HABITAT USE BY UNGULATES IN THANDA PRIVATE GAME RESERVE, KWAZULU-NATAL

By

Kirsten Canter

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University of KwaZulu-Natal
Westville

As the candidate's supervisor I have/have not approved this thesis for submission

Signed:__________________ Name: __________________

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ABSTRACT

Knowledge of habitat use and selection is essential to managing ungulate populations. This study assesses habitat use by elephant (*Loxodonta Africana*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii)* and impala (*Aepyceros melampus*) in Thanda Private Game Reserve, KwaZulu-Natal. Firstly, I examine the effects of body size dimorphism, sexual segregation and predation on habitat selection and resource partitioning by ungulates. The mechanisms driving resource partitioning strategies were studied at three environmental scales, namely broader habitat (using habitat preference ratios), local environment (using Multi-Dimensional Scaling (MDS) and Analysis of Similarity (ANOSIM)) and plant (feeding heights using Analysis of Variance (ANOVA) and Regression analyses). At the habitat level, ungulates show distinct habitat preferences, independent of body size, which did not overlap, thus promote resource partitioning. Habitat selection, at the local environment level, varied among species but not between sexes. Therefore, body size class may influence selection for particular environmental characteristics. At the plant level, resource partitioning was evident among the larger species (giraffe and elephant) versus the smaller species (nyala and impala), but there was no apparent segregation among the sexes within species. Therefore, resource partitioning was strongest at the habitat level, bit less noticeable at the intermediate and finer plant scale. Secondly, I assessed the antipredator behaviour of multi-species assemblage in an experimental context (before vs. after lion reintroduction). I examined herbivore responses in terms of aggregation (forming safer groups), predator avoidance (selecting areas that predators avoid), and habitat selection in terms of habitat structure (selecting areas where capture is less likely), in response to lion reintroduction. Ungulates shifted habitats to avoid lion presence, i.e. into habitats least preferred by lion, and dominant species (based on body size) forced subordinate species into suboptimal habitats. However, counter predictions, ungulates did not increase their group size after lion were released. With the development of small private game reserves, intensive management is essential to maintain ecological heterogeneity, in this case through trophic cascades which promote coexistence. Managing ungulates as ecologically different according to body size will accommodate differences among herbivore populations. Long-term studies of habitat use by ungulates and predators will provide management with information to manipulate factors affecting habitat selection and predation, and thus sustainability of ungulate populations.

PREFACE

The study represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any other University. Where use has been made of the work of others, it is duly acknowledged in the text.

Fieldwork was carried out in Thanda Private Game Reserve, KwaZulu-Natal, under the supervision of Simon Pillinger from March 2004 – October 2005. Writing up the study was conducted in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville, from July 2006 to June 2008, under the supervision of Professor Rob Slotow and co-supervision of Bruce Page and Dr Robin Mackey.

Kirsten Canter

December 2008

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DECLARATION 1 - PLAGIARISM

I, ……………………………………..………………………., declare that

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

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication)

Publication 1: Kirsten J. Canter, Robin L. Mackey & Rob Slotow. Ungulate habitat use and aggregation in response to predator reintroduction in a relatively small private nature reserve in South Africa: A Case Study.

Publication 2: Kirsten J. Canter, Rob Slotow, Robin L. Mackey & Alain Smith. Ungulate resource partitioning at habitat, local environment and feeding levels in a relatively small private nature reserve in South Africa.

Publication 3

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CHAPTER 1
GENERAL INTRODUCTION

Within game reserves, large herbivores are an important source of revenue through hunting (van der Waal & Dekker, 2000; Leader-Williams *et al.* 2001) and ecotourism (Duffus & Dearden, 1990; Giannencchini, 1993; Ogutu, 2002). Private ecotourism ventures have led to the development of smaller, fenced, reserves (Roux, 2006) where conservation management aims to prevent the loss of biodiversity (Pelletier, 2006) by ensuring wildlife populations are maintained within economic sustainable limits (du Toit, 2002; Gordon *et al.* 2004). Understanding plant – herbivore dynamics, and thus, animal habitat requirements is key for wildlife managers to predict animal distribution (Dörgeloh, 2001) and consequently their impact on vegetation (van Aarde *et al*. 2006).

Habitat Selection

In any wildlife ecology study, knowledge of habitat selection is essential in understanding ecological systems (Henley, 2001). A number of theories dealing with habitat selection by ungulates and ungulate spatial distribution within different habitats have been developed to assist ecologists with predicting habitat selection (Rosenzweig, 1981; Druce, 2005). The core assumption within these theories is that animals utilise their environment to improve their fitness by making trade-offs between potential costs and benefits (Krebs & Davies, 1993). Habitat selection is the process whereby individuals occupy and utilise areas, within a reserve, which supply the necessary resources for survival (Morrison *et al.* 1998; Morris, 2003; Olivier, 2007). A preferred habitat type is one that is used more than expected from its availability (Aebischer *et al*. 1993; Garshelis, 2000; Alldredge & Griswold, 2006). Habitat selection and preference are also more easily understood in terms of differential use of habitat types (Garshelis, 2000). Thus, habitat use results from habitat selection, habitat selection results from habitat preference, and habitat preference presumably results from resource-specific differential fitness. (Garshelis, 2000).

Animals would attempt to maximise gains from a particular habitat by selecting vegetation types that offer maximum gains to the animal's physiology (Pulliam, 1988; Pullium & Danielson, 1991). Thus, animal physiology will influence the type of vegetation selected and these differences in physiologies of different animals will allow animals to coexist by occupying and utilising different vegetation types within a habitat (Ben-Shahar, 1998). Differential habitat selection is fundamental to coexistence among similar species (Rosenzweig, 1981). Resource partitioning is the process that allows species living in the same ecosystem to divide the resources, thus maximising the available habitat, forming competitive refuges and facilitating co-existence among species (Durant, 1998; Kozlowski 2007). Coexistence is further promoted when animals switch diets between seasons as the plant densities change (Hambäck, 1998). The different use of resources among species results in different habitat preferences, therefore resource selection is a multilevel, hierarchal decision-making process (Senft *et al.* 1987; Rettie & Messier, 2000).

Acquiring food and avoiding predators are two essential components for survival for most animals (Cowlishaw, 1997; Orians, 2000). Other factors include access to shelter and water (Orians, 2000). Animals are forced to balance these components (Lima & Dill, 1990) through the strategic use of habitats and shifts in behaviour (Lima & Dill, 1990; Brown *et al.* 1999, 2001). A habitat's quality can change rapidly, and the quality, availability and abundance of resources, which affects potential contribution of a habitat to fitness, will influence the extent of habitat use (Boyce & McDonald 1999). Any measure of habitat is variable since the vegetation is patchy, (i.e. non uniform over space and time) (Kristan, 2003; MacGregor & O'Connor, 2004; Nams, 2005). Once a patch no longer meets the animal's requirements, they will shift to a patch with superior resources (Charnov, 1976; Bailey *et al.* 1996; MacGregor & O'Connor, 2004). This mobility between patches creates spatial variation within vegetation at different levels (Laws, 1970; McNaughton, 1984). The cost to the animal of acquiring information and the time of travelling between vegetation types can be substantial (Charnov, 1976; Gross *et al*. 1995). Therefore, knowledge of habitat selection and spatial distribution of herbivores is vital to understanding spatial heterogeneity (McNaughton & Georgiadis, 1985; Schlesinger *et al*. 1990; Pastor & Naiman, 1992).

Animals respond to environmental cues, which will change over space and time (Williams & Nichols, 1984). Consequently, temporal and spatial scales affect habitat selection decisions (Orians & Wittenberger, 1991; Bailey *et al.* 1996). At the macro-habitat scale, selection may be influenced by the presence of water, vegetation type, or substrate (Druce, 2005). At the landscape level, presence, absence, or abundance of potential forage plants will influence which habitats ungulates select (Druce, 2005). Biotic and abiotic factors may determine herbivore distribution patterns at the landscape level (Redfern *et al*. 2003) as animals may have preferences for specific topographical features, for example geological formations such as rocky outcrops or cliffs or for level or sloped terrain. Soil texture may also influence plant production and plant species biodiversity (Campbell, 1986; Scholes, 1991). At the smallest micro-habitat scale, factors such as extent of cover and patch use (Orians & Wittenberger, 1991) will determine an individual's habitat choice (Druce, 2005). However, abiotic and temporal factors (i.e. season and weather conditions) may alter the nature and nutritive value of the plant community, thus altering ungulate foraging preferences (Stuth, 1991; Augustine, 2003). Knowledge of ungulate's response to environmental variations at the different scales, is crucial managing abundance and diversity (Boshoff & Kerley, 2001; Graham & Blake, 2001; Boshoff *et al.* 2002) at these scales (Druce, 2005).

Ungulates can affect vegetation community patterns and ecosystem functioning through processes such as grazing, browsing, trampling, defecation and urination (Hobbs, 1996; Mysterud, 2006; Wisdom *et al.* 2006). Ungulates may reduce forage availability by consuming vegetation and altering plant species composition (Augustine & McNaughton, 1998; Weickert *et al.* 2001). Reduction and prevention of tree and shrub regeneration, as a result of ungulates browsing in highly structured habitats (Putman, 1986; Gill, 1992), may result in long-term changes in canopy species composition and structure (Healy, 1997; Singer *et al.* 1998). Feeding, trampling, and wallowing by ungulates may reduce protective vegetation cover, thus potentially increasing the vulnerability of ungulates to predation (Grant *et al.* 1982; Bock *et al.* 1984). In general, negative impacts of ungulates on biodiversity are relatively greater for browsers than grazers (Mysterud, 2006). However, ungulate defecation can contribute to seed dispersal (Malo & Suarez, 1995; Weickert *et al.* 2001) and accelerated nutrient cycling (McNaughton, 1985). Therefore, ungulates may increase or decrease plant species richness and biodiversity, depending on factors such as grazing intensity (Hobbs & Huenneke, 1992; Mysterud, 2006) and nutrient availability (Proulx & Mazumder, 1998). The evaluation of ungulate foraging behaviour and diet will provide information towards understanding the trophic relationships of different species within ecosystems, and may provide insight into the influences ungulates have within the relatively small reserves (Bookhout, 1996; Roux, 2006).

Predation

Many ungulates shift between habitats that differ in energetic gain and risk of predation (Gilliam & Fraser, 1987; Repasky, 1996), and may be forced to forage in high risk habitats in order to satisfy their requirements (Slotow & Rothstein, 1995; Hopcraft *et al.* 2005). Predation is concurrent with foraging behaviour because ungulates are at a greater risk while foraging (Rangeley & Kramer, 1998). Predation, through intimidation, affects ungulate spatial distribution, by influencing ungulate predator avoidance behaviour (Gilliam & Fraser, 1987; Rangeley & Kramer, 1998).

The formation of herds (Bertram, 1978; Hobson, 1978; Pitcher, 1986) and utilising structured habitats as refuge areas (Finke & Denno, 2002) are common antipredator behaviours that reduce predation risk of ungulates (Sih, 1987; Lima & Dill, 1990). Antipredator behaviours of ungulates are density dependent, high densities utilise aggregation (Bertram 1978; Hobson 1978; Pitcher 1986), and low densities utilise structured habitats (Fretwell, 1972; Rosenzweig, 1986; Savino & Stein, 1989). A heterogeneous landscape will influence predation risk (Druce, 2005), where animals in areas of high perceived predation risk would alter their behaviour before animals in areas of low perceived risk (Laundré *et al.* 2001). Therefore, predation risk promotes coexistence through different habitat selection (Repasky, 1996).

Competition & Resource Partitioning

Interspecific competition and facilitation have been suggested to explain species separation and coexistence in ungulates (Sinclair & Norton-Griffiths, 1982; Roughgarden, 1983; Chase *et al.* 2002). Competition is perceived to be an evolutionary driver among species that have similar resource requirements, as one species will eventually out compete and exclude the other (Schoener, 1983). Interspecific competition has been inferred as the process that allows ecologically similar species to coexist by means of resource partitioning (MacArthur, 1970; Schoener, 1974; Chase *et al.* 2002). Interspecific competition may result in either species exclusion from its preferred habitat or encourage species to specialise in a preferred habitat type (Lawlor & Maynard Smith, 1976; Chase *et al.* 2002). In contrast, intraspecific competition may force subordinate individuals to accept suboptimal habitats, which resources are poorer quality (Pimm & Rosenweig, 1981; Latham, 1999; Orians, 2000).

Facilitation allows more than one species in a habitat to coexist (Huisman & Olff, 1998; Farnsworth *et al.* 2002). Habitat patches allow different habitat selection among herbivores, which enables niche separation and ultimately facilitates species coexistence by reducing competition between species (Schoener, 1983; McNaughton & Georgiadis, 1986; Shannon, 2006a). Therefore, competition and/or facilitation are significant factors in ecological community structure (Sinclair, 1985; Dublin *et al*. 1990).

Sexual Segregation

Sexual segregation is the separation of male and female ungulates outside the breeding season (Ruckstuhl, 2000, 2001, 2002; Mooring *et al.* 2005). Sexual segregation is evident at different levels (Conradt, 1998), where males and females occupy different home ranges (spatial), utilise different habitats within an area (habitat), exist in single-sex groups within a habitat (social) and have different foraging behaviours (diet) (Mysterud, 2000; Ruckstuhl & Neuhaus, 2000, 2002; Coulson *et al.* 2006). Hypotheses to explain the evolution of sexual segregation include differences in predator avoidance strategies (reproductive-strategy hypothesis), forage requirements (body-size hypothesis), and social activities (social factors hypothesis) (Main *et al.* 1996; Ruckstuhl, 1998, 1999; Shannon 2006b).

The Reproductive Strategy Hypothesis (Main *et al*. 1996) states that larger bodied male ungulates are less at risk of predation than the smaller bodied female and juvenile ungulates (Ruckstuhl & Neuhaus, 2000, 2002). Therefore, females select habitats, which firstly provide cover from predators, and secondly, include forage to meet their nutritional requirements (Jakimchuk *et al.* 1987; Berger, 1991; Young & Isbell, 1991). Males, on the other hand, select habitats with high forage availability so that they maximize their strength for the breeding season (Jakimchuk *et al.* 1987; Main & Coblentz, 1990, Main *et al.* 1996).

The Body size (sexual dimorphism) hypothesis (Main *et al.* 1996) states that different foraging behaviour in ungulates is explained by the difference in nutritional requirements, which is a result of differences in physiology due to body size dimorphism (Bell, 1971; Illius & Gordon, 1992; Wilmshurst *et al*. 2000). Smaller bodied females select habitats that provide high-quality forage to meet their higher nutritional requirements due to pregnancy and lactation (Stokke, 1999; Stokke & du Toit, 2000). Larger bodied males are able to utilise low quality food because of higher intake rates and longer retention times (Du Toit & Owen-Smith, 1989; Du Toit & Cumming, 1999).

The social factors hypothesis (Bon & Campan, 1996) states that sexual segregation of ungulates exists so that males and females can develop and maintain skills necessary for survival and reproduction (Conradt, 1998). Males learn fighting skills and how to establish dominance hierarchies, and females learn the general location of key resources (e.g. water, forage and suitable birthing areas) (Clutton-Brock *et al*. 1987; Conradt, 1998; Ruckstuhl, 1998, 1999).

Sexual segregation is most noticeable when the variation of high- and low-quality forage is greatest (Main *et al*. 1996). Differential habitat and forage selection, and spatial distribution by male and female groups have significant consequences for survival and reproduction since they will ultimately influence the fundamental processes of ecosystems (e.g. nutrient cycling and biodiversity) (Bowyer, 2004; Mooring *et al*. 2005). Therefore, herbivore management should vary to accommodate segregated species (Kie & Bowyer, 1999; Bowyer, 2004; Mooring *et al.* 2005).

