ADAPTIVE RESOURCE USE IN A RE-INTRODUCED BLACK RHINOCEROS POPULATION

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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ABSTRACT

The aim of biological management for black rhinoceros (*Diceros bicornis*) conservation is to maximise meta-population growth rates to aid species recovery. This research investigated how adaptive resource use in response to seasonal variation in resource availability could affect maximum productive habitat capacity for this critically endangered species. Analysis was based on a population of rhinos which had shown excellent annual growth rates and low inter-calving intervals since re-introduction to Tswalu Kalahari Reserve in the Northern Cape of South Africa in 1995.

Acacia haematoxylon, a semi-evergreen species, was identified as the key resource forming the majority of diet contents during the late dry season. Use of this species resulted in a low level of seasonal variation in dietary contents of energy and protein. During the data collection period, energy and protein gains of individual female rhinos were estimated to exceed maximum requirements for reproduction throughout the seasonal cycle. An experiment designed to test the compensatory growth response of *A. haematoxylon* found that clipping trees in a way that simulated rhino browsing stimulated an increased growth response in the following wet season. This response indicated potential for a facilitatory relationship in the short term. A large proportion of the available area at Tswalu was not used by black rhinos. Home range location and habitat type selection within home ranges during the dry season were positively associated with two shrubveld habitat types containing greater *A. haematoxylon* biomass than other habitat types. Results from all aspects of field data analysis emphasized the importance of *A. haematoxylon* as the key dry season resource for black rhino at Tswalu.

Field data were used to develop a conceptual model of how seasonally adaptive resource use by black rhinos could determine maximum productive habitat capacity. The crux of the model was to estimate the highest population density at which female rhinos could attain maximum energetic gains for reproduction throughout the entire seasonal cycle. The most limiting period was the nutritional bottleneck during the late dry season. The rationale behind this approach was to enable females to maintain body condition and be capable of meeting nutritional requirements for reproduction throughout the year, thus minimizing inter-calving intervals and maximising population growth rates. Model projections indicated that female rhinos could not attain energy gains for reproduction throughout the dry season in certain habitat types due to low availability of *A. haematoxylon*. However, model outputs indicated potential for an increase in rhino density by approximately one third in the two favoured shrubveld habitat types, assuming that habitat conditions remained unchanged.

Availability of semi-evergreen *A. haematoxylon* was identified as the key vegetation component determining maximum productive habitat capacity for black rhino at Tswalu. Monitoring available biomass of this species at the end of the dry season could provide a simple plant-based indicator of how close the population is to maximum productive habitat capacity. Managing rhino densities in fenced reserves elsewhere around spatial and temporal availability of key resources may assist in achieving black rhino conservation goals of maximising metapopulation growth rates.

DEDICATION

Pour ma merveilleuse Pa et ma Maman brillante avec tout mon amour
et ma gratitude pour votre soutien incroyable dans toutes ses formes.

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In 1971, Joubert and Eloff stated that, "One finds many descriptions in literature of typical black rhino habitats… rhino are found in a wide variety of habitats, from sea level to about 12,000 feet, from plain and desert to high rain forests and cloud-soaked mountain ranges." Despite catastrophic losses, these ancient beasts are still hanging on in some of the last remaining wilderness. It is very much hoped that they will continue to do so.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

LIST OF TABLES

Chapter 2

Chapter 4

Chapter 5

Chapter 6

LIST OF APPENDICES

1. INTRODUCTION

1.1 Motivation for research

The catalyst for this research came from the management team at Tswalu Kalahari Reserve (Tswalu) due to concerns about increased levels of intraspecific aggression observed within the black rhinoceros population. Tswalu is a private wildlife reserve in the semi-arid savanna region of the Northern Cape of South Africa (Fig. 1), established in 1995 when 900 km^2 were converted from cattle farming. The reserve had grown to 1,080 km^2 by 2003 and was fenced into three separate sections, two of which contained black rhinos. Eight black rhinos of the *Diceros bicornis bicornis* south-western subspecies (Ashley *et al*., 1990) had been translocated to Tswalu in June 1995 from Etosha National Park in Namibia. The south-western subspecies (desert-adapted or arid ecotype) of black rhino (*D. b. bicornis*) is listed as critically endangered in the South Africa Red Data book (Friedman and Daly, 2004). The Tswalu population numbered 25 individuals by 2005 and had shown excellent population performance indicators (du Toit, 2001) since introduction with inter-calving intervals of 2.2 ± 0.1 years and annual growth rate of 13.2 ± 2.8 %. The exceptionally high annual growth rate was due in part to the adult female bias in population structure.

Recognition of the need for this research occurred during 2002, when levels of intraspecific aggression were observed to have increased. One female subadult was killed by the original adult bull and there were incidents in which other sub-adults were injured. Three independent sub-adults were translocated to a separate fenced area to prevent any further occurrences. Reserve management requested research to investigate this issue and develop strategies to mitigate future threats. This study was focussed on the five adult females in the Korannaberg section at Tswalu, of all which originated from the founder group. The remainder of the population consisted of two adult males, five subadult females, eight subadult males and five dependent calves by the end of the data collection period in December 2005. The four eldest males were exchanged with new males from Vaalbos National Park and Addo Elephant Park in South Africa during 2005 to augment genetic diversity in the founder population. In

2008, the five eldest male calves were removed and four new founders from Namibia (two male, two female) were introduced to a separate fenced area (Shaw, 2008).

It was suggested that social pressures causing intraspecific aggression could be an indication of incipient density dependence (Owen-Smith, 2001). Specifically, that the population was close to or had reached habitat capacity meaning individuals were experiencing nutritional restrictions due to limitations on resource availability (Fowler, 1987). Sustained high growth rate since introduction indicated that some habitat types within the reserve offered high quality habitat for black rhino, but the suitability of all habitat types was not known. Hence the intention of this research was to estimate capacity of the different habitat types to support black rhino to provide an indication of recommended stocking rates for managers.

The situation at Tswalu is symptomatic of a wider concern for black rhino conservation (Rachlow and Berger, 1998; Emslie, 2001a; Okita-Ouma *et al*., 2007). Current conservation strategies for black rhinos aim to maximise metapopulation growth rates by maintaining population growth rates above 5 % per annum, to minimize the loss of genetic diversity and mitigate impacts of poaching (Emslie and Brooks, 1999; Emslie, 2001a; Emslie, 2001b; Okita-Ouma *et al*., 2007). However, pressures on land use have forced most remaining populations into fenced reserves (Hall-Martin and Knight, 1994; Emslie, 2001a; Hall-Martin and Castley, 2003; Okita-Ouma *et al*., 2007) with a finite vegetation resource base upon which to support animal biomass. Without opportunities for dispersal, density dependent impacts can cause rhino population growth rates to decline in the longer-term (see case studies SADC RMG workshop, 2001; Patton *et al*., 2008; Okita-Ouma *et al*., 2010). There are also indications that at high population densities black rhino browsing may have negative impacts on important food plant species reducing longer-term habitat capacity (Hall-Martin *et al*., 1982; Brett, 2001; Heilman *et al*., 2006; Luske *et al*., 2009). Hence, credible estimates of carrying capacity of an area and active intervention policy to remove animals when this is exceeded are essential to achieve stated goals of maximum growth rates (Emslie, 2001a).

The IUCN African Rhino Specialist Group (AfRSG) has adopted a set figure of 75 % of total estimated ecological carrying capacity as the recommended black rhino stocking density to prevent density dependence issues and maximize productivity and population growth (Emslie and Brooks, 1999; Emslie, 2001b). This is intended to represent the maximum sustainable yield (MSY) (Caughley, 1976) or maximum productive carrying capacity (MPCC). That is, the population density that can sustain the highest annual removals, i.e. the highest population density where nutritional quality of the diet still allows females to breed rapidly (Emslie and Brooks, 1999). The SADC RMG black rhino carrying capacity model has been developed as a tool for calculating the carrying capacity for black rhino (Adcock, 2003; Adcock, 2006) based on four multiple-regression coefficients of six environmental variables (browse availability, browse suitability, annual rainfall, rainfall concentration, soil fertility and minimum temperatures). However, the RMG model is designed for use at a broad scale, using baseline data from fifteen rhino populations throughout southern and eastern Africa and does not explicitly consider the diminishing quantity and nutritional quality of woody plant food resources for black rhino during the dry season (Owen-Smith, 2002). Key resources eaten during the critical late dry period have been shown to form the major influence upon the density of herbivore populations that can be sustained in the long term in seasonally variable environments (Illius and O'Connor, 2000; Owen-Smith, 2002).

This thesis develops an alternative conceptual approach to estimating maximum productive habitat capacity for black rhino, which incorporates seasonal variation in food resource availability and focuses on maintaining individual female body condition, hence maximising their reproductive success. Tswalu offered an apt study site to achieve this; the semi-arid savanna ecosystem, with comparatively low woody plant species diversity, offered a simple system in which to determine seasonal patterns in rhino diet. Furthermore, there was a low level of inter-specific competition for browse resources as there are no elephants (*Loxodonta africana*) on the reserve and comparatively low numbers of kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*). The impact of predation of rhino calves on population success (Mills *et al*., 2006) was not a concern as there are no lions (*Panthera leo*) or spotted hyenas (*Crocuta crocuta*) in the Korannaberg section. There is no prescribed burning regime at Tswalu and natural fires are extinguished. Water availability did not restrict rhino movements, as the Korannaberg section contained 23 artificial waterholes distributed such that no part of the area was more than 5km from water.

1.2 Research aim

The focus of this research was initially envisaged as an assessment of "Black rhino home range use and habitat capacity" looking at how changing resource availability influenced black rhino resource use and movements at Tswalu and how this could limit habitat capacity.

Hence, the original objectives were;

1. To establish how changing food availability influenced black rhino resource use and movements
2. To assess the resultant dietary status of black rhino throughout the year
3. To assess woody vegetation impacts caused by black rhino browsing
4. To determine how intraspecific social influences on home ranges and sub-adult dispersal
5. To develop a habitat capacity model for black rhino at Tswalu Kalahari Reserve

However, preliminary data collection and analysis showed that one woody plant species, *Acacia haematoxylon*, formed the main dry season dietary resource in this area. The study was re-orientated around the concept that it is the quantity and quality of this key resource that determined habitat capacity for black rhino at Tswalu. This work was enhanced by collaboration with Dr Stephane Helary and his PhD research project assessing "Black Rhinoceros Nutritional Ecology". Inclusion of Tswalu as a study site in his project provided analysis of seasonal chemical content of key dietary plant species. Details of seasonal plant chemistry allowed greater understanding the chemical factors influencing seasonal diet selection and the resultant nutritional status of the rhinos throughout the year.

Therefore, the thesis title was updated to "Adaptive resource use in a re-introduced black rhinoceros population" to reflect the new focus. The overall aim shifted towards developing a more broadly applicable concept of maximum habitat capacity for black rhino based on data gathered from Tswalu. Adaptive resource use refers to the adaptive herbivore ecology approach (Owen-Smith, 2002), used to conceptualise the ways in which herbivores adapt their behaviour in relation to temporal and spatial changes in vegetation quality and quantity in seasonal environments.

The broad aim of this research was thus to gather data to develop a conceptual model of how adaptive resource use in response to seasonal changes in resource availability could influence maximum productive habitat capacity for black rhino.

1.3 Research objectives

1. To document the seasonal changes in plant species contribution to the diet of black rhinos at Tswalu and relate diet selection to plant phenology and chemistry.
2. To determine resultant seasonal changes in the nutritional gains of female black rhinos at Tswalu and make comparisons with estimated nutritional requirements for reproduction.
3. To quantify the growth response of the key dry season resource, *Acacia haematoxylon*, to simulated browsing by black rhinos.
4. To establish seasonal habitat selection and use by black rhinos at Tswalu in relation to the distribution of seasonal dietary resources.
5. To develop a habitat capacity model to project recommended densities for maximum productivity of a black rhino population, incorporating seasonal changes in resource availability and quality.

1.4 Literature Review

1.4.1 Diet selection in browsing herbivores

The process of diet selection determines both the quantity and the quality of food intake and subsequently, the nutritional gains of individual animals, their physiological condition, growth rates and potential reproductive and survival rates (Owen-Smith and Novellie, 1982; Hanley, 1997; Owen-Smith, 2002). Hence, understanding of herbivore diet selection forms the fundamental basis for assessing the suitability and ultimately capacity of different habitat types and geographic areas (Owen-Smith, 2002; Owen-Smith, 2003). The diet selection process for herbivores is highly complex due to interactions between physiological constraints and different possible objectives as well as the great heterogeneity of food resources available (Owen-Smith and Novellie, 1982). For browsing herbivores in savanna environments the decisions of diet selection are further compounded by seasonal changes in available plant quantity and quality (Owen-Smith and Novellie, 1982; Owen-Smith and Cooper, 1987; Cooper *et al*., 1988; Owen-Smith, 2002). In African savannas, trees and shrubs regenerate much of their above-ground biomass within a few weeks of the start of the wet season in the form of leaves and shoots (Rutherford, 1980). This photosynthetic material is retained throughout the wet season until shed completely at the beginning of the dry season. As the remaining stems are less nutritious than actively metabolizing plant parts, herbivores must respond to these seasonal changes in food quality and quantity. During the late dry season herbivores may be forced to utilise the dormant twigs from deciduous species and broaden their diet selection to include physically-defended species with a lower intake rate as well as chemically-defended leaves on evergreen species (Owen-Smith, 2002). Nutritional gains will therefore vary dependent upon the intake rates of plant species selected, as spinescent and physically defended species require longer handling times than non-defended species (Cooper and Owen-Smith, 1986; Illius *et al*., 2002).

Nutritional quality of woody plants for browsers is determined by their proportional chemical contents which fall into three main categories (Cooper *et al*., 1988) i) nutrients, including protein and minerals, ii) fibre levels which influence digestion rates and iii) plant secondary metabolites such as tannins which have a negative impact on digestion rates or function as toxins forming a chemical defense to deter browsing (Robbins *et al.*, 1987). Diet selection of available browse by herbivores is thus influenced by physical and chemical defences of woody plants (Freeland and Janzen, 1974; Bryant *et al.,* 1991), as well as nutritional characteristics of leaves in different phenological stages (Cooper and Owen-Smith, 1985; Owen-Smith and Cooper, 1987; Cooper *et al.*, 1988).

