushveld
Malelane Mountain Bushveld
Mopane Basalt Shrubland
Mopane Gabbro Shrubland
Northern Lebombo Bushveld
Nwambyia-Pumbe Sandy Bushveld
Phalaborwa-Timbavati Mopaneveld
Pretoriuskop Sour Bushveld
Sand Forest
Subtropical Alluvial Vegetation
Subtropical Salt Pans
Tsende Mopaneveld
Tshokwane-Hlane Basalt Lowveld
N

Appendix 2: Distance categories for the continuous variable features

Feature	A	B	C	D	E
Fence	0-7.05	7.06-14.10	14.11-21.14	21.15-28.19	28.20-35.24
Road	< 0.6	0.6-102	> 1.2		
Railway line	0-39.08	39.09 - 78.16	78.17-117.24	117.25-195.46	
Infrastructure	0-5.00	5.01-10.00	10.01-15.00	15.01-40.16	
Rivers	< 2	2-5	> 5		