With the development of private game reserves, intensive management to prevent habitat degradation due to the over-utilisation by herbivores has become an important part of conservation planning (Behr & Groenewald, 1990; Bothma, 1995; Van Rooyen *et al*. 2000). Animals live in a heterogeneous environment (Real, 1991) and localized impacts on vegetation, changing vegetation structure and composition affect the biodiversity and habitat suitability for other species (Gordon *et al.* 2004). Most management strategies focus on the management at the population level (Gordon *et al.* 2004). Effective management strategies should consider ungulate responses at different scales, include individual to population interactions (Gordon *et al.* 2004), and acknowledge that species, on the basis of sex, are ecologically different (Bowyer, 2004; Gordon *et al.* 2004). Therefore a holistic view, incorporating abiotic and biotic factors, will produce the most effective management system.

Aims & Objectives

The aims of this study were: (1) to investigate the habitat selection strategies by ungulates within a small reserve; (2) determine the role of sexual dimorphism on habitat selection at various scales; and (3) examine the effects of predation on habitat selection by ungulates.

The purpose of chapter two was to investigate the effect of body size on ungulate habitat presence, to explain competition, facilitation and resource partitioning among ungulates. I examined three levels of scale namely habitat, local environment and feeding level. This provided information on how animals, of differing body sizes, selected specific environmental characteristics at different levels. Chapter three investigated ungulate responses to predator introduction. This chapter examined common ungulate antipredator behaviours based on habitat characteristics and predator awareness, where a multi-species assemblage was assessed in an experimental context (before vs. after lion reintroduction). The final chapter unifies the previous chapters, highlighting the key factors driving habitat selection. This research will undoubtedly provide insight for conservation strategies as well as effective management tools regarding the dynamics of ungulate and predator populations.

CHAPTER 2

STUDY AREA & ANIMALS

Study Area

The 50 km^2 Thanda Private Game Reserve (TPGR), situated in northern Zululand (Figure 1), South Africa (27^{o}52' S; 32^{o}10' E), was established in 2002. The mean annual rainfall is 610 mm (range is 400-700 mm). Rainfall is highly seasonal, with peaks in February, and lowest levels in July, however, during the study, there were relatively low rainfall. The climate is warm to hot, with the mean minimum of 5^{o}C and mean maximum of 38^{o}C. Prior to establishment in July 2002, cattle were present on the reserve. Old cotton fields, created by histrorical farming practices, were left undisturbed to return to natural veld. The data collection study period was March 2004- October 2005. Ungulate densities were below carrying capacity (Brousse-James & Associates, 2002)

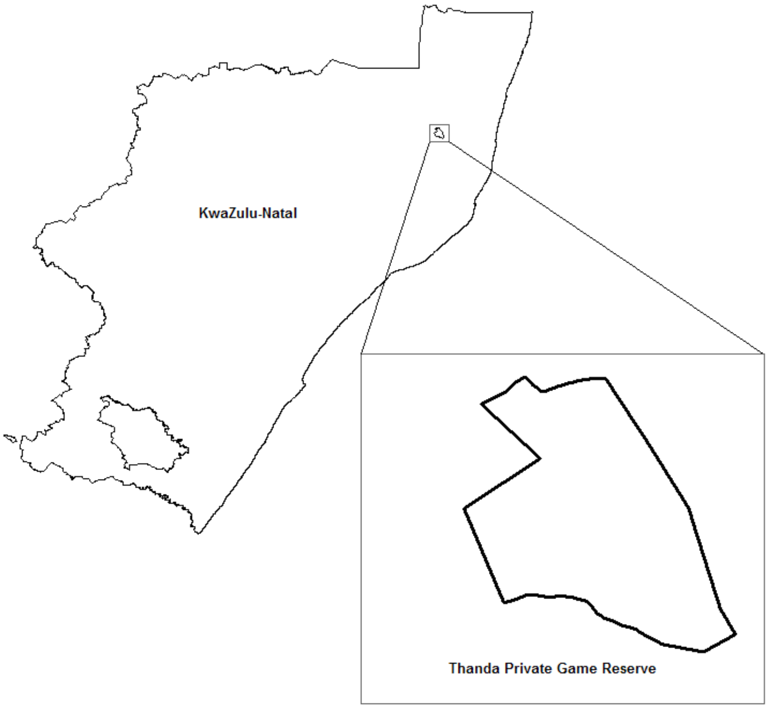

Figure 1: The location of the Thanda Private Game Reserve (TPGR) in KwaZulu-Natal, South Africa.

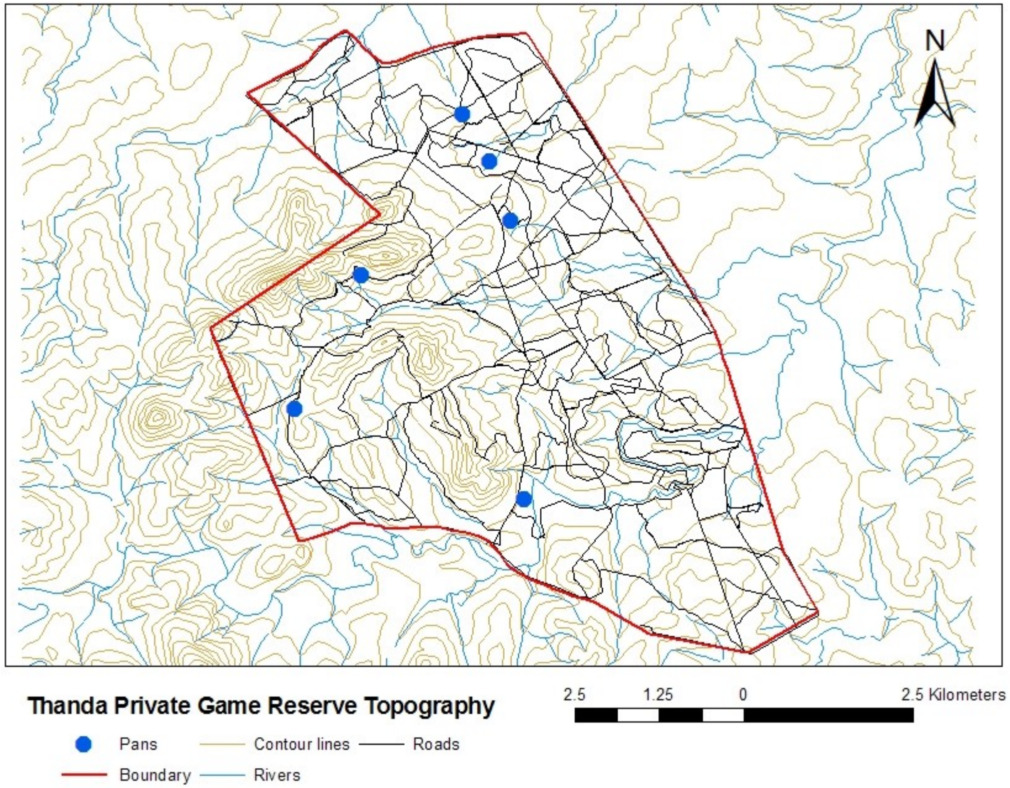

Figure 2: Thanda Private Game Reserve topography and occurrence of pans and streams.

There are two major streams in TPGR, but neither hold perennial water. There are four pans in the reserve, which are supplemented from boreholes to establish permanent surface water. The furthest distance an animal needs to walk to find water is 4.2 km, therefore, water was not a limiting factor in habitat preference, i.e. all parts of the reserve were available for use, even by water-dependent species.

The elevation of TPGR varies from 137 m on the eastern boundary to 438 m in the hills along the western boundary. Two major relief units exist: the western portion has high relief and ridge tops being formed by breccia and quartz porphyry dykes, while the eastern half which has a gentle undulating low relief on a predominantly basalitic landscape (Brouse-James & Associates, 2002). The western relief unit, which acts as the source of a number of small ephemeral streams, has deep valleys and a moderate drainage pattern. The eastern relief unit of TPGR is flat with shallow valleys.

The vegetation communities can be classified broadly as Lowveld Bioregion (SV1BRG22) according to Mucina & Rutherford (2006). The dominant trees which characterise Lowveld include *Acacia nigrescens, A. tortillis, A. burkei, Schotia brachypetala, Spirostachys africana, Sclerocarya birrea* and *Ziziphus mucronata* (Brousse-James & Associates, 2002). Grass species include *Themeda triandra*, *Panicum coloratum, P. maximum, P. deustum*, and *Setaria incrassate* (Brousse-James & Associates, 2002). A vegetation map was created by Brousse-James & Associates (2002), containing 14 different vegetation categories (Appendix A.1.). I simplified their vegetation map using situation on the slope (lowland, midslope or uplands) and structure (woody plant density), into five categories including three low-density categories (lowland woodlands, upland woodlands, old cultivated lands) (maximum habitat structure of 50% cover) and two high density categories (midslope woodlands, riverine) (minimum habitat structure of 50% cover) (Figure 2). Riverine and old lands were kept separate because they differed from the woodland habitat structure. Old lands were created by historical farming practices (old cotton fields prior to 2002) which have been left undisturbed to return to natural veld. Bush encroachment was evident within these old lands. The riverine habitat is a separate ecosystem, with lush, dense vegetation along to the drainage line. Vegetation characteristics of the five habitat categories are described in Appendix A.2.

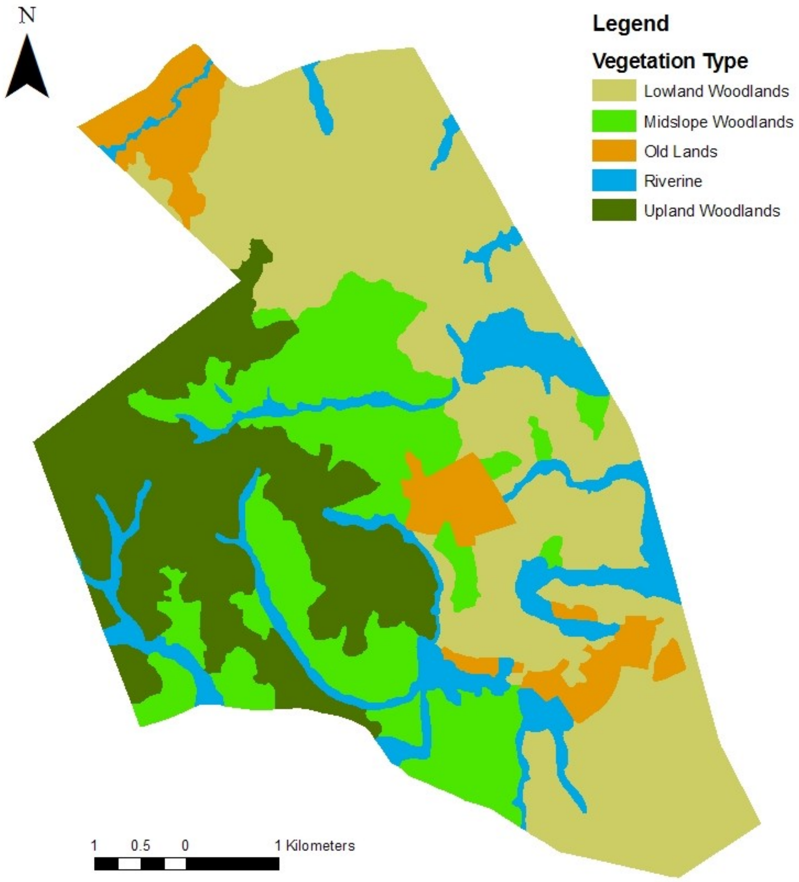

Figure 3: Simplified habitat types in TPGR based on the vegetation map by Brousse-James & Associates (2002) (Appendix A.1.).

Study Animals

The African elephant (*Loxodonta africana*) is an unspecialised, mixed feeder (Owen-Smith, 1988; Codron *et al.* 2006) preferring grazing to browsing (Van Soest, 1994; Codron *et al.* 2006) due to their large body size (Laws, 1970; Demment & van Soest, 1985). Elephants are extremely adaptable, occupying a variety of habitats (Laursen & Bekoff, 1978; Owen-Smith, 2004); however, water (preferably fresh) and shade, in which to shelter during the hottest hours of the day (Poole, 1996), are essential habitat requirements. Sexual dimorphism is obvious in elephant with an adult female mass being 3,000 kg (Poole, 1994; Spinage, 1994), half the size of an adult male (6,000 kg) (Laws & Parker, 1968; Laws, 1969). Elephant are sexually segregated throughout the year, unless males join the breeding herd to mate (Poole & Moss, 1981; Poole 1987, 1989). In 2002 a breeding herd of 10 individuals was introduced to TPGR. Two adult bulls were introduced in 2003 (Table 1). One young bull from the family group died in 2003, therefore for the duration of the study (March 2004 – October 2005) there were 11 elephants (Table 1). Each adult bull had a VHF collar, which allowed for tracking their location on a daily basis using telemetry. The matriarch had a VHF/satellite collar, where her location was downloaded once a day via satellite, and telemetry could be used to track her location.

Giraffe (*Giraffa camelopardalis*) are selective browsers, able to reach up to 5 m (Pellew, 1984; Young & Isbell, 1991). Sexual segregation is evident in feeding heights as males can feed 45cm higher than females (Pellew, 1984; Young & Isbell, 1991; Ginnett & Demment, 1999). Giraffe are non-territorial and gregarious, with no obvious sexual segregation (Young & Isbell, 1991; Ginnett & Demment, 1999). Their large body size renders it unnecessary for them to aggregate for mutual security (Omphile & Powell, 2006). Giraffe were introduced to TPGR in 2002 (n = 17) and 2003 (n = 5) (Table 1). The Giraffe population increased at a high rate because of the high fecundity and lack of predation to approximately 25 animals in 2005 (including mortalities and births) (Table 1).

Greater kudu (*Tragelaphus strepsiceros*) are predominantly browsers, although they are able to tolerate many plants generally avoided by other browsing species or known to be poisonous (Owen-Smith, 1997; Garine-Wichatisky *et al*. 2004). They are sexually dimorphic with males reaching a shoulder height of 1.25-1.5 m and weight of 200-315 kg; while females only reach 1–1.4 m shoulder height and weigh 120-200 kg (du Toit, 1995). Kudu are usually sexually segregated into male and female herds, with males joining the herds during the mating season (June) (du Toit, 1995). The need for concealment limits kudu habitat choices, partially offset by the ability to live in waterless areas (Owen-Smith, 1997; Dörgeloh, 2001; Owen-Smith & Mills, 2008). Kudus generally concentrate along drainage lines and valleys (Owen-Smith, 1994; Garine-Wichatisky *et al*. 2004). Kudu were naturally occurring in TPGR, however additional kudu were introduced in 2002 (n = 9); 2004 (1 bull); and 2005 (n = 14) (Table 1). Upon lion release (2004) the kudu population was approximately 60 animals (including births and mortalities) (Table 1).

Nyala (*Tragelaphus angasii)* are mixed feeders, feeding on leaves, twigs, flowers, a variety of fruits, and grass, especially when it is fresh after rain (Grunow, 1980; Van Rooyen, 1993). Nyala are sexually dimorphic with larger males (95-125 kg weight; 1.05 m shoulder height) and smaller females (55-60 kg weight; 90 cm shoulder height) (Kirby *et al.* 2008). Nyala breed throughout the year, and occur in single sex or mixed herds (van Rooyen, 1993; Kirby *et al.* 2008). Nyala are generally associated with thickets and densely wooded areas, with habitat preferences overlapping with kudu, common and red duiker, and bushbuck (Van Rooyen, 1992; Owen-Smith, 1997). Water is not an apparent essential habitat requirement, however, where it is available they drink daily (Kirby *et al.* 2008). No nyala were introduced to TPGR as populations were abundant. Nyala were removed (live capture) in 2003 (n = 93); and 2004 (n = 7). The population estimate in 2005 was approximately 600 animals (Table 1).

Impala (*Aepyceros melampus*) are mixed feeders (Van Rooyen, 1992; Brashares & Arcese, 2002), although browse forms the majority of their diet (Van Rooyen, 1992; Garine-Wichatisky *et al*. 2004). Sexual segregation is evident in the herd structure, with the females living in breeding herds (5-35 individuals), and males in bachelor herds (5-15) (Brashares & Arcese, 2002). Impala males are territorial during the breeding season. Bachelor herds are however formed during the rest of the year. Impala thrive in areas where the natural vegetation has degenerated because of overgrazing or bush encroachment (Augustine, 2004; Garine-Wichatisky *et al*. 2004; Van Bommel *et al.* 2006) and are dependent on the availability of drinking water (Augustine, 2004; Van Bommel *et al.* 2006). No impala were introduced during the study and the population estimate was 1 150 impala in 2005 (Table 1).