For example, acceptance ratings for plant species by kudu are closely related to indices of nutritional value based on relative nutrient content, as represented by crude protein, and anti-nutrient content, as represented by condensed tannins (Cooper *et al.*, 1988; Owen-Smith, 1994). During the dry season, woody plant species were added to kudu diet approximately in the order of their relative protein-condensed tannin difference or estimate of available protein. However, the high acceptability of certain otherwise unpalatable species during the new leaf phenophase was related to elevation of protein levels relative to condensed tannin contents (Owen-Smith and Cooper, 1987).

Black rhino have shown a clear preference for *Acacia* species as food plants in habitats throughout East and southern Africa from both arid regions and more mesic areas (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al.*, 1994; Muya and Oguge, 2000; Kipchumba, 2002; Buk and Knight, 2010). *Grewia* species and *Combretum* species may also contribute to the diet to a significant extent (Joubert and Eloff, 1971; Muya and Oguge, 2000; Kipchumba, 2002; Buk and Knight, 2010). A wide range of forb species form an important part of black rhino diet in most habitats where available during the wet season (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al.*, 1994; Muya and Oguge, 2000; Kipchumba, 2002). The overall diversity of food plants utilised has been found to be greater during the wet season than during the dry season in a range of habitats (Goddard, 1968; Mukinya, 1977; Emslie and Adcock, 1994; Oloo *et al.*, 1994; von Holdt, 1999).

Analyses of the factors determining diet selection in black rhino have shown inconclusive results. Different authors have found rhino to select for high protein content (Dierenfeld *et al.* 1995; Ganqa *et al*., 2005) or for high fibre content (Loutit *et al*., 1987; Muya and Oguge, 2000). Similarly, the impact of secondary metabolites upon black rhino diet selection is unclear. Dierenfeld *et al*. (1995) concluded that black rhino do not select against browse containing levels of soluble tannins. However, the impact of condensed tannins and other secondary metabolites on the diet selection is not well understood (Hall-Martin *et al*., 1982; Loutit *et al*., 1987; Muya and Oguge, 2000; Clauss *et al*., 2006; Ndlovu and Mundy, 2009). Captive black rhino fed on non-native plant species are known to suffer from iron overload and oxidative stress (Paglia and Dennis, 1999). It has been suggested that rather than acting as a deterrent to browsing, some tannins may form a vital component of black rhino diet for binding excess dietary iron and improving antioxidant status (Clauss *et al*., 2006).

Browse availability and quality in some areas maybe fundamentally unsuitable to support black rhino. Black rhino translocated from the Zambezi valley to private conservancies in the midland region of Zimbabwe became emaciated and died. Severe over-utilisation of vegetation growing on termite mounds emphasized the unpalatability or toxicity of most of the browse in the surrounding *Brachystegia* woodland (du Toit *pers. comm.* in Owen-Smith, 1993).

1.4.2 Seasonal nutritional status

For herbivores to be able to survive in a region, vegetation components providing an adequate rate of intake of energy, protein and other essential nutrients must be available throughout the year (Owen-Smith and Novellie, 1982). The end of the dry season is a critical period for browsing herbivores and areas retaining plant species of highest quality or quantity of forage at this time are essential to the survival of a population through this period (Illius and O’Connor, 2000). The animal population size that can be maintained within a region is dependent upon the extent of these dry season resources (Illius and O’Connor, 2000; Owen-Smith, 2002). Hence, for herbivore species to survive and reproduce throughout the year, nutritional balance is dependent on the availability of particular vegetation components to meet nutritional requirements throughout the annual cycle, but most critically during the bottleneck period at the end of the late dry season (Owen-Smith and Cooper, 1989; Owen-Smith, 2002).

Energy has been shown to be the more limiting nutrient for browsers than protein (Bryant *et al*., 1980; Owen-Smith and Novellie, 1982; Owen-Smith and Cooper, 1989). Indigestible fibre content increases in the diet of browsing herbivores during the drier periods when deciduous woody plant species are without leaves and remaining fibre content in twigs is more lignified than that of grass species, hence less digestible (Bryant *et al*., 1980; Pellew, 1984; Owen-Smith and Cooper,1989). However, crude protein contents of browsing herbivore diets may also show a decline during the dry period when most of the forb species have died and deciduous species have shed their leaves. Protein digestibility may be further restricted by secondary metabolites within remaining leaves on evergreen species (Bryant *et al*., 1980; Hall-Martin et al, 1982; Pellew, 1984; Owen-Smith and Cooper, 1982). Regardless, protein has never been shown to be limiting for maintenance for browsers, even during dry periods (Bryant *et al*., 1980; Owen-Smith and Novellie, 1982; Owen-Smith and Cooper, 1989; Atkinson, 1995).

Estimates of seasonal nutritional gains have not been published for free-ranging black rhino. A number of studies have identified the seasonal diet or chemical composition of black rhino browse species (Hall-Martin *et al*., 1982; Loutit *et al*., 1987; Ghebremeskel *et al*., 1991; Oloo *et al*., 1994; Dierenfeld *et al*., 1995), but have not related these to estimated requirements. However, Atkinson (1995) created estimates of seasonal nutritional gains for captive black rhinos in bomas in Zimbabwe. Comparisons of estimated gains in relation to nutritional requirements for maintenance indicated that rhino could attain protein needs throughout the seasonal cycle, but energy gains declined below estimated maintenance requirements during the dry season (Atkinson, 1995).

1.4.3 Browsing herbivore-vegetation dynamics

Browsing by large herbivores can have a positive facilitatory effect on forage production by woody plant species (Crawley 1983; Pellew 1980; du Toit *et al.* 1990; Fornara and du Toit, 2007). By altering plant root:shoot ratio, shoot removal may lessen the competition for nutrients between shoots (McNaughton, 1983; Danell and Bergström, 1989; du Toit *et al.*, 1990). Removal of terminal meristems can also break the apical dominance and suppression of lateral meristems, altering the growth form of a plant (Aarssen, 1995). Hence, plants may increase the number of shoots produced in response to browsing as an adaptation to reduce the impact of further browsing by modifying the herbivores foraging behaviour (Vivås *et al*., 1991). Heavily browsed plants may also have higher browse quality with reduced chemical defence and increased shoot nutrients, therefore attracting increased browsing pressure (du Toit *et al.* 1990). Pellew (1980) found that *Acacia* species are very tolerant of sustained high levels of offtake and suggested that they could lose up to 85% of seasonal growth without any reduction of plant regeneration. Teague (1989) showed that *Acacia karroo* has a very strong compensatory growth response to herbivory by goats and is capable of withstanding very intense and frequent defoliations.

The impact of browsing has been shown to be closely correlated to the amount of biomass removed and seasonal timing. Teague (1984) found that *Acacia karroo* was sensitive to defoliation during the early flush following the dormant dry season and during the reproductive phase normally occurring in the summer. Milton (1988) found that *A. tortilis* trees cut in summer had significantly lower shoot mass production than control or winter pruned trees. Browsing stimulating compensatory growth may thus have a facilitatory effect, creating a 'browsing lawn' (Pellew, 1983; du Toit *et al*., 1990; Fornara and du Toit, 2007).

However, the degree of regrowth following browsing depends on the availability of limiting resources such as water or nitrogen, the level of plant reserves and the plant growth form. Long-term compensatory regrowth is therefore reliant on the ability of the herbivore to alter availability of nutrients and the abilities of the plants to respond to it (Pastor *et al*., 1997).

There have been no experimental analyses on the impact of black rhino browsing on growth response of important browse species. However, high densities of rhino within fenced reserves have had major negative effect on habitat level resources. Black rhino caused a significant depletion of browse resources from the bushland and bushed grassland areas over a twenty year period at Solio Ranch in Kenya (Brett, 2001). Coverage of *Acacia drepanolobium* was steadily reduced from inside the reserve due to black rhino browsing pressure. In Addo Elephant Park, high densities of black rhino resulted in replacement of thicket habitat by open scrub and dwarf shrub communities (Hall-Martin *et al*., 1982). Black rhino in the Eastern Cape of South Africa feed extensively on tree euphorbia (*Euphorbia bothae*) (Ganqa *et al.*, 2005; Brown, 2008) and recent research suggests levels of use by re-introduced black rhino populations may not be sustainable (Heilman *et al*., 2006; Luske *et al*., 2009; Cowling *et al*., 2009). Declines in *Acacia* species abundance due to megaherbivore browsing have been observed in fenced reserves in Kenya (Birkett, 2002; Birkett and Stevens-Wood, 2005) and South Africa (Bond and Loffell, 2001).

1.4.4 Seasonal habitat use and selection

Habitat selection can provide an indication of habitat quality and hence the capacity of an area to support an animal population at optimal population growth (Morris, 2003). However, habitat use is additionally dependent on social factors as well the capacity of the habitat to provide a limiting resource throughout the seasonal cycle (Mace and Harvey, 1983). Hence, animals may utilise habitat types within a home range to different degrees depending on seasonal conditions and careful consideration of appropriate temporal and spatial scales is essential for successful analysis and interpretation (Orians and Wittenberger, 1991). Tufto *et al*. (1996) found that female roe deer (*Capreolus caprelus*) partially expanded the size of their home range in response to decreasing food supply during the dry season. Similarly, grazing female white rhino (*Ceratotherum simum*) restricted their movements within a home range core when water was abundantly available and forage quality was high during the wet season, but increased home range area during the dry season as forage abundance and quality decreased (Owen-Smith, 1973).

Conversely, a number of browsing herbivores have larger home range area during the wet season compared to the dry season, due to animals shifting between distinct habitat types to utilise seasonally available food resources. Hence, habitat use was driven by smaller-scale changes in food availability. Kudu in Kruger Park foraged in both plains and hill ecotone during the wet season, possibly to utilise forbs present within the plains habitat (Owen-Smith, 1979). During the dry season the plains ecotone was largely abandoned and the hill ecotone was more widely utilised as the kudu included a higher proportion of woody species retaining foliage in this area (Owen-Smith, 1979). Kudu at Nylsvley Nature Reserve utilised *Acacia* habitat with higher rates of forbs in the wet season, but in the dry season remained in the predominant *Burkea* habitat with higher levels of woody vegetation (Owen-Smith, 1993; Owen-Smith, 1994). Black rhino populations have also been observed to show a pattern of changing habitat use in response to rainfall and resultant vegetation growth (Owen-Smith, 1988). Black rhino tend to range more widely onto open grassland areas to utilise forbs present during the wet season and have more restricted ranges on woody vegetation in hilly regions or in riverine areas close to water during the dry season (Goddard, 1967; Joubert and Eloff, 1971; Kiwia, 1989; Oloo *et al*., 1994).

1.4.5 Density dependence and carrying capacity.

The theory of ecological carrying capacity has been used to measure the suitability of an area for herbivore species based on the equilibrium where herbivore population and vegetation growth rate is zero (Caughley, 1976). Subsequently, the density at which animal population growth rate is maximised is referred to as the economic carrying capacity (Caughley 1976) or maximum sustained yield (MSY) (McCullough, 1992). An estimate of 75 % of ecological carrying capacity has been adopted as MSY or maximum productive carrying capacity (MPCC) for black rhino population management (Emslie and Brooks, 1999).

Large mammals are regulated largely by direct effects of food limitations on survival and reproduction (Fowler, 1987). As population density increases, the body mass of large herbivores typically declines, affecting individual performance traits such as age of first reproduction and juvenile survival (Bonenfant *et al*., 2009). At high density, nutritional restrictions can delay the age of first calving and increase breeding intervals, thus decreasing reproductive success of adult females. For megaherbivores, with adult body mass in excess of 1000 kg, the major regulatory responses are known to operate through decreasing fecundity (Owen-Smith, 1988). Observed demographic responses by black rhinos to nutritional restrictions are increases in inter-calving intervals and a delay in the age at which females first reproduce (Hitchins and Anderson, 1983; Hrabar and du Toit, 2005). Hence, to achieve maximum productivity within black rhino populations, females should be maintained at a density where no nutritional restrictions affect reproduction rates (Fowler, 1987; Sæther, 1997; Rachlow and Berger, 1998; Bonenfant *et al*., 2009).

1.4.6 Adaptive resource ecology

The theory of adaptive resource use by herbivores in response to seasonal variation in resource availability provides an alternative approach to assessing habitat capacity. This approach has shown habitat suitability is ultimately dependent upon the adaptive responses of herbivores to spatial and temporal variability in resource availability and quality (Owen-Smith, 2002). Fundamental to this approach is the concept that animal population size is primarily regulated by dry season resources and is largely uncoupled from wet season resources (Scoones, 1995; Illius and O'Connor, 2000). Therefore, the suitability of a habitat for herbivore species must take into account seasonal fluxes in resource availability in terms of different vegetation components (Owen-Smith, 2002).

Plant species within herbivore diets can be divided into vegetation components as defined by Owen-Smith (2002). The following categories of Owen-

Smith (2002) were adapted for black rhino at the RMG Black rhino biological management workshop; quality resources needed to support the highest reproductive potential (e.g. high protein plus highly digestible plant material such as forbs and young *Acacia* leaves) which may only be available seasonally; staple resources forming a large part of the wet season diet (e.g. deciduous browse such as *Acacia* species); reserve resources largely supporting rhino during each dry season and may include evergreens and certain succulents. Buffer resources are needed whenever reserve resources run out (e.g. during a particularly bad dry season), and may include chemically defended evergreens which will rarely be used if resources are not limiting at all. Bridging resources are eaten in the crunch period between late dry season and wet season in southern African summer rainfall regions and may include early flushing deciduous plants or specific localities within an area (Adcock *et al*., 2001).

Particularly important is the availability of resources throughout the late dry season, which forms the critical period for browsers in savanna regions when deciduous trees have lost their leaves (Owen-Smith, 2002). These are defined as "key" resources, and it is the available biomass of these plant species which determines the animal biomass which can be sustained throughout the year (Owen-Smith, 2002). The modelling format developed for assessing adaptive resource use is a growth, metabolism and mortality (GMM) model (Owen-Smith, 2002). This is based on the metaphysiological modelling methodology of Getz (1991, 1993). A GMM model for habitat suitability calculates an aggregated herbivore population biomass that can be supported from plant biomass. Animal biomass is gained by consuming different categories of plant resources, relative to animal physiological attrition and mortality losses (Owen-Smith, 2002).

In summary, the adaptive resource use approach is based on the paradigm that it is availability of key resources during the most limiting period, which determines the biomass of animals that can be supported. As discussed, in large herbivores population regulation occurs via impacts on reproductive success rather than adult survival (Fowler, 1987; Sæther, 1997; Bonenfant *et al*., 2009). Hence, the new concept introduced here is the idea of managing black rhino population densities to maximise individual female reproductive performance, based upon spatial and temporal availability of key resources. Rhino numbers can be managed so the nutritional quality of an individual's diet allows females to meet reproductive requirements throughout the entire seasonal cycle. The aim of this approach is to prevent declines in female body condition, hence allowing minimum intervals between calves and maximum population growth rates (Rachlow and Berger, 1998). The resultant rhino density estimate is defined here as the "maximum productive habitat capacity".

1.5 Thesis structure

The focal chapters (Chapters 2 – 6) in this thesis (Fig. 2) have been written in the form of individual scientific papers each containing an Abstract, Introduction, Methods, Results and Discussion section. The rationale behind this approach is to ease the process of submission for publication in peer-reviewed journals, with the hope that this will aid the dissemblance of knowledge to a wider audience and enhance opportunities for practical conservation benefit.

Chapter 1 forms an introduction to this study, showing the evolution of the research aim and objectives. The motivation for this research is explained and a review of the literature relating to the key ecological questions addressed.

The following two chapters are closely linked, with *Chapter 2* describing changes in the diet content of five focal female rhinos throughout the year in relation to key plant species phenology and chemistry and assigning them to the generic resource types of Owen-Smith (2002). *Chapter 3* assesses the resultant seasonal nutritional status of the female rhinos based on the above diet data. Estimated nutritional gains each month are compared with predicted requirements for reproduction. Outputs are related to population performance and habitat capacity at Tswalu.

Chapter 4 describes a simulated browsing experiment designed to quantify the growth response to clipping simulating rhino browsing on the main dry season dietary resource in this area (*A. haematoxylon*). This was motivated by the preliminary findings of *Chapters 2* and *3* indicating the importance of this plant species in rhino diet. The purpose of this experiment was to increase understanding of the impact of rhino browsing on available biomass of this key resource.

Chapter 5 relates seasonal habitat use by female black rhino at Tswalu to seasonal resource availability in eight habitat types within the reserve. Details of seasonal plant phenology and chemistry and plant species biomass in different habitat types were combined in *Chapter 6* to develop a metaphysiological model of maximum productive habitat capacity for black rhino. The model compared weekly energetic gains against requirements for reproduction to project recommended rhino densities in different habitat types. This chapter thus assesses the concept central to the thesis, that is it the temporal and spatial availability of the key resource in the late dry season which determines maximum productive habitat capacity.

Chapter 7 summarises the overall conclusions from this work, highlighting the key ecological and practical outcomes for black rhino management at Tswalu. Further suggestions are made as to how findings from this study could be extended to help achieve goals for black rhino conservation elsewhere.

Although not yet submitted for publication, the findings from most chapters have been presented at national and international conferences:

Chapter 2**:**	South African Wildlife Management Association symposium, Kathu, Northern Cape, South Africa: September 2004
Chapter 3:	*Invited speaker* Rhino Specialists workshop, Society for Conservation Biology, Port Elizabeth, South Africa: July 2007
Chapter 4:	5th Annual Kruger Network Meeting, Skukuza, Kruger National Park, South Africa: April 2007 *Invited speaker* “Game Management in Africa” workshop International Union of Game Biologists, Uppsala, Sweden: August 2007

Chapter 6: 6th Annual Kruger Network Meeting Skukuza, Kruger National Park, South Africa: April 2008

Invited speaker IUCN African Rhino Specialists Group meeting: Lake Manyara, Tanzania: May 2008

1st Annual Diamond Route Conference, Johannesburg, South Africa: November 2010

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Figures

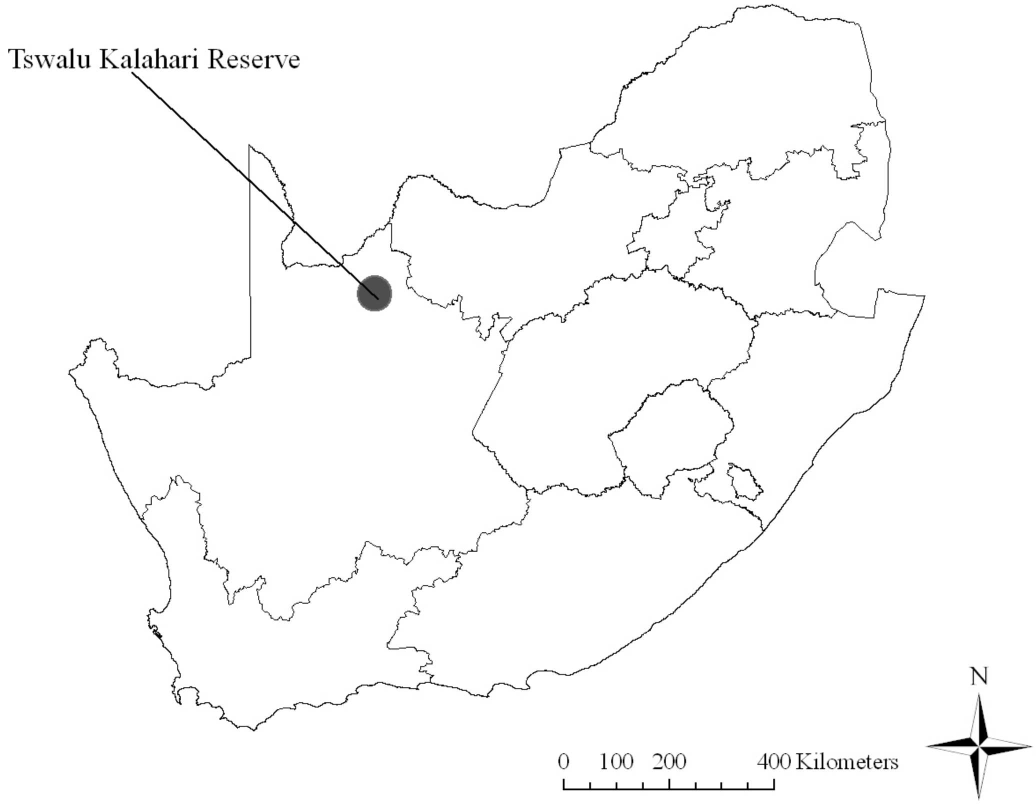

Figure 1. Map of South Africa showing location of Tswalu Kalahari Reserve.

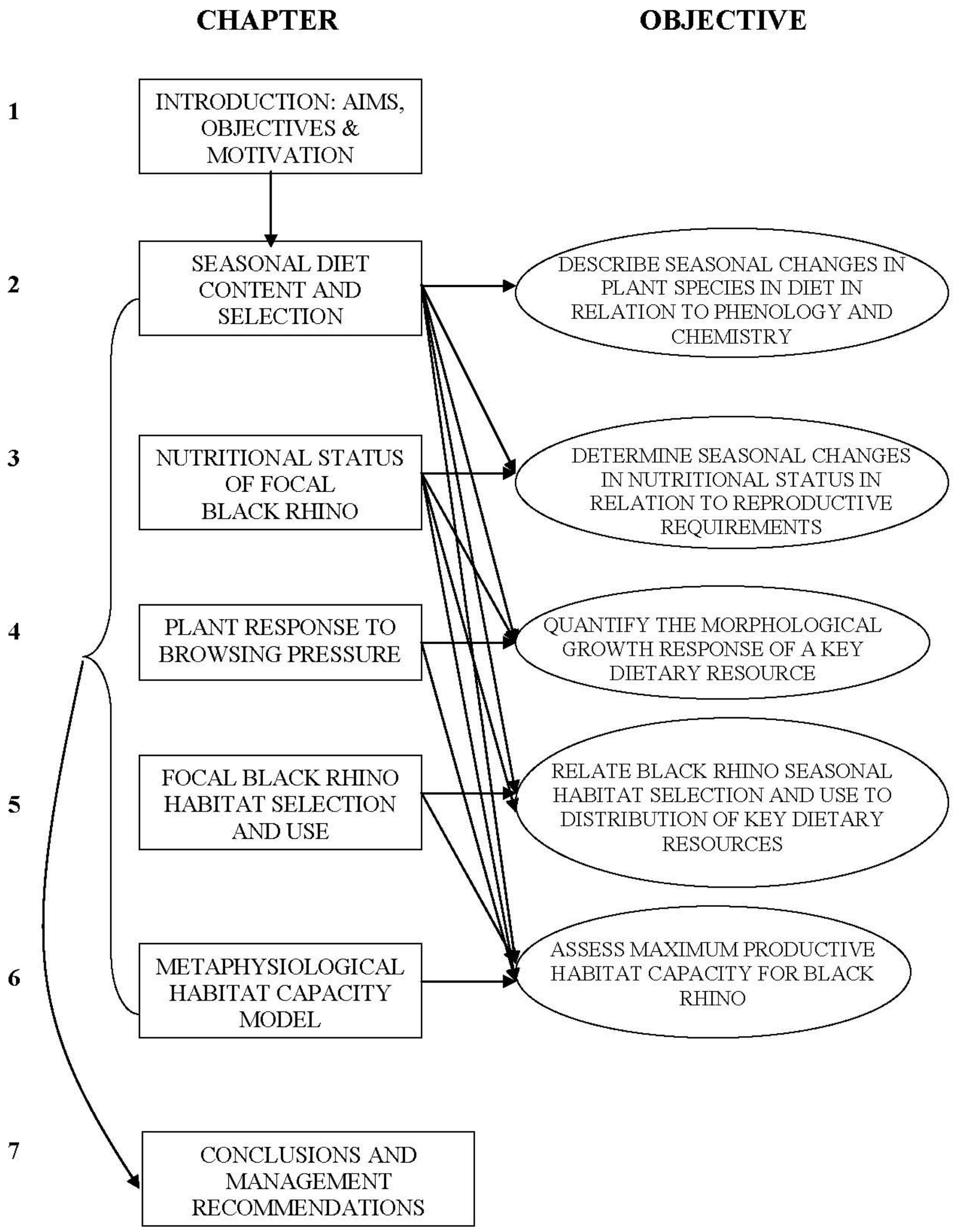

Figure 2. Diagram of research objectives and thesis structure.

2. Seasonal variation in black rhinoceros (*Diceros bicornis*) diet in relation to woody plant species phenology and chemistry in a semi-arid savanna.

2.1 Abstract

Seasonal diet content and the influence of seasonal changes in plant phenology and chemical content on plant species acceptability was determined for black rhinoceros at Tswalu Kalahari Reserve in South Africa. Rhino feeding tracks were followed and the number of bites on each plant species and plant phenology were recorded. A total sample of 29,873 bites was recorded between January 2004 and December 2005. Seven browse species contributing 80% of the estimated dry mass of the diet were analysed for NDF, crude protein and condensed tannins.

During the wet season the diet was divided between three shrub species, *Grewia flava*, *Acacia mellifera* and *Acacia haematoxylon.* As deciduous species lost their leaves, two semi-evergreen species, *A. haematoxylon* and *Monechma incanum,* increased in their dietary contribution. *Acacia haematoxylon* represented more than 75% of diet content for the all the focal black rhino during late dry season months. There was no difference in acceptability indices among individual rhino despite differences in plant species availability suggesting selection was determined by some inherent measure of plant quality.

Plant phenology appeared to be the major factor determining seasonal diet acceptability, with black rhino selecting plant species which retained leaves in the late dry season. Hence, within each season there was a pattern of rhino selecting plant species with highest levels of protein and digestible organic matter. Black rhino at Tswalu consumed shoots containing 9.3 % condensed tannins during the wet season indicating that these levels of plant chemical defence did not act as a deterrent. Neither hooked thorns on *A. mellifera* nor straight, slender thorns on *A. haematoxylon* deterred browsing by black rhino.

Diet selection by black rhinos appears less affected by plant spinescence and condensed tannin content than that of kudu (*Tragelaphus strepsiceros*) or impala

(*Aepyeros melampus*). Accordingly, *A. haematoxylon* was identified as the key resource which sustained black rhino during the late dry period in this area.

Key words: Crude protein; digestible organic matter; condensed tannins; plant spinescence; plant phenology; leaf retention; *Acacia haematoxylon*

2.2 Introduction

Diet selection by herbivores determines the quantity and quality of their food intake and therefore nutritional status, physiological condition and potential reproductive and survival rates (Hanley, 1997). Knowledge of herbivore species dietary content and understanding of the factors influencing plant species selection therefore forms a fundamental basis for assessing habitat capacity and population success for endangered species. In African savannas, most woody plant species are deciduous and lose their leaves during the dry season, leading to restrictions in availability of food resources for browsing herbivores at this time. The nutritional content of woody plant parts is related to phenological stages (Westoby, 1978) and as most shoot and leaf growth on woody plants takes place prior to or early in the wet season (Rutherford, 1980), diet quality also varies between seasons due to variable conditions for plant growth. Hence, there is a cycle of high resource availability and quality during the wet season when deciduous species retain leaves, followed by a decrease in availability and quality as leaves are lost throughout the drier periods (Owen-Smith, 2002).