The benefit of using these species for this study includes their morphological and behavioural adaptations to the habitat. These ungulates, because of their low densities in TPGR, are able to exploit favourable conditions and are not limited to specific habitats by the availability of water (due to the size of the reserve and distributions of water points), which results in a distribution that reflects responses to current environmental conditions. These ungulates also vary in body size both between and within species. These ungulates will adjust their diet, spatial movements and predator awareness in response to the changes in the environment, therefore making it possible to evaluate their optimal habitat selection.

Table 1: Species introductions and population estimates for TPGR (Brousse-James & Associates, 2002; Brousse-James & Associates, 2002, 2003, 2004; 2005).

Species		**2002**		**2003**		**2004**		**2005**	
Common Name	**Latin Name**	**Introduced**	**Population Estimate**	**Introduced**	**Population Estimate**	**Introduced**	**Population Estimate**	**Introduced**	**Population Estimate**
Buffalo	*Syncerus caffer*	20	20	7	27	5	33		39
Bushbuck	*Tragelaphus scriptus*						10		10
Cheetah	*Acinonyx jubatus*	5	5		5		2	1	4
Duiker Common	*Sylvicapra grimmia*		30		58		25		23
Duiker Red	*Cephalophus natalensis*		15		217		29		43
Elephant	*Loxodonta africana*	10	10	2	12		11		11
Giraffe	*Giraffa camelopardalis*	17	17	5	20		23		25
Impala	*Aepyceros melampus*		800		623		1193		1296
Kudu	*Tragelaphus strepsiceros*	9	50		50	1	62	14	72
Leopard	*Panthera pardis*				2	1	3		3
Lion	*Panthera leo*					4	3	2	4
Nyala	*Tragelaphus angassi*		340		987		296		590
Reedbuck Common	*Redunca arundinum*		30		30		30		30
Reedbuck Mtn	*Redunca fulvorufula*						20		20
Steenbuck	*Raphicerus campestris*		10		40		21		24
Warthog	*Phacochoerus africanus*		80		161		234		297
Waterbuck	*Kobus ellipsiprymnus*	14	14		14		16		23
White Rhino	*Ceratotherium simon*	3	3	2	5	2	6		8
Wild dog	*Lycaon pictus*					2	2		2
Wildebeest Blue	*Connochaetes taurinus*	60	64	48	87		129		157
Zebra	*Equus burchelli*	17	8	39	56	44	95		122

Population estimates included mortalities, births and introductions

CHAPTER 3

UNGULATE RESOURCE PARTITIONING AT HABITAT, LOCAL ENVIRONMENT AND FEEDING LEVELS IN A RELATIVELY SMALL PRIVATE NATURE RESERVE IN SOUTH AFRICA

Abstract

The differences in African ungulate body size will determine differential utilisation of resources at different scales for elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), nyala (*Tragelaphus angasii)*, and impala (*Aepyceros melampus*) in TPGR. I examined the effects of body size on resource partitioning at three spatial scales, namely habitat (using habitat preference indices), local environment (using MDS and ANOSIM) and plant (feeding heights using ANOVA and regression analyses) scales. The ungulates studied showed distinct habitat partitioning, which did not overlap, thereby reducing competition and enhancing resource partitioning at the habitat level. The habitat preference rankings for the different body size classes were not concordant among species, nor sex, i.e. habitat selection at the habitat level was independent of body size class. Habitat selection, at the local environment level, showed segregation among species but not between sexes. Therefore, body size class may influence selection for a particular environmental characteristics. Giraffe and impala were more general in their selection of local environment characteristics, when compared with elephant and nyala. At the plant scale, there was distinct segregation in feeding heights among the larger species (giraffe and elephant) versus the smaller species (nyala and impala), but no sexual segregation was evident. Thus, resource partitioning was influenced by body size at the plant level (feeding heights). Resource partitioning was therefore strongest at the largest spatial scale (habitat), less noticeable at the intermediate scale (local environment), and relatively coarse when present at the plant scale (feeding heights). Ungulates should be managed in order to accommodate differences between herbivore populations as ecologically different according to body size. To retain the complete ungulate suite, particularly in small reserves, management should focus on promoting resource partitioning through maintaining habitat heterogeneity.

Introduction

Habitat selection is a multilevel process, as environments offer potential opportunities and hazards, which vary with scale, within diverse spatial heterogeneities, (Johnson, 1980; Orians, 1991). The fitness of a habitat is affected by the quality and abundance of resources, which will influence habitat utilisation (Boyce & McDonald, 1999). At the largest scale (macro-habitat), habitat selection may be influenced by the presence or absence of water, vegetation type or substrate (Melton, 1987; Orians, 1991). However, patch use and available forage will determine individual habitat choice at the smallest scale (micro-habitat) (Orians, 1991; Vernes, 2003). Knowledge of ungulate response to environmental variations at the different scales is essential to manage diversity and vegetation abundance (Boshoff & Kerley, 2001; Graham & Blake, 2001; Boshoff *et al.* 2002) at each scale or level (Cumming *et al.* 2006) i.e. emphasize importance of avoiding mismatch.

Understanding coexistence among species within the same environment, but with different resource use, has long provided a challenge for ecologists (Lamprey, 1963; Ferrar & Walker, 1974; Sinclair, 1977). Ungulates may coexist by using different types of food, foraging heights, activity times or areas, or because of allometric physiological differences (Smith, 1990; du Toit & Cumming, 1990; Main *et al*. 1996). The mechanism whereby many species coexist within a habitat, and are able to select resources to satisfy their requirements, is resource partitioning (McNaughton & Georgiadis, 1986). Ungulates vary their distribution over space and time, shift habitats to optimise seasonal plant composition changes, and differentiate their feeding behaviour in response to available plant species (McNaughton & Georgiadis, 1986). Two major physiological adaptations that can be used to classify ungulates on the basis of resource partitioning are animal forage behaviour (for example graze or browse (McNaughton & Georgiadis, 1986)) and method of digestion (ruminant vs. non-ruminant (Van Soest, 1996)).

The physiological and metabolic requirements of an animal influence foraging behaviour (Sinclair & Gwynne, 1972; McNaughton & Georgiadis, 1986). Body size imposes constraints on physiology which influence the nutritional requirements of an animal (Owen-Smith, 1988; Bailey *et al.* 1996; Demetrius, 2000), which will affect resource use (Ben-Shahar, 1998). Body size differences among animals influence habitat utilisation and foraging behaviour due to allometric relationships associated with increasing body size (Ruckstuhl, 1998; Barboza & Bowyer, 2000; Stokke & du Toit, 2000; 2002). Thus, larger herbivores are able to tolerate a wider range of forage quality (Jarman-Bell principle) (Bell, 1971; Jarman, 1974), and tend to be more generalist in their foraging approach, than smaller herbivores which target fewer plant species and tend to feed selectively (Bell, 1971; Stokke & du Toit, 2000; Shannon *et al.* 2006b).

Sexual dimorphism, where males differ in size from females, influences spatial and foraging ecology (Main *et al.* 1996; Bowyer 2004; Mooring *et al.* 2005). Female and juveniles have higher nutritional requirements due to pregnancy and lactation (Du Toit & Owen-Smith, 1989; Du Toit & Cumming, 1999), and therefore select habitats that provide high-quality forage to satisfy their requirements (Stokke, 1999; Stokke & du Toit, 2000). Larger bodied males are able to utilise low quality food because of higher intake rates and longer retention times (Du Toit & Owen-Smith, 1989; Du Toit & Cumming, 1999). Sexually dimorphic species are able to reduce intra-specific competition as males are able to feed at greater heights than females (Pellew, 1984). This is evident in nyala *Tragelaphus angasi* (Kirby *et al.* 2008), elephant *Loxodonta africana* (Poole, 1994; Shannon *et al.* 2006b) and giraffe *Giraffa camelopardalis* (Pellew, 1984). Therefore, sexes may perceive their environment and feeding opportunities differently (Houston & Shine 1993; Ruckstuhl 1998; Kie & Bowyer 1999).

Resource partitioning was attributed to the selection of specific characteristics within the vegetation, which were essential in supplying the required resources to the animal (Brown & Alkon, 1990; Wilmshurst *et al.* 1999). Here I examined the effect of body size of a range of ungulates in a relatively small game reserve across a range of spatial scales at which resource partitioning occurred, i.e. at the habitat, local environment or feeding level. At the habitat level, I expected ungulates to minimise competition by utilising different vegetation types. At the local environment, where ungulates were selecting specific habitat characteristics, I expected the smaller bodied ungulates to be more selective of resources. I tested the feeding height hypothesis which states that feeding height differences between species facilitates resource partitioning. I predicted that the larger bodied ungulates feed higher than smaller bodied ungulates. I determined whether sexual segregation was evident at the three spatial scales, which may influence the level of intraspecific competition, and thus coexistence of this diverse species suite.

Methods:

The 50-km^2 Thanda Private Game Reserve (TPGR), situated in northern Zululand, South Africa (27^{o}52’ S; 32^{o}10’ E), was established in 2002. The environment is semi-arid with temperature ranges between 5-35^{o}C and a mean annual rainfall of 400-700 mm. Rainfall is highly seasonal, with levels lowest in July and peaking in February. There are two main seasonal streams, and four natural pans which are supplemented from boreholes to establish permanent surface water. The furthest distance an animal needs to walk to find water is 4.2 km, therefore, water was not a limiting factor in habitat distribution, i.e. all parts of the reserve were available for use, even by water-dependent species. The vegetation communities can be classified broadly as Lowveld bioregion (SVI) according to Mucina & Rutherford (2006). The dominant trees which characterise Lowveld include *Acacia nigrescens, A. tortillis, A. burkei, Schotia brachypetala, Spirostachys africana, Sclerocarya birrea* and *Ziziphus mucronata*. A vegetation map was created by Brousse-James & Associates (2002), containing 14 different vegetation categories (Appendix A.1). I simplified their vegetation map using situation on the slope (lowland, midslope or uplands) and structure (woody plant density), into five categories including three low-density categories (lowland woodlands, upland woodlands, old cultivated lands) (maximum canopy cover of 50% cover) and two high density categories (midslope woodlands, riverine) (minimum canopy cover of 50% cover). Riverine and old lands were kept separate because they differed from the woodland habitat structure. Old lands were created by historical farming practices (old cotton fields) which have been left vacant to return to natural veld. The riverine habitat is a separate ecosystem, with lush, dense vegetation due to the drainage line.

Herbivore observations were made during daylight hours (winter: 07h00 – 17h30; summer: 05h30 – 18h30) along road transects (pers. obs). A systematic search pattern (routes) was laid down to cover the entire area of TPGR, thus avoiding sampling bias. The choice of which routes to drive on each day was randomised to prevent autocorrelation of data by evening out the sampling effort among routes (Stokke & du Toit, 2002). The hottest hours of the day (winter: 11:30 - 14:00; summer: 10:30 - 15:30) were excluded as animal activity was minimal (Owen-Smith, 1998). Data were therefore collected where activity peaked i.e. the early morning and late afternoon (Owen-Smith, 1998). Areas that were densely vegetated made it difficult to see the animal, resulting in fewer sightings in these areas. Therefore, I calculated the visible area along the road, to account for difficulties in spotting animals due to differences in habitat density. The visible area was measured in summer, when the chance of spotting an animal obscured by the lush vegetation was lowest. A GPS location was recorded at the furthest visible point perpendicular to the road. The procedure was performed on the left and right side of the road, at 75-100 m intervals along the road or when the habitat changed (n = 1212 points used to create visibility profiles). I imported these points into ArcView 3.3 (ESRI, New Dehli, India) where the X-tools extension was used to calculate the visible area along each transect. I assigned habitats to each sighting by performing a spatial join of the habitat and location data. I calculated the visible area across the reserve (m^2) for each habitat type.

Feeding data were recorded when the ungulate species were foraging, but not when they were alarmed or on the move. If the animal was not feeding, I waited until feeding was initiated and ceased recording when the animal moved off or fed on another plant species. If there was a group of animals foraging, a focal animal was selected to represent the group foraging behaviour (Altmann, 1974; du Toit & Cumming, 1990). At each observation, I recorded sex (male vs. female), age (adult, sub-adult, and juvenile), plant species, feeding mode (browsing, grazing), and feeding height (m).

Once the animal(s) moved off, I completed a Point Centre Quadrat (PCQ) (Mitchell, 2001) on the browsed vegetation. The recently browsed woody plant was at the PCQ centre (n = 139). The plant fed upon was identified; the height, height below canopy, and feeding height were recorded. The PCQ data were used to measure the relative vegetation density (Mitchell, 2001), which was analysed to determine whether there were differences in forage resources available to ungulates and what characteristics were selected (Glover & Mitchell, 2001; Mitchell, 2001; Sparks *et al.* 2002). An animal standing in the centre of the quadrant should be potentially aware of and able to reach each food type within the area described by the PCQ. Data on food types eaten within each PCQ together with available browse are therefore assumed to reflect the animal's diet choice (Stokke, 1999). In instances where animals were located, but did not resume browsing, the animal's location became the centre point of the PCQ (n = 159). This was to show animal habitat occupation, which would assist in determining habitat preferences.

For each PCQ, I recorded a woody plant species at three height classes (< 0.5 m; 0.5 - 1.5 m; > 1.5 m) in each quadrant. For each plant species, I noted plant height, height below canopy and distance to the centre point. In a 2 x 2 m quadrant from the PCQ centre point, rock and grass cover were measured as the percentage of total cover, and grass height was measured in meters. I used a GPS to determine the aspect, and gradient was categorised into 4 classes (1 = flat, 2 = shallow, 3 = medium, and 4 = steep). I assigned habitats to each PCQ quadrant by performing a spatial join of the habitat and location data in ArcView 3.3 (ESRI, New Dehli, India). The PCQ method provides the least variable results for distance measures (Cottam & Curtis, 1954), however it may underestimate trees with low frequencies and overestimate dominant tree species (Mitchell, 2001).

Statistical Analysis

To test the effect of body size at each level (habitat, local environment, and feeding height), I combined the sex and species into one category of body size from largest to smallest e.g. 1 = elephant bull; 2 = elephant cow, etc. This provided a way to compare different body sizes, as different species and sexes had varying body sizes. Given the nature of the data, and the small sample sizes, it was not possible to combine all spatial scales into a single analysis, with scale as a factor.

To test whether ungulates were using the available habitats (lowland woodlands, midslope woodlands, upland woodlands, old lands and riverine) at random, I used a Chi-Square Test. I did not separate male and female giraffe as they were monitored in mixed herds. I assessed habitat preference for each body size class using preference ratios (Viljoen, 1989; Shannon *et al*. 2006a). These were calculated as the proportion of locations within a particular habitat divided by the proportion visible area of that specific habitat type within the reserve (based on our visibility profiles) (i.e. (number of sightings (in habitat) / total number of sightings (species)) / (visible area (for specific habitat) / total visible area of all habitats). If the preference ratio was 1, the habitats were used in direct proportion to their occurrence within the reserve. If the preference ratio was greater than 1, preference for a specific habitat was suggested. If, however, the preference ratio was less than 1, the specific habitat was avoided. The preference ratio thus provided a method of contrasting habitat use among size classes, with any possible biases being consistent for our contrasts. I used Kendall's coefficient of concordance (Siegel & Castellan, 1988) to assess the habitat preference ranking separately for body size class, and then for species. I used a Spearman's correlation to examine whether different sexes (within a species) were selecting habitats in a similar ranking.