Nutritional quality of woody plants for browsers is determined by their proportional chemical contents which fall into three main categories (Cooper *et al*., 1988) i) nutrients, including protein and minerals, ii) fibre levels which influence digestion rates and iii) plant secondary metabolites such as tannins which have a negative impact on digestion rates or function as toxins forming a chemical defense to deter browsing (Robbins *et al*., 1987). Condensed tannins are especially important as a defence mechanism in woody plants (Furstenburg and van Hoven, 1994; Hagerman *et al.,* 1992; Cooper and Owen-Smith, 1985). Diet selection of available browse by herbivores is thus influenced by chemical defences of woody plants (Freeland and Janzen, 1974; Bryant *et al.,* 1991), as well as nutritional characteristics of leaves in different phenological stages (Cooper and Owen-Smith, 1985; Owen-Smith and Cooper, 1987; Cooper *et al*., 1988). The effectiveness of these defences may vary among browsers and woody species. Three species of browsing ruminants (kudu, *Tragelaphus strepsiceros*, impala, *Aepyeros melampus* and Boer goats) showed a threshold response to condensed tannins, with plant species containing leaf concentrations of more than 5 % being mostly rejected as food during the wet season period (Cooper and Owen-Smith, 1985). Cooper *et al*. (1988) showed that in fact the palatability of woody plant foliage to kudu and impala was not dependent upon any single chemical factor but rather upon the difference between nutrient contents, as represented by protein, and secondary metabolites, as represented by condensed tannins. During the dry season, species were added to the diet approximately in the order of their relative protein-condensed tannin difference or estimate of available protein. The high acceptability of certain otherwise unpalatable species during the new leaf phenophase was related to elevation of protein levels relative to condensed tannin contents. Herbivore diet selection can be seen as a matter of balancing nutritional benefits against various costs and restrictions (Stephens and Krebs, 1986; Owen-Smith, 2002).

Alternatively, woody plant species may develop thorns or other physical barriers to reduce foliage losses to browsing herbivores. Cooper and Owen-Smith (1986) found that plant thorns and spines restricted intake in terms of bite sizes or eating rates by kudu, impala and Boer goats. It was shown that plants which are chemically defended against vertebrate herbivory tend to be more prominent on nutrient-deficient soils, while those with physical defences (e.g. thorns) are predominant on fertile soils (Owen-Smith and Cooper, 1987). However, the influence of plant chemical and physical defences is dependent upon the body size and feeding adaptation of a particular species of browsers. The effectiveness of physical deterrents against very large mammalian herbivores such as black rhino is questionable, given their wide use of *Acacia* species and *Euphorbia* species with thorns (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Loutit *et al*., 1987; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al*., 1994; Bhima and Dudley, 1996; von Holdt, 1999; Muya and Oguge, 2000; Ganqa *et al*., 2005).

Analysis of patterns of diet selection by kudu revealed categories of vegetation components which serve as nutritional stepping-stones throughout the year (Owen-Smith, 2002). Generic resource types included (i) quality resources needed to support the highest reproductive potential which may only be available seasonally; (ii) staple resources which form a large part of the wet season diet and often consist of deciduous browse; (iii) reserve resources forming key resources necessary to support animals through the critical period at the end of the dry season, which may include evergreens and certain succulents; (iv) buffer resources which are needed whenever reserve resources run out (e.g. during a particularly bad dry season) and will rarely be used if resources are not limiting and (v) bridging resources which are eaten in the crunch period between late dry season and wet season in southern African summer rainfall regions and may include early flushing deciduous plants or specific localities within an area (Owen-Smith, 2002). For herbivores in savannas, the resource type upon which the animals are dependent during the bottleneck in the late dry period is defined as the key resource, upon which potential animal density is primarily reliant (Scoones, 1995; Illius and O'Connor, 2000).

Studies from southern and eastern Africa have found that black rhino diets tend to contain a large overall number of species, though only a small number of these contribute the majority of the biomass consumed (Goddard, 1968; Goddard, 1970; Joubert and Eloff, 1971; Hall-Martin *et al*., 1982; Loutit *et al*., 1987; Oloo *et al*., 1994; Muya and Oguge, 2000; Lieverloo *et al.,* 2009; Buk and Knight, 2010). The overall diversity of plant species utilised has been found to be greater during the wet season than during the dry season in a range of habitats (Goddard, 1968; Mukinya, 1977; Emslie and Adcock, 1994; Oloo *et al*., 1994). Black rhino have been shown to modify their diet seasonally throughout their range; generally consuming deciduous woody plant species and herbaceous browse when available in the wet season and becoming more dependent on succulents or evergreen species where available during the dry season (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Oloo *et al*., 1994; Hall-Martin *et al*., 1982; Atkinson, 1995; Ganqa *et al*., 2005). A preference for *Acacia* species has been observed in both arid regions and more mesic areas (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al*., 1994; Bhima and Dudley, 1996; von Holdt, 1999; Muya and Oguge, 2000; Kipchumba, 2002; Ganqa *et* *al*., 2005; Ndlovu and Mundy, 2009). *Grewia* species have also been found to contribute to the diet to a substantial extent in both Eastern and Southern Africa (Joubert and Eloff, 1971; Mukinya, 1977; Hall-Martin *et al*., 1982; Emslie and Adcock, 1994; Muya and Oguge, 2000; Kipchumba, 2002).

Most literature published to date does not consider seasonal changes in plant availability or quality and perhaps for this reason does not provide clear explanations for black rhino diet selection in relation to plant chemical contents. Some studies have found high protein levels to be the major factor relating to plant species preference (Dierenfeld *et al.* 1995; Ganqa *et al*., 2005). Other work suggests black rhino appear to avoid species with high protein levels (Muya and Oguge, 2000) and show an apparent selection for high fibre levels (Loutit *et al*., 1987; Muya and Oguge, 2000). This apparent negative selection for protein may actually be due to avoidance of plant secondary metabolites content (Hall-Martin *et al*., 1982; Loutit *et al*., 1987; Muya and Oguge, 2000; Ndlovu and Mundy, 2009). Van Lieverloo *et al.* (2009) found no correlation between utilization of plant species by black rhino and their digestibility, macro-elements, water content, fibre and leaf:twig ratios or availability.

The aim of this paper was to determine seasonal diet content of black rhino at re-introduced to a private game reserve in the Northern Cape of South Africa and assess the influence of seasonal changes in plant phenology and chemical content on plant species acceptability.

The specific objectives and hypotheses were to;

1. Establish rhino diet content in different seasons.

H_1 In the dry season, proportional diet content of species retaining leaves would increase.

2. Determine acceptance of plant species in different seasons and relate these to generic resource types as defined by Owen-Smith (2002).

H_1 Deciduous plant species would form staple resources during the wet season, with acceptance decreasing during the season in which they were without leaves.

H_2 Evergreen species would form reserve resources, with acceptance increased during the early dry, late dry and transition season compared to the wet season.

3. Relate the seasonal acceptance of plant species to their physical and chemical characteristics.

H_1 Black rhino would show higher acceptance for plant species retaining leaves in the dry season than those without.

H_2 Black rhino would not be deterred by presence of thorns.

H_3 Black rhino would show higher acceptance for plant species with highest levels of protein and digestible organic matter in each season.

H_4 Black rhino would show higher acceptance for plant species with condensed tannin content below 5%.

2.3 Methods

Study site

This study was conducted at Tswalu Kalahari Reserve (Tswalu), a private game reserve covering 1,080 km^2 in the Northern Cape of South Africa (S 27°04’ - 27°44’ and E 22°10’ - 22°36’). The geology of this area is predominantly aeolian sand and vegetated dunes of the Kalahari Group Formation, with some alluvium, gravel, limestone and silcrete (van Rooyen, 1999). The predominant vegetation type has been classified as Shrubby Kalahari Dune Bushveld (Low and Rebelo, 1996) which has a relatively open structure. Abundant tree and shrub species in the area include *Acacia erioloba¸ Acacia haematoxylon*, *Acacia mellifera*, *Boscia albutrunca*, *Grewia flava*, *Rhus tenuinervis* and *Terminalia sericea* (van Rooyen, 1999). Water was provided by man-made waterholes sourced from dams and boreholes on the property and the Kalahari pipeline, which were distributed such that no part of the study area was greater than 5 km from a waterpoint.

The climate is semi-arid and rainfall is seasonal, generally occurring as thunderstorms between October and March, and is highly variable between years. On average over 80 % of annual rainfall (82.8 % from 1973 to 2005) occurs between October and March. Monthly rainfall data were compiled from daily farm records

(1973-2002) and daily records maintained by staff at Tswalu (2003-2005). Mean annual rainfall in the area from 1973 to 2005 was 280 ± 164 mm (mean ± SD) (Unpublished data). Rainfall was slightly below average (229 mm) during January 2004 - December 2004 and above average (428 mm) during January 2005 - December 2005.

Data collection took place over two years from the beginning of the wet season in January 2004 to the end of the transition season in December 2005. Both years of the study period were divided into four seasons based on records of mean monthly rainfall and plant phenology (defined as the percentage of mature green leaves retained) observed in the field; wet (January-March), early dry (April-June), late dry (July-September) and transition to the wet (October-December) season (Fig. 1). New leaf flush began in late October prior to the rains in *G. flava*, *A. mellifera* and *A. haematoxylon* and occurred roughly one month later in *Rhigozum trichotomum*. Therefore, all deciduous woody plant species retained green leaves during the wet season, experienced leaf loss during the early dry season, were primarily without mature green leaves during the late dry season and produced the majority of new leaves prior to and during the start of the rains in the transition season (Fig. 1).

Study animals

Eight black rhinoceroses of the south-western subspecies (*Diceros bicornis bicornis*) (Ashley *et al*., 1990) were translocated to the reserve from Etosha National Park in Namibia in June 1995. This founder population consisted of six adult females (age range: 8 to 20 years) and two adult males (age 7 and 8 years). Of these founders, one adult female and one adult male were sold in 1998. The remaining five females formed the focal animals for this study. The focal area for this study was the fenced 479 km^2 Korannaberg section containing the five female rhinos.

The reserve also contained a number of other browsing and mixed feeding ungulate species. The numbers recorded throughout the entire 1,080 km^2 reserve during the 2002 game count were 1,474 kudu (*T. strepsiceros*), 51 giraffe (*Giraffa* *camelopardalis*), 855 eland (*Tragelaphus oryx*) and 332 impala (*Aepyceros melampus*). There were no elephants (*Loxodonta africana*) present at Tswalu and no lions (*Leo panthera*) or spotted hyenas (*Crocuta crocuta*) present within the fenced Korannaberg section.

Data collection

Rhino diet data

An indirect track-based method more commonly referred to as backtracking was used for collection of rhino diet data (Joubert and Eloff, 1971; Mukinya, 1977; Loutit *et al*., 1987; Hall-Martin *et al*., 1982; Oloo *et al*., 1994; Ganqa *et al*., 2005). The basis of this technique is to follow footprints left by black rhino and record all fresh signs of browsing activity. Waterholes and roads in the areas utilised by rhinos were checked early in the morning looking for fresh spoor. Only spoor classified by experienced field scouts as being fresh black rhino tracks from the previous night were followed. The sandy substrate in the area retained tracks clearly which aided identification of rhino's movements. Use of this technique was facilitated by the tight network of sandy tracks used as roads within the reserve. Focal black rhinos were not fitted with radio-transmitters in their horns as this was not considered necessary because it was possible to locate them from their spoor.

Initially, individuals were tracked until they were sighted and could be identified by their unique ear-notch patterns. With time it was possible to differentiate individual females indirectly using the ratio of female and calf spoor diameter (Purchase, 2007) and marks left by distinctive cracks on the soles of the feet (*pers. obs.*; Kretzschmar, 2002). Only one rhino track was observed each day. A minimum of five feeding tracks were analysed each month (*n*=5); consecutive months were combined for months in which fewer than five tracks were recorded. In order to prevent bias towards individual rhino that were easier to locate, a systematic sampling technique was used to ensure roughly equal amounts of data from each of the five focal females throughout each season. Data were recorded from 147 tracks totalling 274.5 km (daily range: 0.5 to 5.1 km).

When a suitable spoor was located, details of that rhino individual foraging were recorded on a PDA (Palm III) connected to a GPS using a sequence written in CyberTracker software (www.cybertracker.org) along the rhino spoor trail. Data collection began at the first identified sign of feeding. Foraging tracks were divided into 100 m sections by counting 140 observer strides whilst walking (mean stride length = 0.71 m).

At each feeding station (Goddard, 1968) the plant species were identified and the number of new bites recorded for each individual tree. Bites were identified by the characteristic "pruning" of vegetation, where the twig is cut off by the proximal molars leaving a distinctive diagonal cut which was easily detectable (Joubert and Eloff, 1971). A single bite was scored for any isolated severed shoot or branch, or where numbers of contiguous shoots or branches were bitten off at the same level. All severed shoots less than 5 mm thick occurring within a hypothetical circle of 5 cm in diameter were recorded as one bite (Hall-Martin *et al.*, 1982). Recent browsing was distinguished from older use by comparing the colour of the wood at point of bite (Emslie and Adcock, 1994). In addition, leaf phenology (immature, mature, yellow and dry) and total leaf retention using a five point scale (0, 1 < 5, 6 < 33, 34 < 66, 67 < 100%; Dekker and Smit, 1996) was recorded for each species. It was not possible to differentiate immature leaves from mature leaves of *Monechma incanum,* so this category was not used for this species. The total number of bites recorded was 29,873 (see Table 1 for details).

Dry mass regression and bite mass

Mean dry mass of bite contents was estimated for the most important woody plant species in the diet. Twenty twigs each of *A. haematoxylon*, *A. mellifera*, *G. flava*, *R. trichotomum*, *M. incanum*, *L. cinerum* and *L. hirsutum* in each of the three diameter size classes (0 - 1 mm, 1 - 3 mm, 3 - 6 mm) were collected in the wet season when mature leaf retention was greatest. Collecting samples in the wet season allowed maximum values to be obtained, which could then be adjusted for different seasonal values in relation to leaf retention patterns on different species. Twigs and leaves were stored in paper bags and air-dried for two years throughout the data collection period before the mass was obtained on an Ohaus Precision Plus TP4000D scale calibrated to an accuracy of three decimal places. The dry mass values were plotted against the associated twig diameter values for the sixty samples of each species, and the diameter (x) converted to twig and leaf dry weight (y) using equations of the type $y = ax^b$ where a and b are constants (Basile and Hutchings, 1966). Mean bite mass for each plant species in each season could then be calculated from mean diameter class of twigs in bites from each plant species. For additional plant species, mass of the plant diet species with the most similar structure were substituted (Helary *et al.*, 2009). Herbaceous browse species were found to represent less than 5% of total bites per month at Tswalu and dry mass estimates for these species were based on leaf matter from *M. incanum* as this was considered to have the most similar structure. The mass of each leaf and twig fraction was also used to calculate a leaf:twig (=wet season leaf mass / wet season twig mass) ratio for each plant species. This was then modified dependent upon the proportion of mature leaves recorded as present for each species in different seasons as above.

Plant species availability and acceptability

As measures of diet content alone do not indicate the relative availability to the herbivore of different plant species contributing to the diet, the presence of plants of important dietary species which had not been browsed along the feeding track was also recorded. The presence/absence of the main diet species *A. haematoxylon*, *A. mellifera*, *G. flava*, *Lycium cinerum*, *Lycium hirsutum, M. incanum* and *R. trichotomum* plants within each 100 m section of the feeding track was recorded. The foraging track width was taken as 2 metres based on the observed neck reach of 1 metre by the rhinos. Only plants with foliage within rhino browsing height (i.e. less than 2 metres above ground: Adcock, 2003) were recorded, along with details of leaf phenology and retention as described above.

Availability for each season along the feeding track was calculated as the number of sections in which a plant species was present (S_p) divided by the total number of sections (S_t) recorded during that season (availability = S_p/S_t). A distance of 100 m was considered approximately the distance covered by rhino in 30 minutes whilst foraging, hence this formed the equivalent of the 30 minute units considered as independent feeding choices by Owen-Smith and Cooper, 1987b).

Acceptability indices (AI) for each individual rhino in each season were calculated as the total number of 100 m sections in which a plant species was eaten (S_e) divided by the total number of 100 m sections in which the species was recorded as present (S_p) (AI = S_e/S_p) within that season. This section-based approach was adapted from the site-based acceptance (SA) for kudu of Owen-Smith and Cooper (1987b) as data was recorded over distance rather than time.

Plant sample collection

For each of the plant species that together contributed over 80 % of the diet in the four different seasons, samples from five unbrowsed plants were taken, to be analysed for chemical contents. Twig samples were pruned at approximately 5-6 mm diameter to match analysed samples with material ingested by browsing rhinos (*pers. obs.*; Ganqa and Scogings, 2007). Plants assessed were *A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum* and *R. trichotomum* in November 2004 (transition), September 2005 (late dry) and January 2006 (wet) and *A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum*, *L. cinerum* and *L. hirsutum* in May 2005 (early dry). There were insufficient leaves on *G. flava* or *A. mellifera* in September 2005 for analysis. All samples were collected prior to 10 a. m. to prevent the effects of prolonged exposure to sunlight, and, where present, leaves were immediately separated from twig at the base of the petiole (Dierenfeld *et al.*, 1995). The samples were air dried and stored in paper bags prior to being oven dried where necessary in preparation for chemical analysis. Analyses were performed separately on leaf and twig fractions. For each plant species, a mean chemical value for leaf and twig content was calculated from the five replicate samples in each season. Plant shoot values were then calculated by combining chemical concentrations within leaf and twig fractions with proportion of leaf:twig ratio for each species in each season.

Chemical analysis

Initially, standard wet chemical analyses were performed on a subset of the total sample using techniques outlined by AOAC (American Organization of Analytical Chemists, 1990). Neutral detergent fibre constituents (NDF) were determined using procedures from ANKOM technology fibre analysis (Goering and van Soest, 1970). Nitrogen was extracted using the macro-Kjeldahl procedure (AOAC, 1990) and converted to crude protein by multiplying by 6.25. Condensed tannin analyses were performed as described in Hagerman (2002), the acid butanol assay was used with Sorghum tannin standard. All concentrations were expressed on the basis of dry matter.

Additional plant chemical analysis was performed in conjunction with a wider study relating black rhino diet content and nutritional status to reproductive success (Helary *et al.,* 2009). Due to the large number of plant samples in the larger study, it was possible to utilise Near Infrared Reflectance Spectroscopy (NIRS) calibrated from wet chemistry data on the initial sub sample to assess fibre and condensed tannin contents. Inductively coupled plasma-optical emission spectrometer (ICP-OES) and an ANKOM 200/220 Fibre Analyzer were used to measure the samples from the calibration set. Wet chemistry analysis of fibre and tannin content was performed by Dawood Hattas from the Botany Department of the University of Cape Town. Mineral analysis was undertaken by BEMLAB in Cape Town. NIRS analyses were conducted at the Dairy Research Institute at Irene in Pretoria (Table 2 and Table 3).

Available protein was calculated by subtracting half the condensed tannin content from the crude protein content, following the approach of Owen-Smith and Cooper (1989) for browsing ruminants. Although rhinos are not ruminants, this approach was included to provide an approximation of the seasonal impact of condensed tannins on protein availability. The measure of NDF was converted to digestible organic matter (dOM g/g) using the equation; dOM = (-NDF*0.98) + 101 for browsing rhinos following Clauss *et al*. (2006a).

Data analysis

Data for the proportional dietary contributions, availability and acceptability of the five main diet species (*A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum*, *R. trichotomum*) were arcsine transformed prior to analysis to conform to normality requirements (Zar, 1999). A four-way ANOVA was used to assess the effects of four predictive factors - plant species, individual rhino (Bogale, Inyani, Kagale, Nantoni and Usuk), season (wet, early dry, late dry and transition) and year (2004 and 2005) on dietary contribution, availability and acceptability. The response variable for dietary contribution was the proportion of the diet content formed from each plant species with replicates of daily samples. The response variable for the availability (S_p/S_t) was calculated as the number of sections in which a plant species was present (S_p) divided by the total number of sections (S_t) recorded during that season (availability = S_p/S_t). The response variable for acceptability indices (AI) for each individual rhino in each season were calculated as the total number of 100 m sections in which a plant species was eaten (S_e) divided by the total number of 100 m sections in which the species was recorded as present (S_p) (AI = S_e/S_p) within that season. Post-hoc analysis was performed using a Tukey honest significant difference test (Zar, 1999). The *P*-level for rejection of null hypotheses was <0.05. All values are reported as mean ± standard error. Analyses were performed using the statistical package Statistica 6 (Statsoft, Inc. 2001).

2.4 Results

Seasonal dietary composition

Thirty six plant species were recorded as consumed by black rhino in total during the data collection period. Seven woody plant species (*A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum*, *R. trichotomum*, *L. cinerum* and *L. hirsutum*) contributed over 83% of the dry mass of the diet of all five rhino throughout the year (Fig. 2). Individual rhinos showed differences in the total proportions of different plant species in the overall diet ($F_{24,742}$=1.825, P=0.0095), however, there was no significant difference in dietary proportions of plant species in individual rhino’s diets in different seasons ($F_{72, 742}$=1.151, *P*=0.192). Hence, data from all rhinos was combined for seasonal analysis. As expected, there were strong seasonal differences in plant species contribution to rhino diet ($F_{18, 742}$=12.317, *P*<0.0005).

In the wet season, three woody plant species formed over 70 % of the diet of the five female rhinos: *G. flava* (34.0 %), *A. mellifera* (25.3 %) and *A. haematoxylon* (22.4 %) (Fig. 2). Herbaceous browse was not widely available at Tswalu and was found to form only a minor component of black rhino diet even during the wet season (maximum dietary proportion of 3.5 % in February 2004). The majority of forb species eaten were from the *Hermannia* family, principally *H. comosa* and *H. tomentosa*. Occasional bites were recorded from grass species (*Centropodia glauca* and *Schmidtia pappophoroides*) during the late wet season, but contributed less than 1 % of the total estimated dietary composition.

After the wet season, the semi-evergreen species, *A. haematoxylon* increased in dietary contribution to 43.1 % in the early dry season, peaked at 76.8 % in the late dry season then decreased to 45.5 % in the transition season (Fig. 2). Another semi-evergreen species, *M. incanum*, also increased in dietary proportion from 3.6 % in the wet season to 8.3 % in the late dry season. The deciduous species, *R. trichotomum*, formed the greatest contribution to the diet (16.6 %) in the transition season, when it was without leaves.

Overall dietary content of the seven major plant species did not differ between the two years of data collection ($F_{6, 742}$=1.204, *P*=0.302) but there were seasonal differences between years ($F_{18, 742}$=1.787, *P*=0.023). Notable differences included lower dietary contribution by *A. haematoxylon* during the late dry season in 2004 in comparison to the same period in 2005 and a concurrent decrease in *M. incanum* dietary contribution in late dry season 2005 compared to 2004 ($F_{6, 203}$=2.5363, *P*=0.02172). The dietary content of *G. flava* was greater during the early dry season 2005 than 2004 ($F_{6, 133}$=3.1826, *P*=0.00597) which may have been related to the higher rainfall causing longer leaf retention in this year. In 2004, *R. trichotomum* was included in the diet in greater quantities in the late dry season compared to 2005 when the seasonal increase in use of this species only occurred during the transition period.

Plant species availability and acceptability

Seasonal availability of different woody plant species was different for individual rhinos ($F_{72, 740}$=1.3695, *P*=0.02702). *Monechma incanum* showed higher availability to two of the five animals, particularly during the late dry season. *G. flava* availability was highest during the wet season for all rhinos (0.72 ± 0.03) and declined to 0.51 ± 0.03 during the late wet season (Fig. 3a). The pattern for *A. mellifera* was similar, peaking at 0.53 ± 0.05 in the wet season and declining to 0.40 ± 0.03 during the late dry season (Fig. 3b). Conversely, *A. haematoxylon* was more available during the late dry season (0.48 ± 0.04) than the wet season (0.22 ± 0.04) (Fig 3c).

Individual rhinos showed no difference in their acceptance of different plant species thorough the year ($F_{24, 740}$=0.971, *P*=0.503) or within different seasons ($F_{72, 740}$=1.144, *P*=0.202). The acceptability of *G. flava* decreased from a maximum of 0.61 in the wet season to a minimum of 0.08 in the late dry season (Fig. 3a). *Acacia mellifera* remained more constant in levels of acceptability; however it also showed a decline from 0.39 in the wet season to 0.26 in the dry season (Fig. 3b). Conversely, the acceptability of *A. haematoxylon* increased from 0.58 in the wet season to 0.79 in the late dry season (Fig. 3c). Acceptability indices for *M. incanum* were also higher in the late dry season (0.67) and transition season (0.78) than the early dry season (0.45) or wet season (0.55) (Fig. 3d). *Rhigozum trichotomum* was most highly accepted during the transition season (0.51) and much lower during the wet (0.08) and early dry (0.05) (Fig. 3e).

Based on the acceptability indices the woody plant species were grouped in each season as favoured (AI > 0.5), neither favoured nor neglected (0.3 < AI < 0.5) and neglected (AI < 0.3). The first group consisted of *A. haematoxylon* in all seasons, *M. incanum* in the wet, late dry and transition seasons, *G. flava* in the wet season and *R. trichotomum* in the transition (Figs. 3a-e). *A. mellifera* in the early dry, wet and transition seasons formed the second group. Species that were neglected were the three deciduous species in the late dry season (*A. mellifera*, *G. flava* and *R. trichotomum*) and *R. trichotomum* in the wet and early dry season (Figs. 3b, c and e).

From these groupings it was possible to identify generic resource types categories following the classification developed for browsers by Owen-Smith (2002). *G. flava* and *A. mellifera* formed the staple dietary resource, as deciduous species providing much of the wet season diet. *Grewia flava* appeared more highly favoured than *A. mellifera*. More unusually, *A. haematoxylon* also formed a staple resource type during the wet season, despite being a semi-evergreen species which continued to form a major dietary contribution during the late dry season as a reserve resource. Another semi-evergreen species, *Monechma incanum*, which increased in dietary importance during the late dry season, was also a type of reserve resource. None of the plant species in the diet at Tswalu were identified as buffer resources as these would only be eaten during severe drought conditions which were not experienced during the study period (Owen-Smith, 2002). The addition of *R. trichotomum* to the diet during the transition season when it is without leaves suggests that this species could be used as a bridging species during this crunch period between the wet and late dry seasons. Given the low forb content of the diet, there were no plant species that could be categorised as quality resource type in black rhino diet at Tswalu.

Physical and chemical characteristics

Plant species phenology

Two deciduous species, *G. flava* and *A. mellifera,* began to shed foliage during May and retained only a low proportion of leaves during the late dry season until the flush of new growth prior to the rains (Fig. 1). *R. trichotomum* started to lose leaves during July and retained least leaves prior to new leaf flush in October (Fig. 1). Two plant species, *A. haematoxylon* and *M. incanum* were semi-evergreen, retaining leaves throughout the year, with new foliage production coinciding with leaf shed in September and hence no period of total leaf loss.

Assessment of plant species acceptability in relation to leaf:twig proportions show that there was no clear pattern in the wet season (Fig. 4a) when deciduous species retained leaves. As leaf loss occurred from the early dry (Fig. 4b) into the late dry season (Fig. 4c) species with decreasing leaf:twig ratio also showed a decline in acceptance. Hence we accept the hypothesis that rhino were selecting for plant species retaining leaves during the dry season. The exception is *R. trichotomum* which increased in acceptability during the transition season when without leaves.

Plant spinescence

Two of the three woody plant species forming the bulk of rhino diet (*A. haematoxylon* and *A. mellifera*) were physically defended with paired thorns. These were small and hooked in the case of *A. mellifera* and longer, straight and slender in *A. haematoxylon* (Coates-Palgrave, 2002). This confirmed the hypothesis that black rhino would not be deterred by the presence of thorns.

Chemical composition of leaves and twigs

Protein and digestible organic matter content in leaves and twigs in the transition and wet seasons were generally greater in comparison with the early or late dry seasons for all species (Table 2 and Table 3). During the wet season digestible organic matter content of plant shoots was greatest in *M. incanum* (54.5 %) and *A. haematoxylon* (50.7 %) (Fig. 5a). Crude protein content was highest in *A. mellifera* (13.4 %) and *G. flava* (11.3 %), but available protein was greater in *M. incanum* (11.2 %).