From the PCQ data, I separated the woody vegetation according to height class and absolute density of each species (Mitchell, 2001). For the three height classes (< 0.5 m; 0.5 - 1.5 m; > 1.5 m), a database was constructed showing the plant density at each PCQ, animal species and sex, and local environment characteristics (rock and grass cover, grass height, aspect, and gradient). I used an arcsine transformation to convert the percentage data from grass and rock cover, to normalise data. I used an ordination analysis (Multi-dimensional scaling (MDS) analysis) in Primer (Version 5.1) (Clarke & Gorley, 2001) to determine whether animals of differing body size (categorised by species and sex) were selecting habitats based on different local environmental characteristics (gradient, aspect, rock cover, grass cover, grass height, density < 0.5 m, density 0.5-1.5 m, density > 1.5 m). I varied the number of variables (local environmental characteristics (n = 8)) for each run of the analysis to detect which local environmental characteristic caused a separation in habitat selection among the body size classes. I converted the data to a Bray-Curtis similarity matrix, and then ran a multi-dimensional scaling analysis. The stress value was calculated and a two dimensional ordinal plot detects trends in similarity (Clarke & Warwick, 2001). Points that are close together represent samples that are very similar in composition. I ran an ANOSIM (analysis of similarity) (Clark, 1993) to determine whether any grouping according to the body size class was evident at the local environmental level using the Bray-Curtis Similarity matrix that was created for the MDS analysis.

To assess changes in feeding height (browsing data only), for different body size classes among different habitat types, I used a 2-way ANOVA (data were normally distributed, Kolmogorov-Smirnov test, P > 0.05) (n = 96 sightings). The independent variables were body size classes and habitats. I used a linear regression to determine the relationship between feeding heights and body size class (ranked from largest to smallest). To determine differences in feeding heights between sexes I separated the body size class into two categories according to species and sex. I used a 2-way ANOVA (data were normally distributed, Kolmogorov-Smirnov test, P > 0.05) (n = 96 sightings) to test differences in feeding heights between sexes.

Results

Habitat Level

Male elephant (male: $\chi^2_{4,36} = 11.78$, $p < 0.019$), giraffe (male: $\chi^2_{4,29} = 46.45$, $p < 0.0001$; female: $\chi^2_{4,26} = 107.84$, $p < 0.001$), and impala (male: $\chi^2_{4,57} = 28.53$, $p < 0.0001$; female: $\chi^2_{4,53} = 40.30$, $p < 0.0001$) showed significant habitat preferences, as they did not use habitats in a random fashion. Both male and female nyala (male: $\chi^2_{4,42} = 6.81$, $p = 0.146$; female: $\chi^2_{4,37} = 9.35$, $p = 0.053$), and female elephant used habitats randomly ($\chi^2_{3,6} = 0.67$, $p = 0.881$), but the latter could have been a result of few samples (n = 6).

In terms of habitat preference ratios (Figure 1), elephant males preferred old lands (Preference Index (P.I.) = 3.2), used lowland woodlands, midslope woodlands, and riverine areas in equal proportion to the habitat occurrence (no preference), but avoided upland woodlands. Female elephant preferred upland woodlands (P.I. = 2.7), but avoided lowland woodlands and riverine

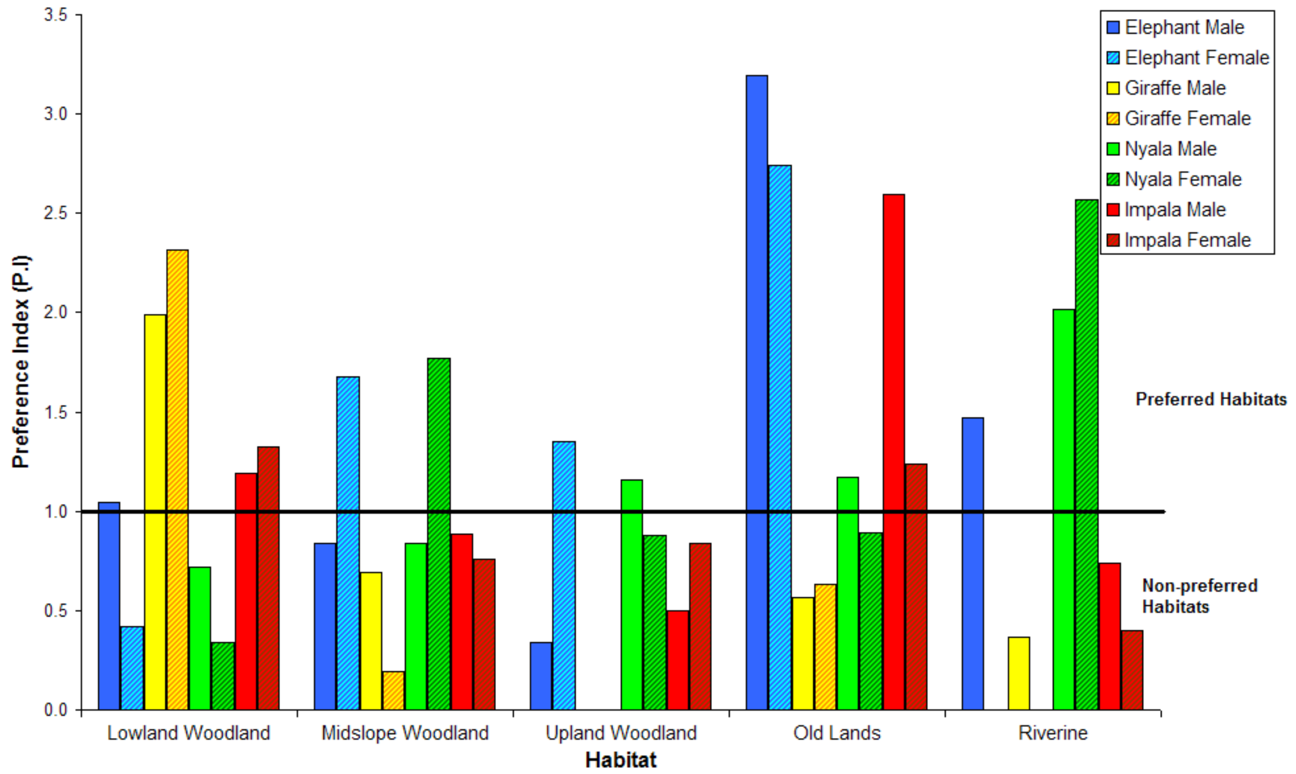

Figure 1: Preference indices for each ungulate species within each habitat category in TPGR. Preference indices were calculated as the proportion of locations within a habitat divided by the proportion of visible habitat types within TPGR. Any index above 1 would indicate a preference; similarly any index less than 1 would indicate avoidance of the habitat. Any index equal to 1 would indicate that the habitat was used in proportion to its occurrence.

areas. Both male and female giraffe preferred lowland woodlands (P.I. = 2.0 and 2.3 respectively), and avoided upland woodlands, riverine (no sightings) and midslope woodlands (n = 6). Both male and female nyala preferred riverine (P.I. = 2.0 and 2.6 respectively), and female nyala avoided lowland woodlands, a less dense habitat. Male impala preferred old lands (P.I. = 2.6), and avoided upland woodlands. Female impala had no preferred habitat, but avoided riverine areas.

Body size classes (species and sex) had different habitat preferences i.e. ranked habitats differently (Kendall's W test of concordance: W = 0.257; P = 0.740) (Table 1). Impala males were the most similar in habitat preference rankings when compared with other species (Bonferonni p = 0.070). The habitat preference ranking of the ungulate species was not concordant (W = 0.388; P = 0.202), which meant that each species had independent habitat preference rankings (Table 2).

There was no correlation of habitat preference rankings between sexes (within species) (Table 3). Therefore, the preference rank order of male (within species) was not correlated with female (within species) (e.g. impala: $r_s = 0.60$; p = 0.285) (Table 3). I expected male and female giraffe habitat preferences to be similar, as sexual segregation occurs infrequently within this species (Young & Isbell, 1991; Ginnett & Demment, 1999), however this was not the case (giraffe: $r_s = 0.872$; p = 0.054).

Local Environment Level

From the multi-dimensional scaling (MDS) analysis there was segregation (or grouping) in body size classes (n = 159; stress value = 0.06) (Figure 2). The ANOSIM analysis showed significant differences in habitat selection at the local environment level between species (R = 0.071; p < 0.001). There was no significant differences in habitat selection at the local environment level between sexes (R = 0.05; p = 0.369). Therefore habitat selection strategies, at the local environment level, follow those at the habitat level, where there are differences among species, but not between sexes. However, these patterns, although significant, were not strong as there was clearly a lot of scatter within each species/sex, and overlap among species/sex (Figure 2).

Table 1: Habitat selection concordance among body size classes at TPGR for the period March 2004 – October 2005. Results from Kendall's W test of concordance for different body size classes. I compared the habitat preference rankings (n = 5) for each body size class (n = 8).

Body Size Class	**W**	**Bonferroni Probability**	**Conclusion**
Impala Female	0.497	0.070	No concordance
Impala Male	0.228	3.407	No concordance
Nyala Female	-0.008	5.326	No concordance
Nyala Male	-0.002	5.334	No concordance
Giraffe Female	0.381	1.109	No concordance
Giraffe Male	0.297	2.312	No concordance
Elephant Female	0.263	2.735	No concordance
Elephant Male	0.407	0.830	No concordance

H_o = the eight body size classes are concordant with one another. The habitat preference rankings were calculated using the preference ratios. The Friedman's Chi-square tests the overall concordance of habitat rankings by different body size classes. The Kendall's W concordance test assumes there the body size classes were independent and tests each body size class in relation to the rest of the classes. The Bonferroni correction is a statistical adjustment for the multiple comparisons thereby examining a wide range of hypotheses simultaneously. The overall Kendall W = 0.257; X^2 = 0.07939, which suggests that we reject the H_o, and therefore conclude that body size classes have different preferences (i.e. ranking habitats differently).

Table 2: Habitat selection similarity among species in TPGR for the period March 2004 – October 2005. Results from Kendall's W test of concordance for different species. I compared the habitat preference rankings (n = 5) for each species (n = 4).

Species	**W**	**Bonferroni Probability**	**Conclusion**
Impala	0.175	1.368	No concordance
Nyala	0.400	2.450	No concordance
Giraffe	0.425	1.251	No concordance
Elephant	0.550	0.458	No concordance

H_o = the four species are concordant with one another. The habitat preference rankings were calculated using the preference ratios. The overall Kendall W = 0.388; $X^2 = 0.202$, which suggests that we reject the H_o, and therefore conclude that species have different preferences (ranking habitats differently).

Table 3: Habitat selection correlation between sexes (within species) in TPGR for the period March 2004 – October 2005. Results from the Spearman correlation on habitat preference ratios for the two sexes within a species.

Species	r_s	**P**	**Conclusion**
Elephant	0.100	0.873	No correlation
Giraffe	0.872	0.054	No correlation
Nyala	0.700	0.188	No correlation
Impala	0.600	0.285	No correlation

H_o = the sexes within a species are correlated (rank habitats similarly). I compared the habitat preference rankings (n = 5) for each sex (n = 2) within a species. Spearman correlation ranks the data, which was necessary as I was comparing the rankings of habitats within species.

Feeding Level

There was a significant difference in feeding heights for the different body size classes (ANOVA: $F_{6,64} = 9.180$; $p < 0.001$), where elephant and giraffe (both males and females) were browsing at significantly higher levels than impala and nyala (Figure 3). The post-hoc LSD test confirmed that elephant (both male and female) feeding heights were significantly different from male giraffe, and nyala and impala males and females. Giraffe males fed at significantly different feeding heights to all other body size classes, with the exception of giraffe females. Giraffe females fed at different heights to both nyala and impala (males and females); however, there were non significant differences between giraffe females and elephant (males and females) and giraffe males. Nyala (males and females) and impala (males) were feeding at significantly different levels to elephant (males and females) and giraffe (males and females).

There was a significant linear relationship between body size classes and feeding heights ($n = 148$; $R^2 = 0.107$; $p < 0.001$). There were no significant differences in feeding heights between the sexes ($F_{1,96} = 1.319$; $p = 0.254$), nor among different habitat types ($F_{4,64} = 0.980$; $p = 0.425$).

Discussion

Animal foraging behaviour is a major feature in habitat studies (Okiria, 1980, Dekker *et al.* 1996; Perrin, 1999), where animals select optimal habitats to maximise gains to their physiology (Sinclair & Gwynne, 1972; Pullium, 1988; Pullium & Danielson, 1991). Differences in requirements between different species and sexes, attributed to physiological factors related to body size in ungulates (Main *et al.* 1996), will cause different species to occupy and exploit different vegetation types. Therefore, differences in physiology and body size will influence habitat selection, with larger species able to tolerate a wider range of vegetation types than smaller species (Jarman, 1974; Bell, 1971; Geist, 1974).

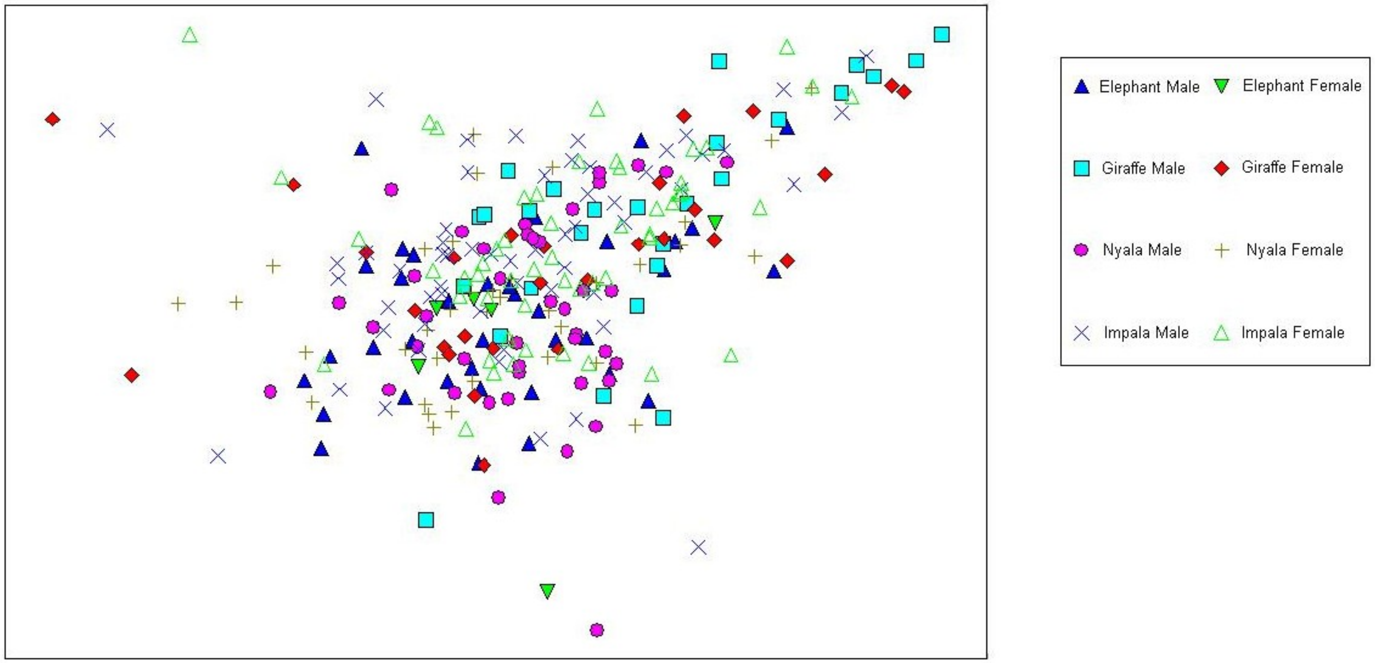

Figure 2: Habitat selection by body size classes based on local environmental characteristics in TPGR. A MDS ordination of the 159 PCQ sites of local environmental characteristics and Bray-Curtis similarities (stress = 0.06). The local environmental characteristics include grass cover (arcsin transformation), grass ht (m), and density of woody plants in three height classes (< 0.5 m, 0.5 - 1.5 m, and > 1.5 m).