In the early dry season, shoots of *A. haematoxylon* (44.9 %) and the two *Lycium* species added to the diet (*L. cinerum*: 44.1 %, *L. hirsutum*: 46.6 %) had the highest levels of digestible organic matter (Fig. 5b). *Lycium* species also the highest proportions of crude protein and available protein: *L. cinerum*: 16.7 % for both, *L. hirsutum*: 15.7 % and 15.6 %. During the critical late dry season, semi-evergreen species showed the highest content of digestible organic matter (*A. haematoxylon* 46.4 %; *M. incanum* 46.3 %) crude protein (*A. haematoxylon* 10.2 %; *M. incanum* 9.1 %) and available protein (*A. haematoxylon* 9.1 %; *M. incanum* 9.6 %) (Fig. 5c). There was a pattern of increased acceptance of semi-evergreen species retaining leaf material during the late dry season (Fig. 5c). These two species also had the highest levels of protein and digestible organic matter during the transition period: dOM (*A. haematoxylon* 48.6 %; *M. incanum* 44.4 %) crude protein (*A. haematoxylon* 10.8 %; *M. incanum* 11.9 %) and available protein (*A. haematoxylon* 8.2 %; *M. incanum* 11.9 %) (Fig. 5d).

Chemical defense

Measures of condensed tannins in leaves of all species also showed a pattern of being higher in the wet and transition seasons than the drier seasons (Table 2). The maximum condensed tannin content was 9.33% within shoots of *G. flava* during the wet season, but this declined to 1.48 % when this species was without leaves in the late dry season (Table 2 and Table 3). Levels of secondary chemicals in plant shoots showed no indication of leading to seasonal avoidance of plant species. The two plant species (*A. haematoxylon* and *G. flava*) contributing the greatest proportion of the black rhino diets and showing high acceptability indices (Fig. 3a and 3c) had higher concentrations of condensed tannins than other plant species in all seasons (Table 2 and Table 3).

2.5 Discussion

Diet content of black rhinos at Tswalu was found to contain relatively few woody plant species and almost no forbs. Just three woody plant species (*G. flava*, *A. mellifera* and *A. haematoxylon*) formed the staple diet of the rhinos throughout the year. Black rhino have been reported using a relatively low proportion of available plant species from a range of geographical areas (Goddard, 1968; Goddard, 1970; Joubert and Eloff, 1971; Hall-Martin *et al.*, 1982; Loutit *et al.*, 1987; Oloo *et al.*, 1994; Muya and Oguge, 2000; Lieverloo *et al.,* (2009); Buk and Knight, 2010). All three of the main dietary components at Tswalu were woody shrub species that do not grow very tall. Black rhino have been shown to be selective for plant sizes within species (Emslie, 1999) and the majority of black rhino browsing occurs below 2 metres (Adcock, 2003).

Rhino diet content followed the same seasonal pattern in both years of data collection; *Grewia flava* and *A. mellifera* formed the staple deciduous resource during the wet season. *Acacia haematoxylon* was also used as part of the wet season diet but increased greatly in dietary content during the drier periods of the year, peaking at 77 % in the late dry season. Another semi-evergreen species, *M. incanum*, was also found to form a reserve resource during the late dry season. *R. trichotomum* was eaten during the transition from the late dry to wet season. The addition of two *Lycium* species to the diet occurred in the early dry season. As the plant species forming the majority of diet content during the late dry season, *A. haematoxylon* was identified as the key reserve resource.

The diet of black rhino at Vaalbos National Park, close to Tswalu in the Northern Cape of South Africa, showed similar seasonal patterns, with *G. flava* and *A. mellifera* forming much of the wet season diet, *M. incanum* eaten most during the late dry season and *R. trichotomum* during the transition period (Buk and Knight, 2010). *Acacia haematoxylon* was not available at Vaalbos and *Acacia tortilis* formed much of the late dry season diet (Buk and Knight, 2010). Black rhino at Tswalu appeared to substitute plant species of similar quality within seasons, based on plant species distribution and relative availability. For example, the reduction in use of *A. haematoxylon* during the late dry season in 2004 in comparison to 2005 seemed to be compensated by increased use of *M. incanum*. There was also an indication that variation in annual rainfall patterns could influence diet content. Use of *G. flava* during the early dry season 2005 was greater than early dry season 2004, possibly due to higher rainfall and longer leaf retention during the second year.

Similar seasonal patterns have been observed more widely for black rhino elsewhere, with higher quality herbaceous or deciduous species generally eaten when available in the wetter periods and evergreen species increasing in importance during drier times in study sites in Eastern and Southern Africa (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Oloo *et al.*, 1994; Hall-Martin *et al.*, 1982; Atkinson, 1995; Ganqa *et al.*, 2005). The use of forbs in black rhino wet season diet has been widely observed in areas with lower density woody vegetation in East Africa, such as the Masai Mara (Mukinya, 1977), Tsavo National Park in Kenya (Goddard, 1970) and Serengeti National Park in Tanzania (Goddard, 1968). Forbs also formed approximately 40 % of the wet season diet of kudu at Nylsvley Nature Reserve (Owen-Smith and Cooper, 1989). Herbs were less important in rhino diet at Tswalu and in other lower rainfall areas in Southern Africa (Hall-Martin *et al*., 1982; Buk and Knight, 2010) perhaps due to lower availability. Black rhino at Tswalu were nevertheless able to achieve high reproductive success without access to this quality resource type during the wet season. Recent literature has highlighted black rhino faecal contents of approximately 15 % grass in thicket vegetation (Parker *et al*., 2009) though little use was made of this resource type at Tswalu, with only a few bites observed during the wet season. Van Lieverloo *et al*. (2009) noted that diet composition for black rhino developed from backtracking data tends to not detect grass consumption and underestimate herb content in comparison to faecal analysis. However, bites were detected on both grass and herb species at Tswalu, perhaps aided by the lower vegetation cover than in thicket areas, and so any underestimate is considered likely to be minor.

Potential staple resources for black rhino in other areas often consist of deciduous *Acacia* species, such as *Acacia nilotica* and *Acacia karoo* in Ithala Game Reserve, South Africa (Kotze and Zacharias, 1993) or other deciduous species such as *Spirostachys africana* in Hluhluwe-iMfolozi Game Reserve in South Africa (Emslie, 1999) similar to the use of *A. mellifera* and *G. flava* at Tswalu. Early dry season use of *Lycium* species by black rhino was also observed in Addo Elephant National Park (Hall-Martin *et al*., 1982).

The identification of species forming reserve and buffer resources for black rhino in other areas during the drier periods of the year in other areas is less well known. In some areas black rhino have been found to use *Euphorbia* and succulent species during the drier periods of the year; north-western Namibia (Loutit *et al*., 1987; Hearn, 2000), Great Fish River Reserve in the Eastern Cape of South Africa (Ganqa *et al*., 2005; Heilmann *et al*., 2006; Brown, 2008; Luske *et al.,* 2009), Addo Elephant Park (Hall-Martin *et al*., 1982). *Euphorbia* species were not present in the

Korannaberg area as an alternate dry season resource for focal black rhino at Tswalu. *Terminalia sericea* forms part of black rhino diet during the dry season at Waterberg Plateau Park in Namibia (Helary *et al*., 2009) and North Luangwa National Park in Zambia (Claire Lewis *pers. comm.*). This species was available at Tswalu but was not recorded being eaten by black rhino during the data collection period. Hence, *T. sericea* is identified as a potential reserve or buffer resource which could be added to black rhino diet at Tswalu in the future. Other potential reserve or buffer species which are available at Tswalu but not utilised at present include *Acacia erioloba, Acacia hebeclada* and *Boscia albutrunca*.

The differences in dietary content of woody plant species in individual rhino diet seemed related to differences in woody plant species availability within different rhino home ranges (Chapter 5). However, acceptability indices of different plant species were not different for individual rhinos, suggesting that this was not affected by habitat use or plant species availability, but other factors such inherent measures of plant quality. In fact, as predicted, in the late dry season rhino were found to be selecting for semi-evergreen woody plant species which retained mature leaves. The seasonal pattern of woody plant species use was strongly tied to plant phenology. *Grewia flava* and *A. mellifera* acceptability followed a similar pattern to leaf retention; peaking in the wet season when mature leaf retention was greatest and decreasing during late dry season when leaves were shed. When the deciduous species lost their leaves at the end of the wet season in other areas, rhino became reliant on *A. haematoxylon*, a semi-evergreen species which retains mature green leaves though the dry season. *Monechma incanum*, a small shrub which also retained leaves throughout the year also formed a type of reserve resource with high acceptability during the late dry and transition seasons. The major dietary contribution and consistently high acceptability levels for *A. haematoxylon* by all focal animals highlighted the importance of this species in the diet of all adult female black rhinoceros at Tswalu, throughout the year, but particularly during the late dry season.

Browsing ruminant species, including giraffe, eland and kudu become dependent upon evergreen or semi-evergreen woody plants during the dry season (Hall-Martin, 1974; Pellew, 1984; Owen-Smith and Cooper, 1989; Watson and Owen-Smith, 2002). Watson and Owen-Smith (2002) found that for eland in Mountain Zebra National Park, total fibre was the most important chemical factor influencing acceptability; the shoots of palatable species contained low fibre concentrations, while the shoots of unpalatable species were more variable in fibre content. As with rhino at Tswalu, this was due not only to the presence or absence of mature leaves, but changes in overall plant shoot chemical content relating to particular leaf phenophases. Ganqa *et al*., (2005) similarly found a positive relationship between leaf:twig ratio and seasonal plant preference of black rhino in Great Fish River Reserve in South Africa.

As predicted, rhinos were not deterred by the presence of thorns as a physical deterrent on woody plant species. Bite size and hence intake rates of kudu, were found to be restricted by the presence of thorns (Cooper and Owen-Smith, 1986). The effect was greater for kudus than impalas and goats, as kudu altered their feeding technique, being forced to remove only leaves or leaf clusters from plant species with straight spines as opposed to shoot ends from unarmed plant species or those with hooked thorns (Cooper and Owen-Smith, 1986). Spinescence was not found to influence rates of food ingestion by giraffe in the Serengeti as food intake rates gained by biting shoots of spinescent species were equivalent to those achieved by leaf-stripping on broad-leafed shrubs (Pellew, 1984).

The use of a range of spinescent plant species, particularly in the *Acacia* and *Euphorbia* families, has been recorded by black rhino in a range of habitat types (Goddard, 1968; Joubert and Eloff, 1971; Mukinya, 1977; Loutit *et al*., 1987; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al*., 1994; Muya and Oguge, 2000; Kipchumba, 2002; Ganqa *et al*., 2005; Ndlovu and Mundy, 2009). Black rhino at Tswalu were not inhibited from twig biting by either the hooked thorns present on *A. mellifera* or straight, slender thorns on *A. haematoxylon*. However, rejection of *Acacia erioloba* and *Acacia hebeclada* by rhino at Tswalu in favour of the aforementioned *Acacia* species could have been linked to the more robust, straight thorns on the latter with potential impacts on food handling time and intake rates.

Rhino did appear to select plant species with highest levels of protein and digestible organic matter in each season. For deciduous species, shoot chemical composition in different seasons was obviously dependent upon leaf retention and acceptance was highest in the wet season when plants retained mature leaves. The semi-evergreen species with high acceptance in the diet, *A. haematoxylon* and *M. incanum*, had consistently high levels of protein and digestible organic matter throughout the seasonal cycle. During the wet season, rhino browse in the Zambezi Valley, Zimbabwe ranged between 4-20 % available protein and 34-72 % NDF (or 30–68 % dOM) (Dierenfeld *et al.*,1995) so results from Tswalu fell within the higher level of both diet quality measures.

Within the woody plant species selected by black rhino at Tswalu there was no indication of seasonal avoidance of plants that were chemically defended by condensed tannins. The hypothesis that rhino would select plant species with condensed tannin content below 5% was rejected as maximum condensed tannin content was 9.33% within shoots of *G. flava* during the wet season. Scogings *et al.* (2004) suggested that the higher condensed tannins levels in *G. flava* may be the result of a strategy to rely on chemical defences to reduce long-term intake by browsers rather than on physical defences. However, condensed tannins were not found to act as a deterrent for black rhino at Tswalu. The impact of condensed tannins on ruminant herbivores is reduction of the microbial fermentation of plant cell walls decreasing their energetic gains (Cooper and Owen-Smith, 1985). Black rhino have been shown to increase production of tannin binding salivary proteins in response to dietary tannins, indicating an evolutionary adaptation to these forms of chemical defense (Clauss *et al.*, 2005). It has been suggested that some level of condensed tannin intake may in fact be beneficial in preventing iron overload in black rhino (Clauss *et al.*, 2006b) which has been shown to lead to disease in captive animals (Paglia and Dennis, 1999).

Black rhino in Nairobi National Park, Kenya were found to avoid phenols and alkaloids as part of their diet selection patterns (Muya and Oguge, 2000). There is some indication that another secondary metabolite such as an alkaloid (Bryant *et al*., 1991) within plant leaves could have acted as a chemical deterrent to rhino browsing at Tswalu, as acceptability levels for *R. trichotomum* increased during the transition season when this species was without leaves. Clauss *et al*. (2005) found that salivary tannin-binding proteins capable of binding hydrolysable tannin were more responsive to dietary stimulation than those of condensed tannins, suggesting that hydrolysable tannins play a greater role in free-ranging black rhino's diet selection. Identification of the specific chemicals acting as deterrents to black rhino browsing would form an interesting avenue for future research to guide habitat suitability assessments for black rhino. Overall, these results suggest that diet selection by black rhinos may be determined by different factors than browsing ruminants, potentially enabling rhinos to use species which are not available to other browsers.

This chapter has established the plant species contributing to black rhino diet at Tswalu and assessed factors influencing seasonal adaptations in diet selection. The aim of this thesis was to gather information which could be used to produce a quantitative assessment of black rhino habitat capacity. Due to financial constraints, it was not possible to analyse the chemical content of the plant species which were not eaten by rhino, hence it is not possible to provide an in-depth analysis of the factors influencing black rhino diet selection. Chemical analysis of the energy, nutrient and anti-nutrient content and intake rates of woody plant species that are available and accessible to black rhino at Tswalu but not eaten, would provide a more comprehensive understanding of the nutritional factors determining diet selection. However, overall patterns of dietary resource use by black rhino at Tswalu showed clear indications of seasonal adaptations to phenological changes in plant species quality and quantity. The seasonal pattern of resource use at Tswalu was unusual, due to availability of *A. haematoxylon* as a palatable evergreen species. This single plant species was established as the key resource forming a major part of diet content during the late dry period.

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Figures and tables

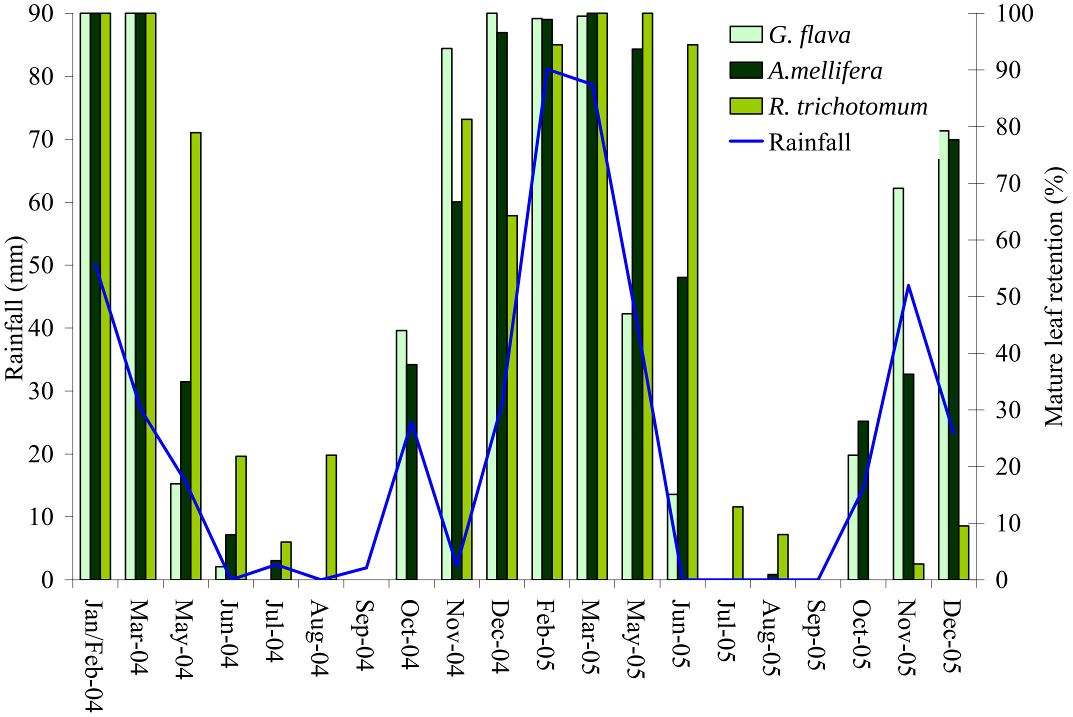


Figure 1. Monthly rainfall and retention of mature green leaves by three deciduous plant species throughout the data collection period, January 2004 – December 2005.

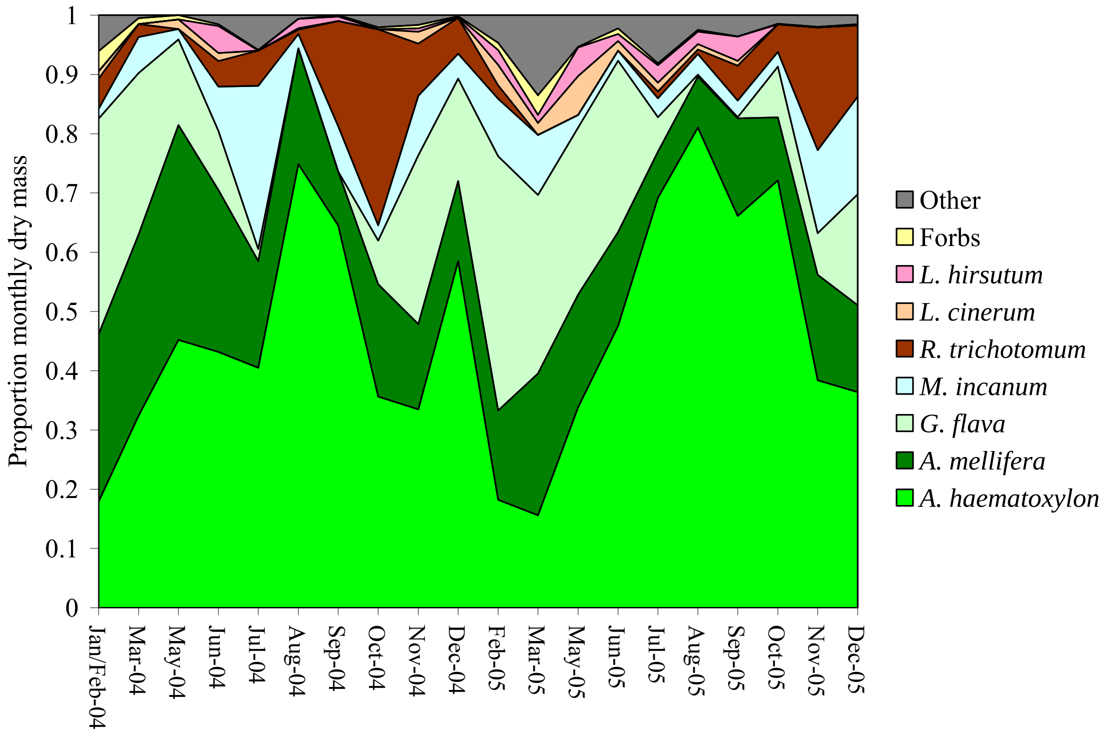


Figure 2. Monthly proportion of plant species in the diet of five focal female black rhinos combined at Tswalu Kalahari Reserve.

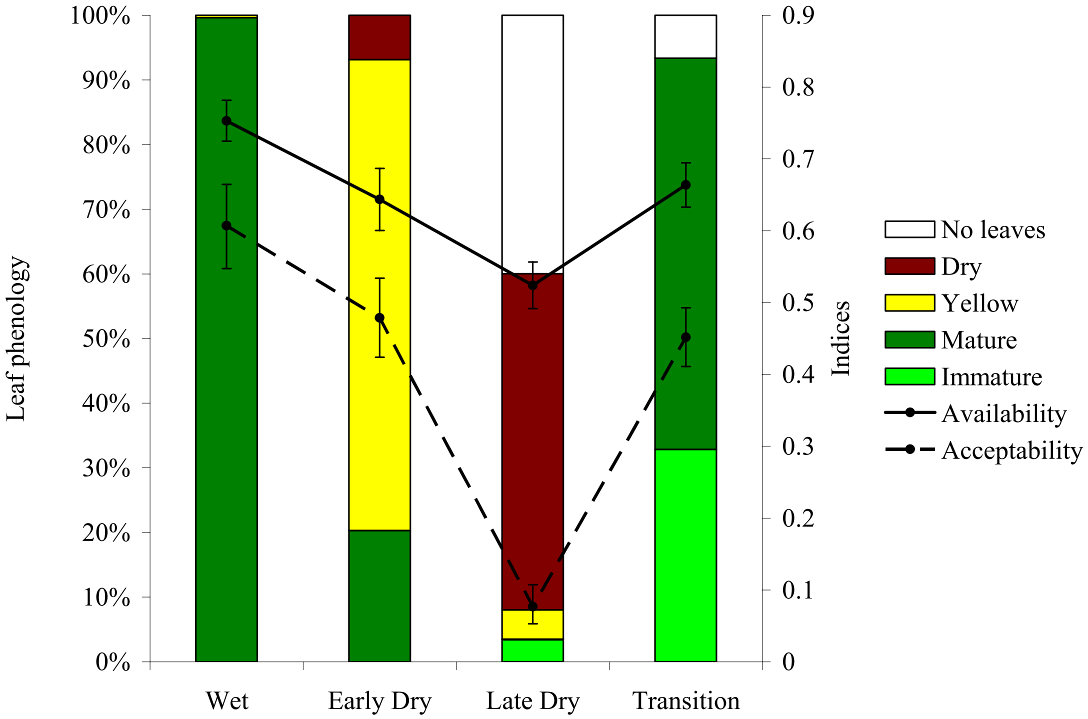


Figure 3a. Availability, acceptability indices (± SE) and proportion of leaves in different phenological stages in *G. flava* over different rainfall periods.

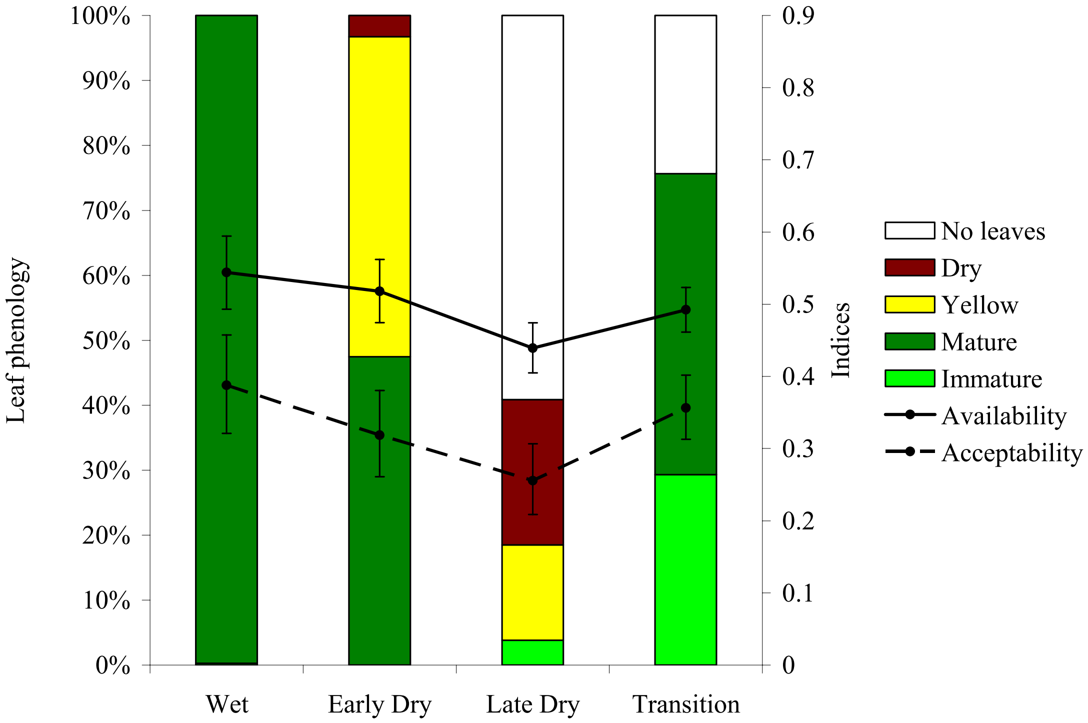


Figure 3b. Availability, acceptability indices (± SE) and proportion of leaves in different phenological stages in *A. mellifera* over different rainfall periods.

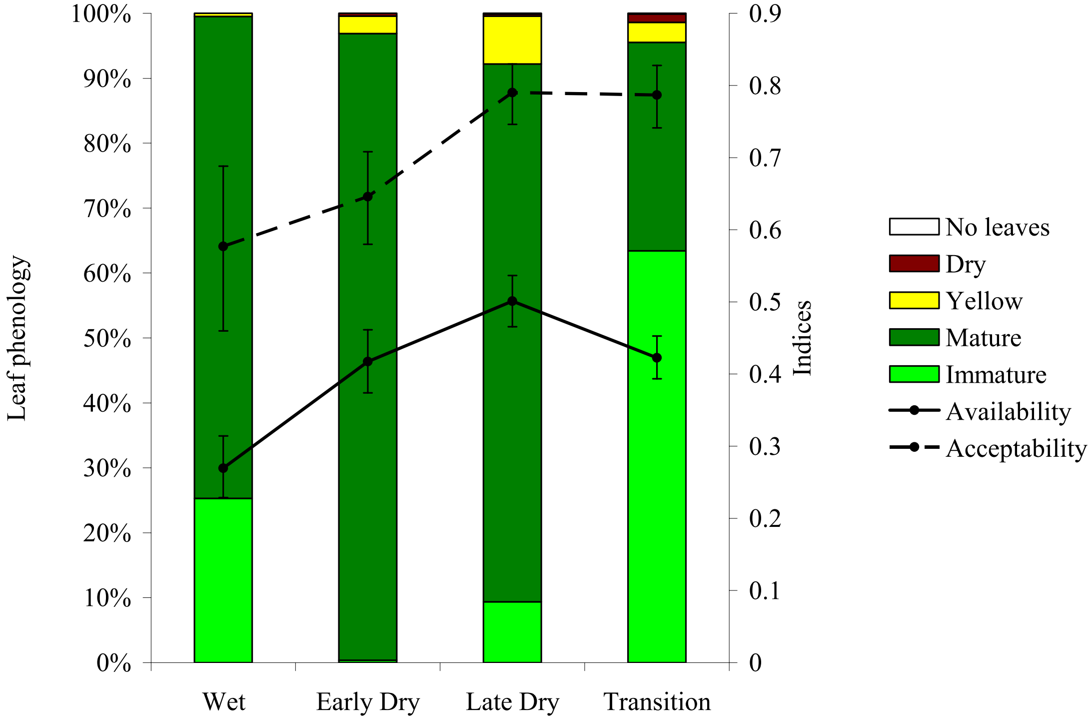


Figure 3c. Availability, acceptability indices (± SE) and proportion of leaves in different phenological stages in *A. haematoxylon* over different rainfall periods.