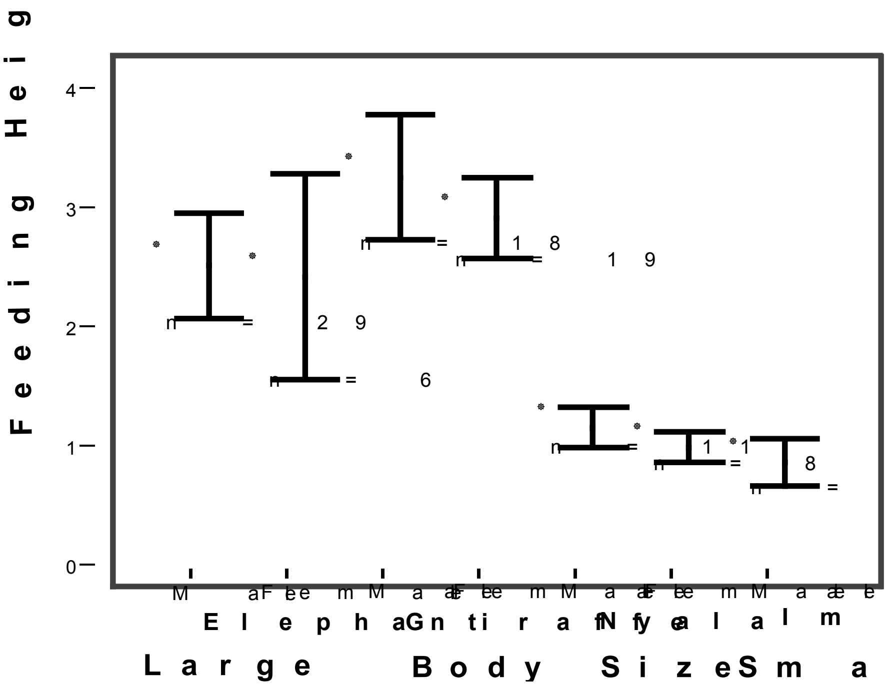

Figure 3: Feeding heights of body size classes in TPGR. The groups are categorized by species and sex and were ranked from smallest to largest body size. There were no browsing sightings recorded for female impala. Feeding heights (m) were recorded at each feeding observation sighting (n = 96). Data were mean ± 95% confidence limits. I expected the larger animals to feed at higher levels than the smaller animals.

The habitat preference rankings for the body size classes of ungulates in this study were not concordant, suggesting that the habitats were selected independently, regardless of the body size class. Therefore, at the habitat level, no overlap of habitats was exhibited, which would reduce competition across the different body size classes, suggesting resource partitioning was driving habitat selection. At the local environment level, there were significant differences in the habitat characteristics selected by the different body size classes. Therefore, the differences in habitat selection at the local environment level imply a lower competition among species. This would suggest that resource partitioning influences habitat selection at the local environmental (intermediate) level. Larger bodied ungulates reduced competition by feeding at different heights to smaller ungulates. Therefore, at the feeding level, partitioning was evident between the body size classes, with the larger bodied ungulates able to utilise different resources to the smaller bodied ungulates.

At the local environmental level, elephant, which tend to be more general in their habitat use due to their large body size (McNaughton & Georgiadis, 1986; du Toit & Cumming, 1990), were more selective, which was not expected. However, it was evident that giraffe, also a large-bodied animal, showed generalist tendencies in their approach to habitat selection, which was to be expected. Nyala were selective, which conforms to their requirements of a relatively smaller-bodied herbivore (Ben-Shahar, 1998). Impala were more generalist in habitat use based on the characteristics at the local environment level, which can be explained by their wide dietary tolerance (van Rooyen, 1992, Van Eeden, 2006). Therefore, the ungulates using habitats with similar characteristics would likely be competing for resources to satisfy their requirements.

Habitat distribution and size affect use by animals since individuals perceive and respond differently to variation in environment (Turner *et al.* 1989; Wiens, 1989). Landscape heterogeneity influences ecosystems processes (Turner *et al.* 1989; Turner & Gardner, 1991), predator-prey relationships (Bowman & Harris, 1980; Pierce *et al*. 2000), interspecific competition (Pacala & Roughgarden, 1982), and population dynamics (Dempster & Pollard, 1986; Dunning *et al.* 1992; Henein *et al.* 1998). Animal habitat use and selection within heterogeneous landscapes will effect nutrient cycling, biological diversity, plant succession and ecosystem development (Bowyer *et al.* 1997; Kie *et al.* 2002). Therefore, landscape heterogeneity influences patterns of movement, home range size, and in turn will impact on the development of succession landscapes (Kie *et al.* 2002).

The utilisation of different vegetation types will influence resource partitioning (Page & Walker, 1978); therefore observations of foraging behaviour will contribute to a better understanding to how species partition resources. Most research has focussed on grazers (Ruckstuhl, 1998; Conradt *et al*. 1999; Bonenfant *et al.* 2004). An example of resource partitioning was where white rhino *(Ceratotherium simon)* grazed on shorter grasses than buffalo (*Synerus caffer*), who shared the same vegetation type (Perrin & Breton-Stiles, 1999). Another well documented example is that of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*), which feed on the same grass species, but at different heights (Bodenstein *et al.* 2000).

In browsers, the feeding-height hypothesis explains the relationship between body size and resource partitioning (Lamprey, 1963; Leuthold, 1978; McNaughton & Georgiadis, 1986). The stratification of feeding heights in browsers (Lamprey, 1963; Sinclair, 1985; McNaughton & Georgiadis, 1986) is suggested to result from inter-specific competition, with larger bodied herbivores using their reach to avoid competing with smaller, more selective species (du Toit & Cumming, 1990; Woolnough & du Toit, 2001). In this study, feeding heights were significantly different between the larger species, elephant and giraffe, and the smaller species, impala and nyala. The intraspecific difference in feeding height stratification has been shown in giraffe (Pellew, 1984; Ginnett & Demment, 1999), nyala (Kirby *et al.* 2008), and elephant (Poole, 1994; Shannon *et al.* 2006b), where larger-bodied males feed at higher levels than smaller-bodied females (du Toit, 1995; Mysterud, 2000). However, sexual segregation in feeding heights was not evident in the study. This may have been an artefact of small sample size (low power) because the trend was in the direction for larger males to feed at higher levels than females.

Elephants are able to feed on trees less than 1 m in height (Ross *et al.* 1976), but focus feeding between 2-4 m (Guy, 1976; Owen-Smith, 1988; Kabigumila, 1993), which is in competition with other browsers (giraffe and kudu) (Guy, 1976; Stokke & du Toit, 2000; Shannon *et al.* 2006b). The upper canopy of mature trees is available to giraffe and to a lesser extent, elephant (Pellew, 1984; du Toit & Cumming, 1990), thereby reducing competition with smaller herbivores and facilitating resource partitioning.

Smaller ungulate species are implicated as browsers of young trees, or trees < 1 m (Belsky, 1984) and ungulates are known to impact on seedling recruitment (Belsky, 1984). Their impact is reduced upon tree maturity, when the available forage grows out of reach for small ungulates (du Toit &

Cumming, 1990; Van de Koppel & Prins, 1998). Changes in habitat structure and composition caused by large and small herbivores, due to localised impacts on the vegetation, have cascading effects on biodiversity and affect the habitat suitability for other species (Gordon *et al.* 2004).

With the development of relatively small private game reserves in South Africa, intensive management to prevent habitat degradation due to the over-utilisation by herbivores has become an important part of conservation (Behr & Groenewald, 1990; Bothma, 1995; Van Rooyen *et al*. 2000). Animals live in a spatially complex environment, containing with many available resources (Real, 1991). Resource partitioning studies evaluate the number of species than can coexist (Schoener, 1974), thereby assisting in management decisions how best to manage the difference between herbivore populations within the restricted area. Knowledge of animal habitat requirements is essential because species reproduction and survival rates would be improved in habitats they prefer (i.e. the habitat fitness should be higher) (Garshelis, 2000). Good veld management can manipulate landscapes to maintain habitat heterogeneity, include preferred habitat types and remove alien invasive plant species, and thus improve population survival rate (Garshelis, 2000; Kie *et al.* 2002). Most management strategies focus on the management at the population level, modelling population growth (Gordon *et al.* 2004). Management should, however, also consider the age and sex structure of the population and interactions between subpopulations to understand population dynamics and resultant productivity. Effective management would benefit from acknowledging sexual dimorphism within species and manage these species as ecologically different on the basis of sex (Bowyer, 2004). Further, in order to promote coexistence of the diverse ungulate guild, management should promote resource partitioning by maintaining habitat heterogeneity, thereby providing optimal resources for multi-species population growth.

CHAPTER 4:

UNGULATE HABITAT USE AND AGGREGATION IN RESPONSE TO PREDATOR REINTRODUCTION IN A RELATIVELY SMALL PRIVATE NATURE RESERVE IN SOUTH AFRICA: A CASE STUDY

Abstract

Anti-predator behaviours by ungulates are essential for ungulate survival where predators are present. Here I examined habitat selection in terms of aggregation (forming safer groups), predator avoidance (selecting areas that predators avoid), and habitat selection in terms of habitat structure (selecting areas where capture is less likely) in an experimental context (before vs. after lion reintroduction). Further, I tested the Reproductive Strategy Hypothesis by determining whether male and female impala and nyala used different habitat selection strategies. I compared the habitat preferences of ungulates before and after lion introduction with lion habitat preferences, to show whether ungulates were moving into or out of a habitat in response to lion habitat preferences. There were no significant changes in ungulate group size before or after lion were released. Giraffe (*Giraffa camelopardalis)* were the only ungulates to move into the habitat most preferred by lion (*Panthera leo*) (riverine). Kudu (*Tragelaphus strepsiceros*) shifted into the habitat least preferred by lions, which would suggest they avoided lions, even though this habitat did not provide cover. Nyala (*Tragelaphus angasii)* avoided lion preferred habitats; however, they selected habitats that provided cover. Impala (*Aepyceros melampus)* and nyala breeding herds avoided lions by moving into the habitat least preferred by lion, which provided support for the Reproductive Strategy hypothesis. The impala and nyala bachelor herds moved out of the habitat least preferred by lion. Therefore, I concluded that ungulates shifted habitats to avoid lion presence i.e. into habitats least preferred by lion. Such predation driven shifts into sub-optimal habitats may affect biodiversity through trophic cascades or reduce herbivore productivity, and thus sustainability of large predator populations.

Introduction

Predator-prey interaction affects the spatial distribution of prey by influencing predator avoidance and vigilance of prey species, which limit predator encounters or capture (Lima, 1998; Rangeley & Kramer, 1998). The animal's fitness will determine the antipredator behaviour as the benefits and costs will vary (Lima, 1998). Local population density and the amount of available cover are two important factors influencing the antipredator tactic used (Rangeley & Kramer, 1998). Numerous studies have shown that in the presence of predators, prey will shift their habitats to avoid predators, even at the cost of lower foraging quality (Dill & Fraser, 1984; Lima *et al.* 1985; Gilliam & Fraser, 1987). The most dangerous places, are usually the most profitable (Gilliam & Fraser, 1987; Slotow & Rothstein 1995; Lima, 1998).

Aggregation, where animals form groups, herds and flocks, is another antipredator tactic, especially by animals utilising less dense, open habitats (Bertram 1978, Hobson 1978, Pitcher 1986). The most abundant Serengeti ungulates (wildebeest (*Connochaetes taurinus)*, zebra (*Equus burchelli)* and Thompson's gazelle (*Eudorcas thomsonii*)) all live in herds (Maddock, 1979; Sinclair, 1985). When the number of individuals within a herd increases, the benefits from dilution (Hamilton, 1971; Bertram, 1978) and confusion effects (Pitcher 1986, Turner and Pitcher 1986) improve, however predation may still occur. Another benefit of aggregation is the increased probability of animals detecting predators (Jarman, 1974; Estes, 1976; Leuthold, 1977). Vigilance is an early warning system of predator presence (Hunter & Skinner, 1998); where more vigilant animals detect approaching predators from greater distances (FitzGibbon, 1989; 1990) and consequently have more time to reduce predator encounters (Hunter & Skinner, 1998). The relative use of these antipredator tactics is likely to be related to population densities, with lower density species selecting habitats to provide cover (taking refuge) and higher density prey species making use of aggregation (Rangeley & Kramer, 1998).

Habitat use by prey species may be a result of the presence of predators because the physical structure of a habitat appears to determine the level of risk (Lima, 1998). Animals scatter in highly structured habitats, which reduces the probability of detection or predation because they are difficult to detect (Sih, 1987; Lima & Dill 1990). In small reserves where structured habitats are limited, animals may break away from herds to avoid detection (Molvar & Bowyer, 1994), as fewer suitable hiding places exist, therefore the effectiveness of anti-predator (refuge) tactics (Rangeley & Kramer, 1998) will be reduced (Fretwell & Lucas, 1970; Rosenzweig, 1986; Savino & Stein, 1989).

The predation risks faced by females and males are described by the Reproductive Strategy Hypothesis (Main *et al.* 1996), which suggests that larger bodied males are less at risk of predation than the relatively smaller bodied females and juveniles. (Ruckstuhl & Neuhaus, 2000, 2002; Corti & Shackleton, 2002). Therefore, some females select habitats, which, firstly, provide cover from predators, and, secondly, include forage to meet their nutritional requirements of pregnancy and lactation (Jakimchuk *et al.* 1987; Berger, 1991; Young & Isbell, 1991). Some males, on the other hand, select habitats with high forage availability so that they maximize their growth for the breeding season (Jakimchuk *et al.* 1987; Main & Coblentz, 1990, 1996). Another aspect of antipredator behaviour includes the various classes of individuals (e.g. juvenile, sub-adult, adult; breeding herds, bachelor herds mixed herds, etc.) that vary their predation risk as a result of their behavioural and morphological characteristics (FitzGibbon & Lazarus, 1995; Prins, 1996).

Interspecific interactions influence spatial distribution of animals (Brown, 1971; Brown & Munger, 1985), which may result in either species exclusion from its preferred habitat or encourage species to specialise in a preferred habitat type (Lawlor & Maynard Smith, 1976). In contrast, intraspecific competition may force subordinate individuals into suboptimal habitats, with poor quality resources (Pimm & Rosenweig, 1981; Orians, 2000). Within the antipredator behaviour research, there is little documentation on determining which approach is used (Rangeley & Kramer, 1998). Depending on the circumstances, some species may be highly specialised for aggregation or taking refuge, however others may be capable of successfully using either (Rangeley & Kramer, 1998). These two effects, both selection for cover and aggregation, work synergistically since predators select vulnerable individuals, whose antipredator behaviour are not effective (FitzGibbon, 1989). Therefore, species with flexible antipredator responses may be particularly useful in determining which antipredator approaches are used (Rangeley & Kramer, 1998).

Impala (*Aepyceros melampus)*, aggregate in open habitats (Leuthold, 1970; Leuthold & Leuthold, 1975) using dilution effects to provide greater predator protection (FitzGibbon, 1990). Nyala (*Tragelaphus angasii*) are non-territorial mixed feeders, with habitat preferences overlapping kudu (*T. strepsiceros*) (Owen-Smith, 1994, 1996; Van Eeden, 2006). The presence of cover in the form of dense vegetation is a vital habitat requirement for both nyala (van Rooyen, 1990; Kirby *et al.* 2008) and kudu (Owen-Smith, 1994, 1996; Friedmann & Daly, 2004). Impala are mixed feeders, utilising a variety of habitats (van Rooyen, 1992; Brashares & Arcese, 2002), but preferring light woodland with little undergrowth (Van Eeden, 2006). Impala can thrive in areas where the natural vegetation has degenerated because of overgrazing or bush encroachment (Augustine, 2004; Garine-Wichatisky *et al*. 2004; Van Bommel *et al.* 2006), due to their wide dietary tolerance (Kingdon, 1997; Van Eeden, 2006). Giraffe (*Giraffa camelopardalis)* are non-territorial selective browsers (Owen-Smith, 1994, 1996). Giraffe prefer open woodland habitats with low densities of shrubs (Dekker *et al.* 1996), remaining near the evergreen vegetation, usually along watercourses, during the dry season, and dispersing more widely after the rains, when forage becomes available (Augustine, 2004; Van Bommel *et al.* 2006).

Ungulates' habitat preferences are potentially influenced by the availability and suitability of food, water, shelter from extreme climatic conditions and cover from predators (Jarman & Sinclair, 1979). Here I manipulated predation risk and tested the subsequent antipredator behavioural responses of a range of browsing prey to an introduction of lions (*Panthera leo).* Specifically, I examined the following anti-predator behaviours where re-introduced lions were absent and then present: (1) Aggregation: I tested whether group size increased after predator reintroduction, predicting that animals selecting open habitats, especially impala and giraffe, will form larger groups. (2) Habitat selection: (a) I compared habitat selection among the species, and habitat shifts before and after the lion's release. (b) I determined whether habitats offering more structure (cover) were selected for after predator introduction, especially by nyala and kudu which prefer denser vegetation. (3) Group structure: By examining group structure and sexual segregation within a habitat, I determined whether competition within a species was affecting habitat selection with regard to predation risk in terms of the Reproductive Strategy hypothesis. I predicted that dominant breeding herds would displace adult bachelor male herds, forcing them into suboptimal (riskier) habitats.

Methods

Study Area

The 50 km^2 Thanda Private Game Reserve (TPGR) was established in 2002. TPGR is situated in northern Zululand, South Africa (27^{o}52' S; 32^{o}10' E). The environment is semi-arid in TPGR with temperature ranges between 5 – 35^{o}C. Rainfall is highly seasonal, with the lowest levels in July and peaking in February, and a mean annual rainfall of 400-700 mm. Four natural pans are supplemented from boreholes in TPGR to maintain a permanent water source, in addition to the two main seasonal streams. Water is not a limiting factor in ungulate distribution because the furthest distance an animal needs to find water is 4.2 km. i.e. all parts of the reserve were available for use, even by water-dependent species. The vegetation communities can be classified broadly as Lowveld bioregion (SVI) according to Mucina & Rutherford (2006). The dominant trees which characterise Lowveld include *Acacia nigrescens, A. tortillis, A. burkei, Schotia brachypetala, Spirostachys africana, Sclerocarya birrea* and *Ziziphus mucronata* (Brousse-James & Associates, 2002). A higher resolution vegetation map was created by Brousse-James & Associates (2002), containing 14 different vegetation categories. I simplified the Brousse-James & Associates (2002) map, which was created with 14 different vegetation categories, using situation on the slope (lowland, midslope or uplands) and structure (woody plant density), into five categories. These categories included three low-density categories (lowland woodlands, upland woodlands, old cultivated lands) (maximum canopy cover of 50% cover) and two high density categories (midslope woodlands, riverine) (minimum canopy cover of 50% cover). Riverine and old lands were kept separate from the other habitats because they differed from the woodland habitat structure. Old cotton fields (old lands), which were created by historical farming practices, have been left vacant to return to natural veld. The riverine habitat is a separate ecosystem, with lush, dense vegetation due to the drainage line.

Animal Distribution

I determined spatial distribution and habitat preference by driving road transects throughout TPGR, where animals were spotted from the vehicle. A systematic search pattern (routes) was laid down, and the choice of which routes to drive was randomised to prevent autocorrelation of data by avoiding sampling bias (Stokke & du Toit, 2002). These routes allow coverage of most habitat types represented in the study area. I avoided transects along the electrified boundary fence. The objective of this systematic sampling was to achieve an even intensity of sampling in all habitats so that species frequencies would reflect both distribution and habitat preference. Areas that were densely vegetated may have made it difficult to see the animal, resulting in fewer sightings in these areas. Therefore, I calculated the visible area along the road, where animals were spotted. A GPS location was recorded at the furthest possible point visible perpendicular to the vehicle. The procedure was repeated on the left and right side of the vehicle, at regular intervals along the transect or when the habitat changed (N = 1212 points used to create visibility profiles). The visible area was measured in summer, when the contrast between habitat structures was obvious. I imported these points into ArcView 3.3 (ESRI, New Dehli, India) where the X-tools extension was used to calculate the visible area along each transect.

Ungulate observations were made during daylight hours (07h00 – 17h30). The hottest hours of the day were excluded as animal activity was minimal, whereas activity peaked in the early morning and late afternoon (Owen-Smith, 1998). A driver and at least two passengers drove the routes at approximately 10 – 20 km/hr. For each animal or group, I stopped and recorded date, time, vehicle GPS location (decimal degrees), distance to animal, the animal's age, sex, number, initial behaviour (most prevalent behaviour if a group of animals was sighted). Distances were estimated by eye.

Three lion, a sub-adult male and two sub-adult females, were released into the reserve on 21st September 2004. One of the females died in October 2004. Lion spatial data were collected from a GPS/GSM Collar, where a location was recorded every 4 hours (the two lions were in a single group) from the time of release (May 2004) till the end of the study (September 2005). The Kernel Home Range calculation in ArcView 3.3 (ESRI, New Dehli, India) showed that lion total home range use (95% Kernel) (hectares) occupied 52% of the total reserve area. This would elicit shifts in ungulate habitat preferences after lion were released. I assigned habitats to each sighting by performing a spatial join of the location data and habitat from vegetation map in ArcView 3.3 (ESRI, New Dehli, India).

Statistical Analysis

Lion spatial data were used from May 2004 till September 2005. Ungulate data used were June to August 2004 (before lion introduction) and June to August 2005 (after lion introduction). This allowed time for the lion to settled into the reserve, and for the ungulates to have responded to the lions. Because data were collected over the same time of the year, I controlled for seasonal responses of ungulates. Winter periods are known for their limiting food resources (Gordon & Illius, 1988; Smith *et al*. 2007), therefore habitat selection based on food preferences and predator avoidance would be pronounced. This would be important for browsers such as giraffe and kudu, whose forage availability is severely restricted to the evergreen plants during the dry season (Van Eeden, 2006).

Group Size

To assess changes in group size before and after lion release, for different species (impala, nyala, kudu and giraffe), and among different habitat types (riverine, midslope woodlands, upland woodlands, lowland woodlands and old lands), I used a 3-way ANOVA (data were normally distributed, Kolmogorov-Smirnov test, $P > 0.05$) ($n = 1605$ sightings). I tested for changes in group size for impala and nyala bachelor and breeding herds before and after lion release using a Mann Whitney U test (data were not normally distributed).

Habitat preference

To test whether habitat use was random, I used a Chi-Square Test. I assessed habitat preference for each ungulate species using preference ratios (Viljoen, 1989; Shannon *et al*. 2006a). These were calculated as the proportion of locations within a particular habitat divided by the proportion visible area of that specific habitat type within the reserve (based on our visibility profiles) (i.e. (number of sightings (in habitat) / total number of sightings (species)) / (visible area (for specific habitat) / total visible area of all habitats). The lion preference ratio was calculated differently, as the location data were used from the GPS collars, which was the actual location within the reserve, including areas not visible from the road (i.e. number of sightings (in habitat) / total number of sightings) / (area (for specific habitat) / total area of reserve). If the preference ratio was 1, the habitats were used in direct proportion to their occurrence within the reserve. If the preference ratio was greater than 1, preference for a specific habitat was suggested. If, however, the preference ratio was less than 1, the specific habitat was avoided. The preference ratio thus provided a method of contrasting habitat change before and after lion introduction, with any possible biases being consistent for our contrasts.

Habitat change was calculated by subtracting the ungulate habitat preference ratio before the lions were released, from the preference ratio after the lions were released. The change of ungulate habitat preference before to after lion release was graphed against lion habitat preference. I predicted that a positive change would be animals shifting into a habitat and a negative change would reflect animals shifting out of a habitat. The baseline ($y = 0$) indicated no change in habitat before to after the lion were released (i.e. no effect) (Figure 1). The $x = 1$ line indicates lion habitat preferences: when $x > 1$, the lion prefers the habitat, spending more time in that habitat; when $x < 1$ the lion avoids the habitat (Figure 1).

To test for predation risks faced by females and males within a species, animals were grouped according to their social class, for example, breeding and bachelor herds. Kudu and giraffe were excluded due to small sample sizes. I calculated habitat preferences for each sex class using preference ratios. Scatter plots of impala and nyala age-sex class habitat changes before and after lion release were assessed against lion habitat preference (Figure 2).

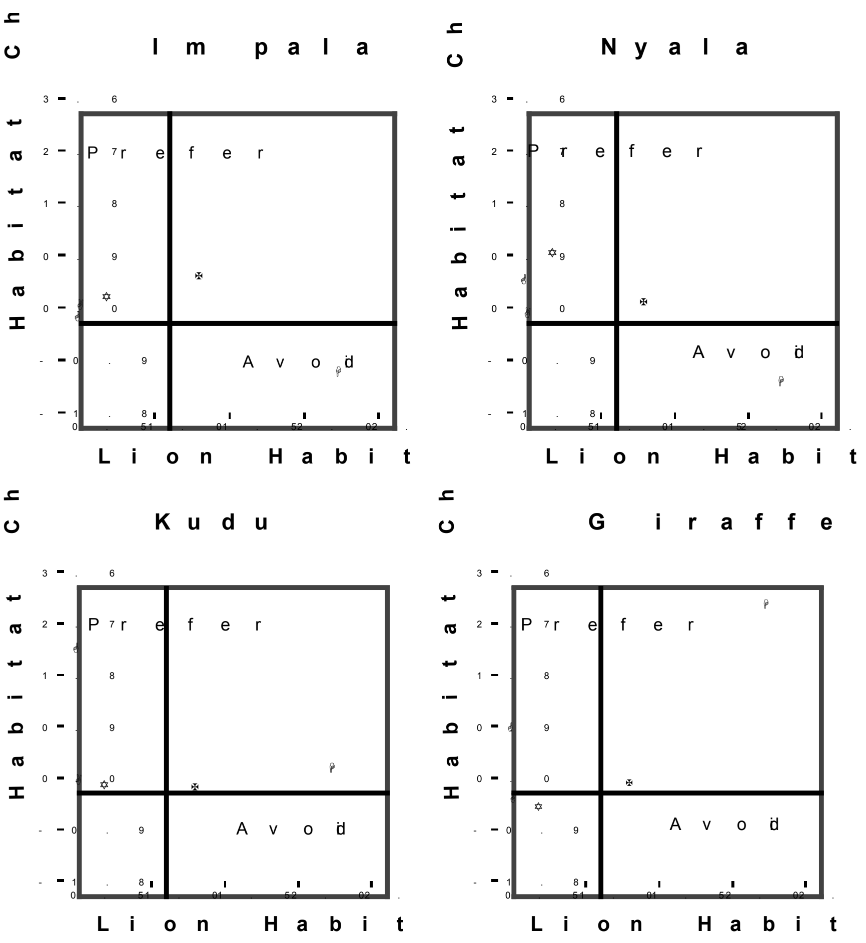

Figure 1: The effect of lion release on ungulate habitat use in TPGR. Ungulate habitat change (preference index (after the lion release) – preference index (before the lion release)) contrasted against lion habitat preferences for impala, nyala, kudu and giraffe. ○ = lowland woodlands ▼ = midslope woodlands ▲ = upland woodlands □ = old lands ◊ = Riverine. A positive change indicated an ungulate moving into a habitat, and a negative change indicated an ungulate moving out of a habitat. I predicted the ungulates would select habitats where the lion were not present (top left) and avoid habitats that the lions preferred (bottom right).

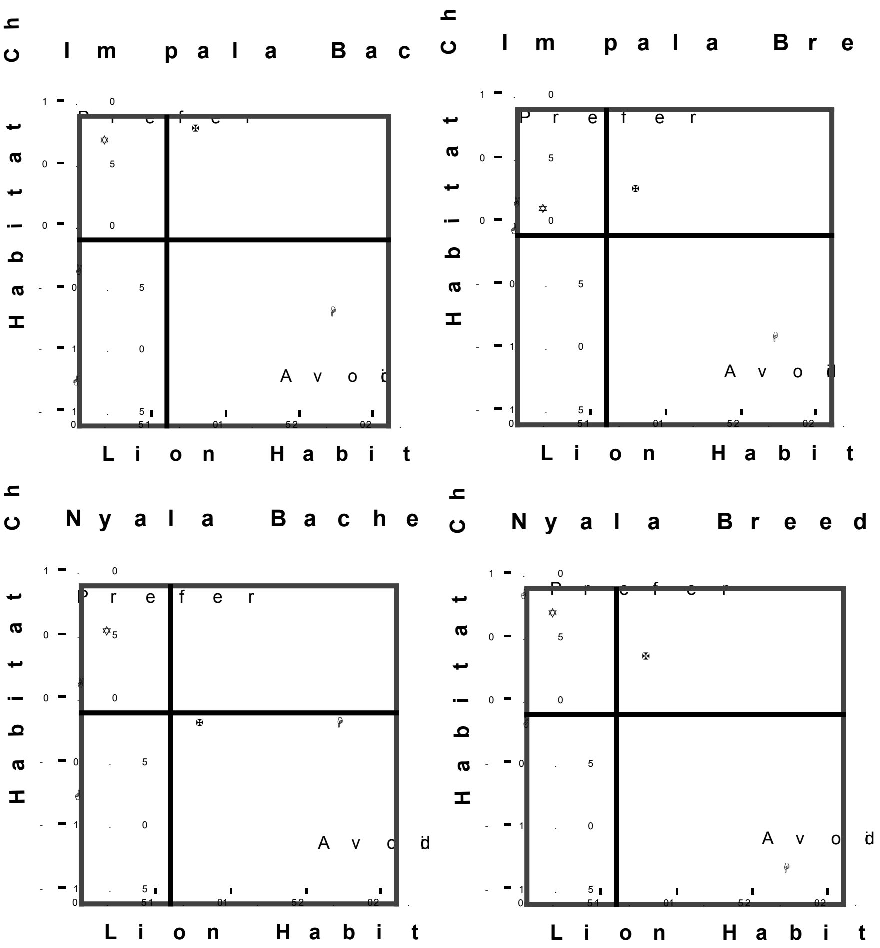

Figure 2: The effect of lion release on habitat use among sex-classes in TPGR. Impala and nyala (bachelor and breeding herds) habitat change (preference index (after the lion release) – preference index (before the lion release)) compared with lion habitat preferences. ○ = lowland woodlands ▼ = midslope woodlands ▲ = upland woodlands □ = old lands ◊ = Riverine. A positive change indicated an ungulate moving into a habitat, and a negative change moving out of a habitat.

Results

There was a significant difference in group size among species (3-way ANOVA: $F_{3,526} = 20.192$, $p < 0.0005$) (Figure 3a). However, group size did not vary among habitats ($F_{4,\,526} = 0.482$, $p = 0.75$) or in response to predator presence (before/after the lion were released: $F_{1,\,526} = 0.973$, $p = 0.324$). There were no significant interaction effect of habitat and before/after lion release on group size ($F_{4,507} = 0.467$, $p = 0.760$), or of species before and after predator release ($F_{3,519} = 0.280$, $p = 0.840$).

There was no significant change in nyala breeding herd (Mann-Whitney U-test: $Z = -1.008$, $N = 55$ before and 62 after, $p = 0.313$) or nyala bachelor herds ($Z = 0.466$, $N = 58$ before and 37 after, $p = 0.641$) (Figure 3b) group size after lion release. Impala breeding and bachelor herds group size did not change after release (breeding: $Z = -0.014$, $N = 95$ before and 51 after, $p = 0.989$; bachelor: $Z = -1.315$, $N = 73$ before and 33 after, $p = 0.188$) (Figure 3b).

Based on the Chi-squared test, lion habitat use was non random, ($\chi^2_4 = 143.19$; $p < 0.0001$), where the lion preferred riverine (Preference Index (P.I) = 2.3), which was a more densely structured habitat. Lion avoided lowland woodlands (P.I. = 0.57) and old lands (P.I = 59), the less dense habitats. Lion did not avoid or prefer midslope and upslope woodlands, using those habitat types in accordance with their occurrence (P.I. = 0.87; P.I = 1.38 respectively).

Ungulate habitat selection was non random (Table 1). Impala (before: $\chi^2_4 = 50.04$, $p < 0.001$ and after: $\chi^2_4 = 80.34$, $p < 0.001$) and nyala (before: $\chi^2_4 = 24.52$, $p < 0.001$ and after: $\chi^2_4 = 40.98$, $p < 0.001$) showed habitat preferences both before and after lion release. Giraffe showed a habitat preference before lion were released (before: $\chi^2_4 = 29.33$, $p < 0.001$), but no preference after lion were released. Impala bachelor and breeding herds showed a preference in habitat selection before (bachelor: $\chi^2_4 = 22.87$, $p < 0.001$; breeding: $\chi^2_4 = 28.40$, $p < 0.001$) and after (bachelor: $\chi^2_4 = 17.15$, $p = 0.002$; and breeding: $\chi^2_3 = 14.80$, $p = 0.002$) lion release (Table 2). Nyala bachelor and breeding herds only showed a preference after lion were released (bachelor: $\chi^2_4 = 12.89$, $p = 0.012$; breeding $\chi^2_4 = 35.5$, $p < 0.001$).

I expected ungulates to select habitats where lions were not present (i.e. the top left and bottom right quadrant), if habitat change was influenced by lion release. Based on the preference index, impala moved out of riverine habitat, which lion preferred, into upland woodlands, which was the

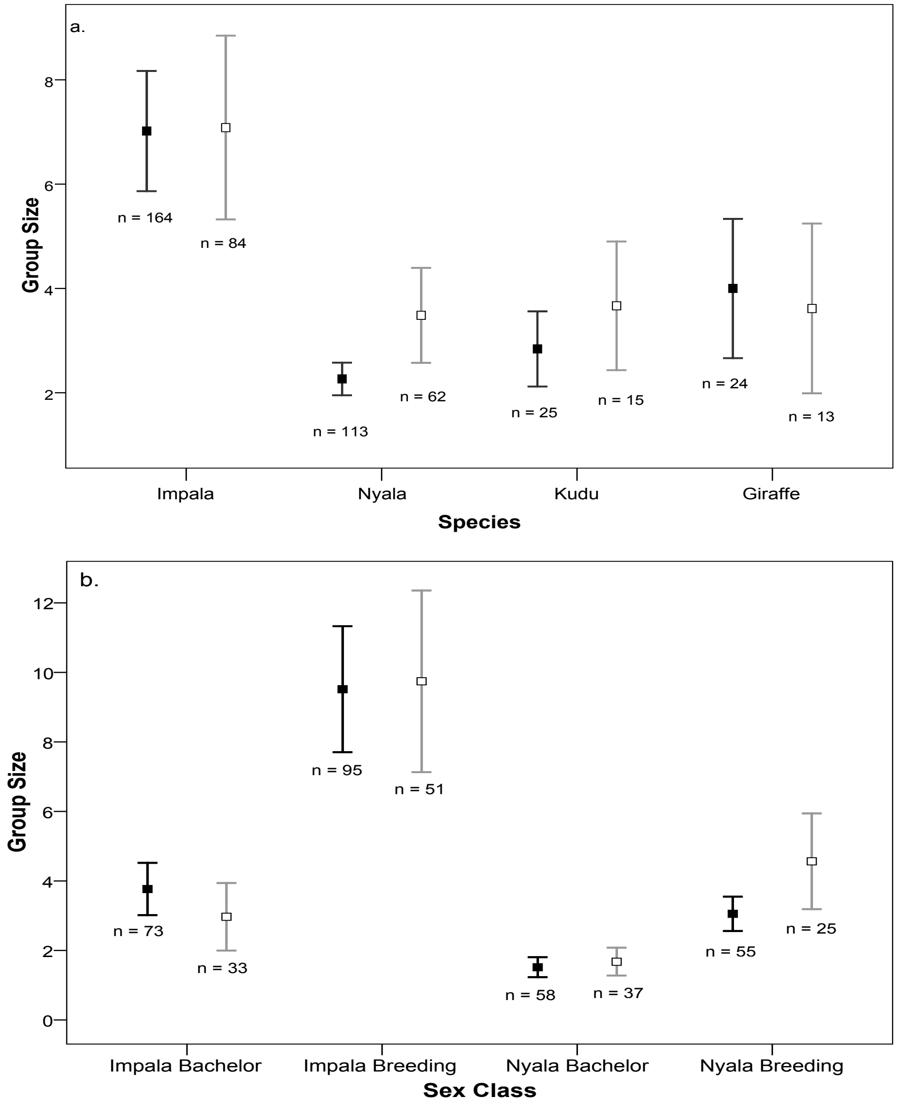

Figure 3: The effect of lion release on ungulate group size (Mean ± 95% confidence intervals) in TPGR. Before lion introduction = ■/black line; after lion introduction = □/grey line. I expected the species selecting open habitats to increase their group size. Variance of each herd's group size is shown by distance of the error bar from the centre square.

second preferred habitat of lions (Figure 2). Nyala moved out of riverine (preferred by lion) and into midslope woodlands and old lands, which lion do not prefer, and nyala did not change their use of upland woodlands, even though lion preferred that habitat (Figure 2). Kudu moved into old lands, which lion do not prefer, but kudu did not change their use of the other habitats (Figure 2). Giraffe moved into riverine, which lion prefer, which contradicted our predictions, but giraffe also moved into old lands, which lion do not prefer (Figure 2).

Impala breeding herds moved out of riverine habitats, which lion preferred, while there were no substantial changes in impala breeding herd use of other habitats (Figure 3). Impala bachelor herds moved out of old lands, riverine and lowland woodlands and into midslope and upland woodlands (Figure 3). Lion showed preference for riverine and upland woodlands, therefore it was unexpected that impala bachelor herds moved out of old lands and lowland woodlands. Nyala breeding herds moved out of riverine habitat, which lion prefer, into old lands and midslope woodlands, which lion do not prefer. Nyala bachelor herds moved out of old lands into midslope woodlands, both habitats that lion do not prefer. However, nyala bachelor herds did not change their use of riverine or upland woodlands, which lion preferred (Figure 3).

Discussion

Aggregation is an evolutionary solution to reduce the risk of predation and decrease the amount of time assigned to anti-predator behaviour, for example vigilance. This has been demonstrated in birds (Diamond & Lazarus, 1974; Powell, 1974; Bertram, 1980) and in mammals (Berger, 1978; Hoogland, 1979; Monaghan & Metcalfe, 1985). Research suggests that ungulates that select open, less dense habitats, benefit from forming large herds (increasing numbers) (Hobson, 1978; Pitcher, 1986; Mattiello *et al*. 2004), however this was not evident in my study. Predators may aggregate and focus their searching effort in areas where prey densities are high (Murdoch & Stewart-Oaten 1989; Ives 1992; Ives *et al.* 1999), therefore the spatial distributions of both predators and prey are important (Nachman, 2006). Within species that select for cover (Sih, 1987, Lima & Dill 1990), in my study the average group size tended to be smaller (nyala = 2.8/group; kudu = 3.15/group), whereas the average group size for species in open habitats e.g. impala was larger (7/group).

Table 1: The effect of predator introduction on habitat selection in TPGR. Results of the Chi-squared test showing that species are using habitats in a non-random manner. The individual habitat records were used. Impala before n = 162; after n = 166; nyala before n = 112; after n = 96; kudu before n = 24; after n = 15; giraffe before n = 24; after n = 11.

Species	**Impala**		**Nyala**		**Kudu**		**Giraffe**	
	χ^2	P Value	χ^2	P Value	χ^2	P Value	χ^2	P Value
Before	50.04	< 0.001	24.52	< 0.001	6.00	0.112	29.33	< 0.001
After	80.34	< 0.001	40.98	< 0.001	4.67	0.323	4.64	0.200

Table 2: Effect of predator introduction on habitat selection within species in TPGR. Results of the Chi-squared test showing sexual segregation in habitat selection. The individual habitat records were used. Impala bachelor herds before n = 71; after n = 33; impala breeding herds before n = 91; after n = 50; nyala bachelor herds before n = 56; after n = 36; nyala breeding herds before n = 55; after n = 60.

	Impala				**Nyala**			
Species	Bachelor Herds		Breeding Herds		Bachelor Herds		Breeding Herds	
	χ^2	P Value	χ^2	P Value	χ^2	P Value	χ^2	P Value
Before	22.87	< 0.001	28.40	< 0.001	7.75	0.101	4.13	0.248
After	17.15	0.002	14.80	0.002	12.89	0.012	35.5	< 0.001

Predator foraging behaviour may adapt in structurally complex habitats because these habitats influence prey susceptibility to predation (Clark & Messina, 1998; Grabowski, 2004) by providing prey refuges (Eklov & Persson, 1995). For example, sedentary ungulates may avoid detection by predators in a simple habitat more effectively than active ungulates (Perry & Pianka, 1997; Rosenheim & Corbett, 2003). Water also influences habitat selection (Augustine, 2004; Van Bommel *et al.* 2006). Kudu and nyala will drink water daily when it is accessible although it is not vital daily requirement (Owen-Smith, 1994; Garine-Wichatisky *et al*. 2004). Giraffe drink every 2-3 days when water is available but are able extract water from green leaves (Cooper *et al.* 1988; Mattielo *et al.* 2004); however, impala require surface water on a daily basis (Western, 1975; Augustine, 2004; Van Bommel *et al.* 2006).

Giraffe showed a preference for riverine habitats, which is consistent with literature, when resources are limiting (Ginnett & Demment, 1999). Impala were found distributed throughout the reserve utilising most habitat types, which is consistent with the literature that the wide habitat ranges of impala are due to their dietary tolerance (Kingdon, 1997; Van Eeden, 2006). Nyala selected the denser vegetation, which is consistent with literature that suggests selection for cover is an important habitat requirement (Vincent *et al.* 1968; Van Rooyen, 1990). In our study kudu did not select denser vegetation (as indicated by Owen-Smith, 1979, 1994; Friedmann & Daly, 2004), but chose the less dense habitats. This habitat selection may have been to avoid predator encounters.

If lion were a factor influencing habitat selection, I expected the ungulates to move into the least preferred lion habitat and move out of the most preferred lion habitat. Kudu followed this trend and shifted into the least preferred lion habitat, old lands, after lion were released. However, kudu did not change their use of the other habitats. Giraffe and Nyala breeding herds moved into old lands (Impala breeding herds showed no change in habitat use of old lands), the habitat least preferred by lion.

Giraffe were the only species to move into the most preferred lion habitat, riverine, after lion release. Note that the small lion group size (two), and young age (sub-adult at release) meant that giraffe were not hunted by lion, and thus did not need to respond to predation risk. Giraffe, with efficient anti-predatory behaviours to this particular lion threat, could thus risk predator encounters (Tikanen *et al.* 1997). Nyala breeding and impala breeding and bachelor herds moved out of riverine after the lion were released, which was consistent with our predictions. Nyala did not minimise their use of upland woodlands, which was the second preferred lion habitat or old lands, which was the least preferred lion habitat, but shifted into midslope woodlands, which was neutral in terms of lion usage.

The Reproductive Strategy hypothesis has received support in explaining sexual segregation in ungulates, where females with young often select relatively safer habitats, avoiding predators even at the expense of forage quality (du Toit, 1995; Main *et al.* 1996; Villaret *et al.* 1997). Increased predator avoidance by females was shown in Asian elephants (*Elephas maximus)* where males may take more risks while foraging than females (Sukumar & Gadgil, 1988). Females stayed in more sheltered habitat, while at the same time males used habitat of superior nutritional quality (Albon & Langvatn 1992). Nyala breeding and impala breeding and bachelor herds moved out of riverine after the lion were released, thereby avoiding predators. Bachelor herds of both nyala and impala may have moved out of the predator-free old lands, providing some support for Reproductive Strategy Hypothesis (Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002), which states that the larger bodied males are less vulnerable to predation. The bachelor herds may have moved as a result of dominance by kudu (in terms of body size) and nyala and impala breeding herds (guarded by dominant males). This pattern followed predictions of subordinates being forced into sub-optimal habitats (with the optimal habitat in this case being defined by low lion predation risk). Therefore, the various species/age-sex classes responded as predicted in changing habitat selection to avoid introduced predators.

Foraging, predation, and reproduction strategy success are inter-related to strategies used by other ungulates (Weitz & Levin, 2006). Ecosystem structure and function (biodiversity) can be influenced by predator and ungulate population dynamics (Bowyer & Kie, 2006). Most research concentrates on the ungulate response to predators because population dynamics of both predators and prey are affected, which is useful for wildlife managers (Nachman, 2006). Lion release onto TPGR, did not influence the ungulate group size, but altered ungulate habitat selection, with ungulates shifting into sub-optimal habitats. Apparent increases in competition may have resulted in least dominant groups being displaced into least-optimal habitat. Competition is known to have a predominant effect on the structure, dynamics and persistence of predator–prey interactions for some ungulate species (Bonsall & Hassell 1997, 2000; Chaneton & Bonsall 2000).

Predator-prey dynamics are influenced by habitat characteristics, and relative densities of predator and prey as well as their behaviour (Hopcraft *et al.* 2005). More lion kills were recorded when prey is ambushed than where prey is abundant, therefore, habitat selection of prey for structure influences prey catchability (Hopcraft, *et al.* 2005). Understanding predator and prey behaviours, and the selection of complex habitats that provide refuge (Hopcraft *et al.* 2005), may expand our understanding of trophic cascades caused by competition and antipredator behaviour (Pimm & Rosenzweig, 1981; Byrnes *et al.* 2006; Finke & Denno, 2006). Therefore, predator introductions have direct costs in terms of the removal of prey (consumed) (Pierce *et al.* 2000; Miller *et al.* 2006; Nachman, 2006), and hidden costs in the reduced population productivity as a result of sub-optimal habitat use (Finke & Denno, 2006). Reduced productivity reduces both the future carrying capacity to sustain predator populations, and potential harvesting income.

CHAPTER 5:
GENERAL DISCUSSION & CONCLUSIONS

Habitat selection choices influence individual success (Kristan, 2003). Animals perceive and react to the heterogeneous nature of the environment (Křivan & Sirot, 2002) at different spatial scales. Each aspect of an animal's biology (e.g. foraging behaviour (Rosenzweig 1991; Fritz *et al.* 2003), dispersal patterns (Blums *et al.* 2003), and population dynamics (Lewis & Murray, 1993)) influence their response to each scale of habitat selection (Senft *et al*. 1987; Real, 1991; Nams, 2005).

A suitable habitat may contain a mixture of patches that provide opportunities for successful reproduction and survival (Orians & Wittenberger, 1991). The effect of scale has been studied in animal population dynamics (Hobbs & Hanley, 1990; Coulson *et al*. 1999), their harvest (McCullough, 1996), and metapopulation dynamics (Bleich *et al*., 1996; DeWoody *et al*. 2005). Scale sensitivity is influenced by the variable nature of interactions of ungulates with their environment (Wallis de Vries *et al*. 1999), and their ability to migrate among patches (Berger, 2004; Alldredge & Griswold, 2006).

Resource selection occurs in a hierarchical fashion (Alldredge, & Griswold, 2006) and will vary at each scale (Kotliar & Wiens, 1990; Schmidt, 1993; Ward & Saltz, 1994). Resource selection studies are useful because they include multiple levels (Aebischer *et al.* 1993; Erickson *et al*. 1998), where the results can be helpful in identifying patterns of habitat selection (Alldredge & Griswold, 2006). Factors influencing selection at each scale will vary (Alldredge & Griswold, 2006), because scales of measurement and environmental heterogeneity may be continuous (Kie *et al.* 2002). For example, home range size and shape, and density levels or competition, are influenced by habitat structure (Alldredge & Griswold, 2006).

The distribution and availability of suitable habitats, together with the density of competitors, affect the probability of an ungulate selecting a suitable habitat (Morris, 1988; Rosenzweig, 1995). Habitat selection may lead to segregation across different parts of the environment (Rice & Salt, 1988; Křivan & Sirot, 2002), provided competition is evident (Křivan & Sirot, 2002). Therefore, habitat overlap is reduced by high levels of competition (Brown, 1971; Křivan & Sirot, 2002). In my study, at the habitat (large scale) level, habitats were selected independently (regardless of the body size class), thus there was no habitat overlap, which would reduce competition, and suggest that resource partitioning may be driving habitat selection.

Animals select optimal habitats to maximise gains to their physiology (Sinclair & Gwynne, 1972; Pullium, 1988; Pullium & Danielson, 1991). Once a habitat patch no longer satisfies an ungulate's requirements, they will move patches (Wilmshurst *et al.* 2000). Individual selection for particular environmental characteristics is influenced by physiological requirements due to body size (Basset & Angelis, 2007). At the local environment (intermediate scale) level, there were significant differences in the habitat characteristics selected by the different body size classes, therefore reducing competition. This would suggest that resource partitioning influences habitat selection at the local environmental level.

The evolution of body size dimorphism has been attributed to the segregation of the sexes because of its influence on spatial and foraging ecology (Ruckstuhl, 1998; Stokke & du Toit, 2000; 2002). Understanding the relationship between the distribution of resources and animals is essential (Brown *et al*. 1995; Gaston, 2004), because resource selection is affected by season, gender, age class, and behaviour (Main *et al.* 1996; Alldredge & Griswold, 2006). Therefore, differences in physiology and body size will influence resource partitioning (Page & Walker, 1978) and habitat selection (Conradt *et al.* 1999), with larger species able to tolerate a wider range of vegetation types than smaller species (Bell, 1971; Geist, 1974; Jarman, 1974). In the study, elephant, which tend to be more general in their habitat selection strategies due to their large body size (McNaughton & Georgiadis, 1986; du Toit, 1990), were more selective at the local environmental level, which was not expected. Giraffe, also a large bodied herbivore, however showed generalist tendencies in their approach to habitat selection. Nyala were selective, which conforms to their requirements of a smaller-bodied herbivore (Ben-Shahar, 1998); however, impala were more generalist in habitat selection based, which can be explained by their wide dietary tolerance (van Rooyen, 1992, Van Eeden, 2006). Therefore, the ungulates selecting habitats with similar characteristics would likely be competing for resources to satisfy their requirements.

Arsenault & Owen-Smith (2008) showed that the largest species, white rhino, consistently utilized shorter grass than three smaller grazers. In addition, the smallest species, impala, tended to use grass heights intermediate between those grazed by wildebeest and zebra, both larger species (Arsenault & Owen-Smith, 2008). The assumption that smaller herbivores should be superior competitors through being able to persist on sparse vegetation may be true (Arsenault & Owen-Smith, 2008). However, large herbivores can survive when only poor quality, abundant vegetation exists; therefore, the nutritional requirements and allometric scaling of intake rate must be taken into account when explaining resource partitioning among herbivores (Wilmshurst *et al.* 2000; Arsenault & Owen-Smith, 2008).

The stratification of feeding heights in browsers (Lamprey, 1963; Sinclair, 1985; McNaughton & Georgiadis, 1986) is suggested to result from inter-specific competition, with larger bodied herbivores using their reach to avoid competing with smaller, more selective species (du Toit, 1990; Woolnough & du Toit, 2001). In this study, there was distinct segregation in feeding heights (small scale) among the larger species (giraffe and elephant) versus the smaller species (nyala and impala). The intraspecific difference in feeding heights have been shown in giraffe (Pellew, 1984; Ginnett & Demment, 1999), nyala (Kirby *et al.* 2008), and elephant (Poole, 1994; Shannon *et al.* 2006b), where larger-bodied males feed at higher levels than smaller-bodied females (du Toit, 1995; Mysterud, 2000). However, there were no differences in feeding heights between sexes, which may have been an artefact of small sample size (low power) because the trend was in the direction for males to feed at higher levels than females.

Knowledge of animal density, and the way animals respond to the heterogeneous environment, is essential to link scale with biodiversity (Morris, 1987; O'Neill *et al*. 1988). Ecosystem processes that relate to biodiversity are influenced by changes in population density (Bowyer *et al*. 1997; Kie *et al*. 2002), e.g. the spatial separation of the sexes outside the mating season (Conradt *et al.* 1999; Bowyer, 2004). Allometric differences between dimorphic sexes (Barboza & Bowyer, 2000; 2001) and predation risk (Bleich *et al*. 1997; Corti & Shackelton, 2002; Bowyer, 2004) influence sexual segregation (Bowyer & Kie, 2006). Females compete more intensely with other females and young ungulates than with males (McCullough *et al.* 1989), because they are responsible for the survival of the young (Bowyer & Kie, 2006), and the sexes are spatially segregated for most of the year (Bowyer, 2004; Bowyer & Kie, 2006). Therefore, during segregation, the scale at which females select resources will affect recruitment, and ultimately, population density (Bowyer, 2004; Bowyer & Kie, 2006).

For optimal habitat selection, animals will need to balance foraging benefits (energy gain) and foraging costs (predation risk) (Lima & Dill, 1990; Kotler, 1995). However, the good foraging areas are often riskier (Orians, 2000; Slotow & Rothstein, 2002). Predator avoidance has been shown to play an important role in habitat selection by herbivores in other ecosystems (Sinclair & Arcese 1995; Kie & Bowyer, 1999; Pierce *et al*. 2004). Predators may influence prey spatial dynamics is by shifting ungulate habitat use (Sinclair & Arcese 1995; Kie & Bowyer, 1999; Pierce *et al*. 2004), possibly due to vigilance behaviour (Frank, 2008). In my study, group size did not increase, which was contrary to what was expected. However, ungulates shifted habitats to avoid predators, i.e. into habitats least preferred by lion. Giraffe were the only species not under threat of predation (lion group size was too small), and were able to move into the most preferred lion habitat, thereby taking advantage of the reduced competition with the other species, which had shifted out of the preferred habitat of the lion.

The Reproductive Strategy hypothesis has received support in explaining sexual segregation in ungulates, where females with young often select safer habitats, avoiding predators even at the expense of forage quality (du Toit, 1995; Main *et al.* 1996; Villaret *et al.* 1997). Increased predator avoidance by females was shown in Asian elephants where males may take more risks while foraging than females (Sukumar & Gadgil, 1988). Females stayed in more sheltered habitat, while males used habitat of superior nutritional quality (Albon & Langvatn 1992). Nyala and impala breeding herds moved out of the most preferred lion habitat into a less risky habitat after the lion were released, thereby avoiding predators. Bachelor herds of both impala and nyala moved out of the predator free habitats, providing some support for Reproductive Strategy Hypothesis (Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002), which states that the larger bodied males are less vulnerable to predation.

Kudu, the second largest herbivore, shifted into the least preferred lion habitat after lion were released. The bachelor herds may have moved out of this habitat due to dominance by kudu (in terms of body size) and nyala and impala breeding herds (guarded by dominant males). This pattern followed predictions of subordinates being forced into sub-optimal habitats (with the optimal habitat in this case being defined by low lion predation risk). Therefore, the various species and sexes responded, as predicted, in changing habitat selection to avoid introduced predators. By manipulating where animals graze, and preventing ungulates from grazing highly productive sites, predators may have had significant, indirect effects (Peacor & Werner, 2001) on prey that may reduce prey condition and predispose them to predation, disease, and starvation (Frank, 2008).

Understanding predator and prey behaviours may expand our understanding of trophic cascades caused by competition (Bowyer & Kie, 2006) and antipredator behaviour (Frank, 2008). Primary production is strongly correlated with biodiversity (Tilman *et al*. 1996), and at high densities, ungulates can promote succession changes in pathways of vegetation communities (Pastor *et al*. 1993) and cause subsequent trophic cascades (Terborgh *et al*. 2001; Ripple & Beschta, 2004) that may affect biodiversity. Habitat selection may vary as a consequence of vegetation succession (Boyce & Merrill, 1991). For example, the population dynamics of large herbivorous mammals can profoundly influence ecosystem structure and function (Bowyer *et al*. 1997; Kie *et al*. 2002; Bowyer & Kie, 2006) via trampling and compaction of soil (Cumming & Cumming, 2003). Ungulates utilise their environment non-uniformly (Hobbs, 1996; Kie *et al*. 2002), through concentrated patches of foraging and defecation (McNaughton, 1985; Day & Detling, 1990). Therefore, depending on population densities, ungulates are capable of driving nutrient cycling and thus ecosystem processes (Molvar *et al*. 1993; Frank & McNaughton, 1993).

The trophic effects of predators have been limited to predator control on prey at lower trophic levels (McLaren & Peterson, 1994; Terborgh *et al*. 2001). These studies suggest that a relatively small number of highly mobile carnivores may have a widespread effect on trophic levels (e.g. prey, plants and soil), change the spatial distribution of prey, and thus, spatial pattern of ecosystem processes, thereby contributing to an overall decline of those processes in this ecosystem (Fortin *et al.* 2005; Kauffman *et al.* 2007; Frank, 2008). Predator conservation, reintroduction or removal policies may have important, cascading consequences beyond the direct effects of predators on prey, which management should consider (Frank, 2008).

From my study I concluded that resource partitioning was therefore strongest at the largest spatial scale, less obvious at the intermediate scale, and relatively coarse when present at the plant scale. Ungulates shifted habitats to avoid lion presence, i.e. into habitats least preferred by lion and dominant species (body size) forced subordinate species into suboptimal habitats.

The spatial distribution of habitat patches influences species coexistence (Orians & Wittenberger, 1991). The variation in the habitat types may not have been large enough to produce differences in habitat selection at the local environment level. Three out of five habitats were classified as woodlands, with variation due to vegetation structure (density) and the geographical location on the slope. Therefore, body size classes may have separated at the environmental level if the woodlands habitats were grouped together, and habitat selection was examined for riverine, old lands and woodlands (grouping the three variants into one category).

Resource selection is influenced by many factors (e.g. season, sex, age, and activity) (Alldredge & Griswold, 2006; Arsenault & Owen-Smith, 2008). If resource use and availability changes across seasons, the study should focus on habitat selection during relatively short periods of time within each season, or allow for use and availability to change across seasons (Cooper *et* *al*. 1988; Arthur *et al*. 1996; Garshelis, 2000). By identifying conditions affecting animal performance, ecologists attempt to predict the animal response (Fretwell & Lucas, 1970; Leibold, 1994). A potential flaw, in this study, was that the focus was the animal's response and did not determine changes in environmental conditions. A major flaw in most habitat selection studies is the lack or replication, as was the case in my study. Replication in habitat studies is difficult because there are multiple factors, which may vary e.g. season, rainfall, burning regimes, and population density, which will modify the vegetation quality and thus habitat selection. This could have been responsible for the relatively low power in some analyses. Information on comparisons of habitat use and availability among individuals, among groups of individuals in different portions of a study area, among study areas, and among time periods (e.g. seasons) may provide significant insights (Garshelis, 2000).

Predator-prey dynamics are not only a function of habitat (cover) but prey densities (Hopcraft *et al*. 2005). Thus developing long-term conservation plans for carnivores must include appropriate hunting habitats as well as high prey densities (Hopcraft *et al.* 2005). By examining prey preferences in this study, and comparing it to surrounding areas, management can plan for future reintroductions (Marker, 1998; Hayward *et al.* 2006). Long term research on predator introductions and comparisons between predators within a reserve, and between reserves, will contribute to understanding the underlying mechanisms of predator-prey interactions (Hayward & Kerley, 2005) and predator avoidance behaviour traits by ungulates, which will allow management to plan rather than respond. Monitoring other predators within a reserve, is essential, particularly those that are competitively inferior e.g. wild dogs (Carbone *et al.* 1997; Mills & Gorman, 1997; Hayward, 2006), cheetahs (Durant, 2000; Hayward *et al.* 2006), and hyaenas (Durant, 1998; Hayward, 2006) so that impact of that predator on other predators can be determined.

Finally, since change is constant, monitoring is essential to quantify that change and regular and rigorous monitoring of the vegetation, will assist management in improved decisions for both vegetation and animal management strategies. Long term studies examining habitat selection strategies, (e.g. seasonal effects; burning regimes) and predator-prey interactions, will provide management with a better understanding on how best to manipulate factors affecting habitat selection to maintain heterogeneity.

An important component of land management planning is the quantitative evaluation of habitats (Hobbs & Hanley, 1990; Fernández *et al*. 2006), where carrying capacity is inferred to be a measure of habitat value (Hobbs & Swift, 1985; Hobbs & Hanley, 1990). Current habitat evaluation models assume that data reflect the value of differential habitat types and rely on habitat use and availability data (Hobbs & Hanley, 1990). Understanding the animal's response to variability (temporal and spatial) at different scales is vital to designing effective monitoring programs (Wiens, 1989; Kie *et al.* 2002). Developing an understanding between scale and biodiversity requires knowledge of how species are related to variation in temporal and spatial scales (Bowyer & Kie, 2006) because scale is necessary to deciding how habitat data should be applied in resource management (Boyce *et al.* 2003).

One problem facing wildlife managers is managing the imbalances in herbivore/habitat relationships (Ferrar & Walker, 1974). With the development of private game reserves in South Africa, intensive management to prevent habitat degradation due to the over-utilisation by herbivores has become an important part of conservation planning (Behr & Groenewald, 1990; Bothma, 1995; Van Rooyen *et al*. 2000). Most mismanagement comes from utilising 'crisis management strategies' (Rosenzweig, 2001; Morris, 2003). However, management planning should accommodate ungulate responses at different scales, include individual to population interactions (Rosenzweig, 2001; Morris, 2003; Gordon *et al.* 2004), and acknowledge that species are ecologically different, on the basis of sex (Bowyer, 2004; Gordon *et al.* 2004), in order to accommodate differences among herbivore populations, and maintain habitat heterogeneity. Therefore, a holistic management view that incorporates all possible biotic and abiotic factors influencing habitat use will produce the most effective management system.

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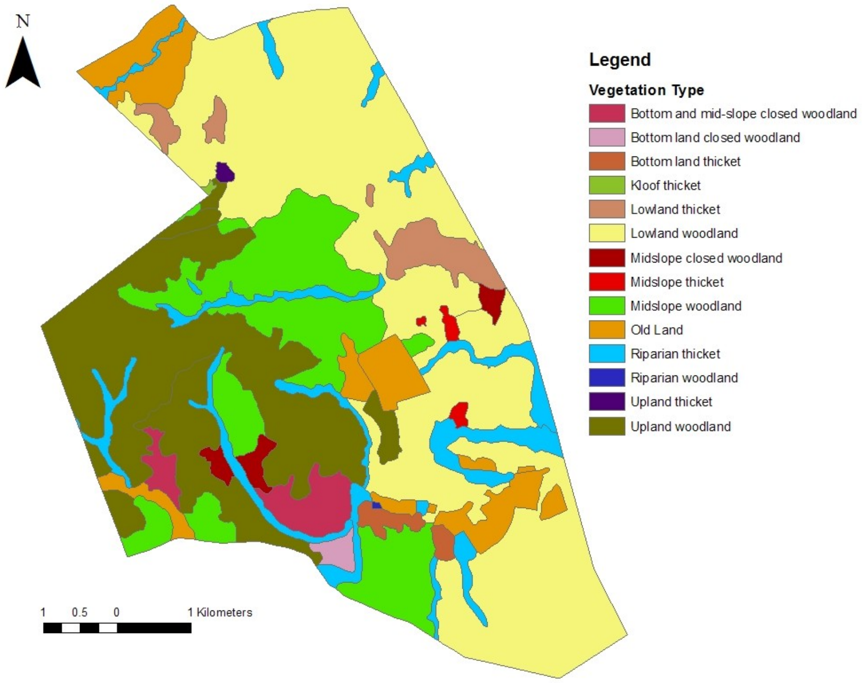
APPENDIX A.1. TPGR Habitat Types as described by Brousse-James & Associates, Thanda Management Plan (2002). Vegetation types were categorised broadly as Lowveld by Acocks (1988), and were separated using an aerial photograph.



APPENDIX A.2. The habitat types, plant composition and area of each habitat in TPGR. Common plant species that categorise each habitat type are included. *Ehretia rigida* and *Euclea spp* were excluded as they were abundant throughout the reserve.

Habitat Type	**Common Plant Species**	**Area (ha)**
Lowland Woodlands	*Acacia tortillis, A.nilotica, A.nigrescens, A. burkei Sclerocarya birrea, Ziziphus mucronata, Ozoroa engleri*	1691.54
Midslope Woodlands	*Spirostachys africana, A. nigrescens, A. burkei, Berchemia zeyheri, Ziziphus mucronata, Combretum apiculatum*	832.08
Upland Woodlands	*A. burkei, Berchemia zeyheri, Olea europa, Aloe marlothii, Combretum apiculatum*	873.76
Riverine	*A. robusta, A. xanthophloea, A. schweinfurtheii, Schotia brachypetala, Ficus sycomorus, Sideroxynon inerme,*	464.00
Old Lands	*A. karroo, A. tortillis, Dychrostachys cinerea,*	311.33

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APPENDIX A.3. The home ranges of lion in Thanda Private Game Reserve, 2004-2005.