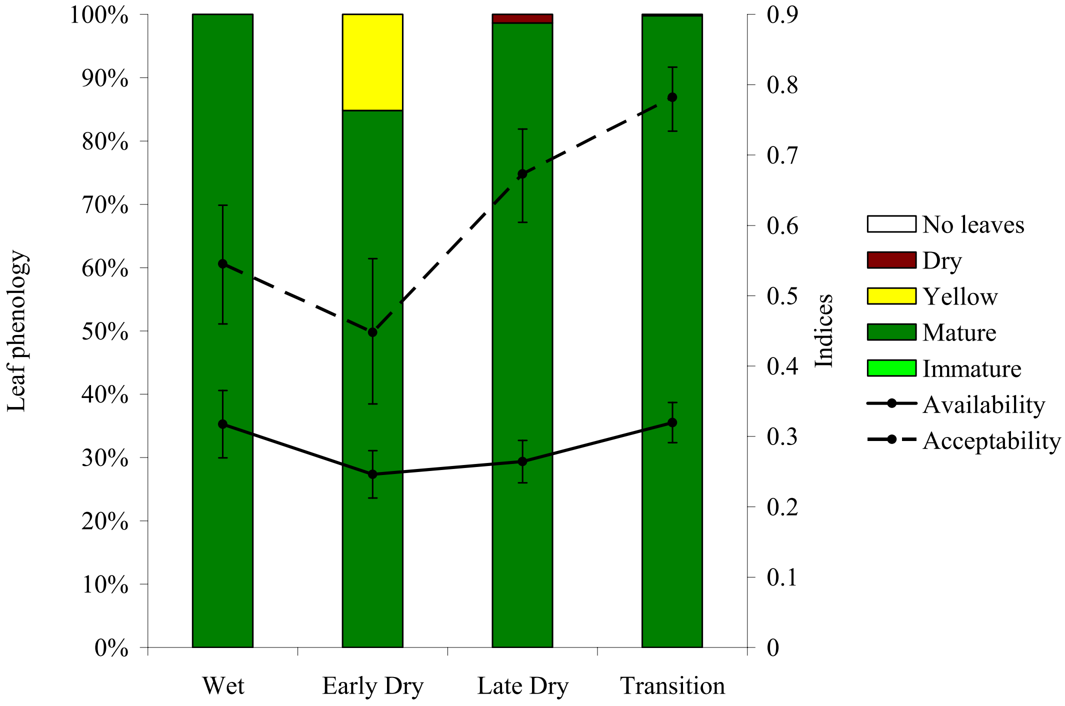


Figure 3d. Availability, acceptability indices (± SE) and proportion of leaves in different phenological stages in *M. incanum* over different rainfall periods.

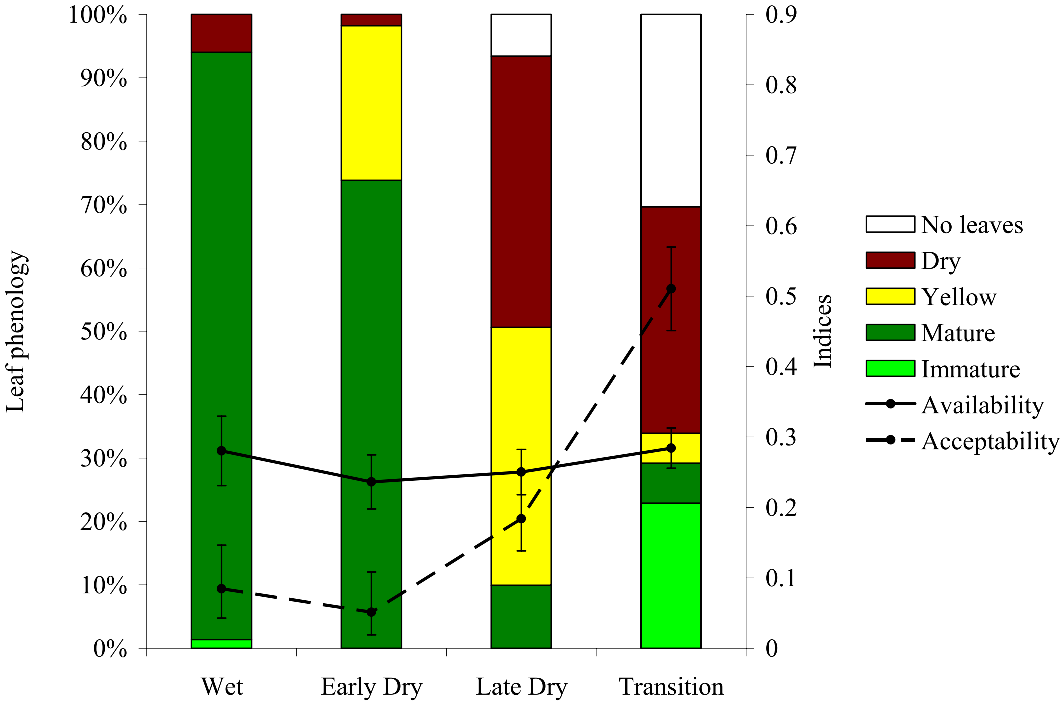
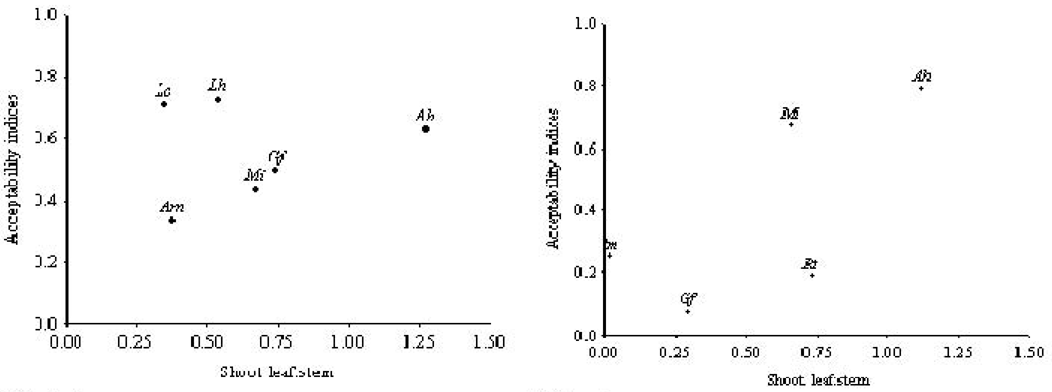


Figure 3e. Availability, acceptability indices (± SE) and proportion of leaves in different phenological stages in *R. trichotomum* over different rainfall periods.

a) Wet season

c) Late dry season



b) Early dry season

d) Transition season

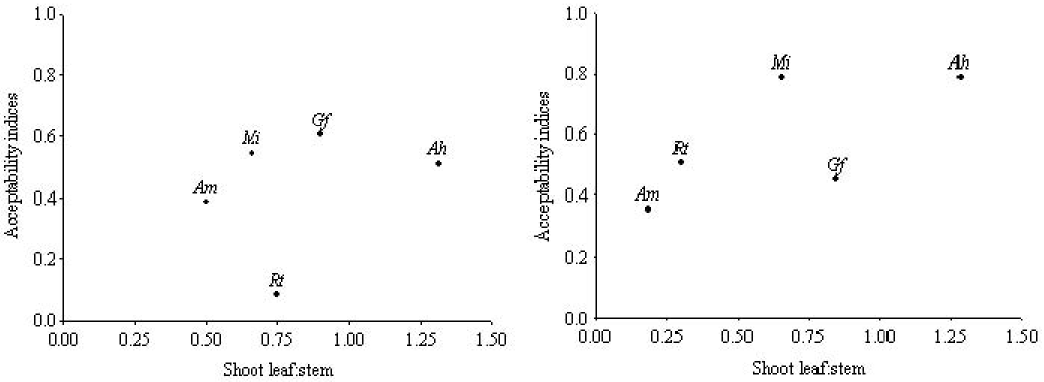
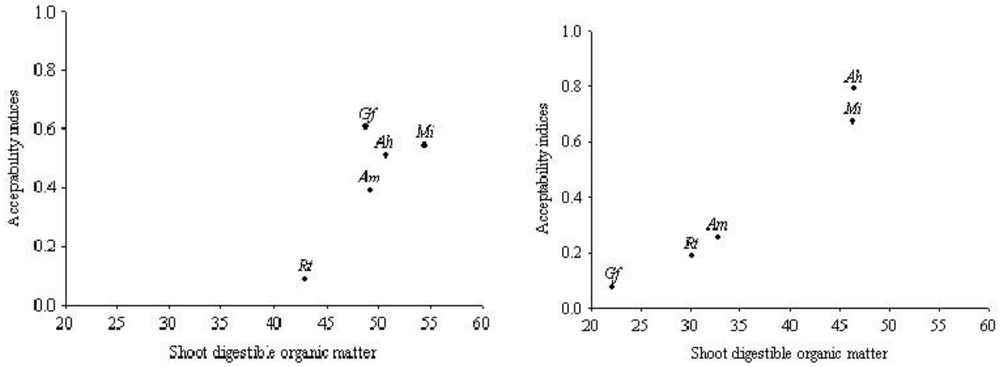


Figure 4. Acceptability indices for plant species in different seasons in relation to leaf:stem ratio.



a) Wet season

c) Late dry season

b) Early dry season

d) Transition season

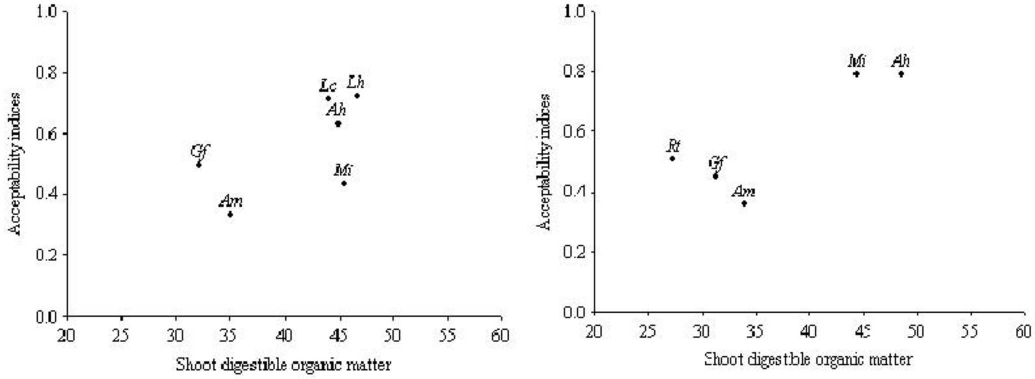


Figure 5. Acceptability indices for plant species in different seasons in relation to digestible organic matter content.

Table 1. Number of bites recorded between January 2004 and December 2005 from five focal rhinos in four different seasons.

Season	Bogale	Inyani	Kagale	Nantoni	Usuk	Total
Wet	1,077	843	1,141	1,137	786	4,984
Early dry	643	1,036	593	1,095	1,063	4,430
Late dry	1,068	1,779	1,068	1,636	2,541	8,092
Transition	1,789	2,625	3,946	2,251	1,756	12,367
Total	4,577	6,283	6,748	6,119	6,146	29,873

Table 2. Mean (± SE) proportional chemical contents of leaves in different seasons (% DM) (*n* = 5).

Chemical content / Species	Wet	Early dry	Late dry	Transition
Digestible organic matter				
A. haematoxylon	60.44 ± 0.95	54.73 ± 0.63	54.6 ± 0.75	57.81 ± 1.05
A. mellifera	68.91 ± 0.91	70.33 ± 2.66	0	67.09 ± 1.12
G. flava	65.57 ± 2.13	65.22 ± 0.49	0	62.24 ± 0.67
M. incanum	70.65 ± 1.03	66.56 ± 2.14	61.30 ± 0.88	64.75 ± 0.53
R. trichotomum	64.26 ± 6.87		74.62 ± 0.79	74.21 ± 6.78
L. cinerum		74.41 ± 2.72		
L. hirsutum		71.90 ± 1.70		
Crude protein				
A. haematoxylon	12.65 ± 0.32	14.03 ± 0.36	12.96 ± 0.43	14.16 ± 0.75
A. mellifera	23.75 ± 0.68	22.16 ± 1.30	0	23.3 ± 0.43
G. flava	16.83 ± 0.62	13.36 ± 0.39	0	17.31 ± 0.57
M. incanum	15.70 ± 0.89	15.56 ± 0.68	12.16 ± 0.82	18.92 ± 0.99
R. trichotomum	15.45 ± 0.63		9.21 ± 0.21	13.6 ± 1.01
L. cinerum		29.64 ± 4.10		
L. hirsutum		25.23 ± 1.37		
Condensed Tannins				
A. haematoxylon	4.67 ± 0.37	2.54 ± 0.38	2.83 ± 0.32	6.32 ± 0.79
A. mellifera	0.30 ± 0.19	0.03 ± 0.01	0	0.12 ± 0.04
G. flava	9.45 ± 0.60	5.31 ± 0.36	0	8.54 ± 0.32
M. incanum	0.07 ± 0.01	0.01 ± 0.01	0.03 ± 0.01	0.08 ± 0.01
R. trichotomum	0.15 ± 0.03		0.13 ± 0.01	0.3 ± 0.07
L. cinerum		0.05 ± 0.02		
L. hirsutum		0.12 ± 0.03		

Table 3. Mean (± SE) proportional chemical contents of twigs in different seasons (% DM) (*n* = 5).

Species	Wet	Early dry	Late dry	Transition
Digestible organic matter				
A. haematoxylon	41.66 ± 1.44	36.14 ± 0.93	38.89 ± 0.62	40.03 ± 1.24
A. mellifera	42.75 ± 0.54	42.5 ± 2.02	43.68 ± 1.06	40.15 ± 0.5
G. flava	39.58 ± 0.58	38.85 ± 1.86	41.12 ± 1.79	39.82 ± 2.03
M. incanum	42.38 ± 1.96	36.22 ± 2.61	39.14 ± 1.35	33.6 ± 1.11
R. trichotomum	39.55 ± 2.16		42.85 ± 0.84	38.9 ± 1.38
L. cinerum		32.06 ± 0.74		
L. hirsutum		33.32 ± 2.26		
Crude protein				
A. haematoxylon	7.38 ± 0.20	7.41 ± 0.17	7.74 ± 0.50	7.79 ± 0.31
A. mellifera	10.05 ± 0.47	9.15 ± 0.45	9.79 ± 0.76	8.8 ± 0.41
G. flava	6.96 ± 0.35	5.09 ± 0.12	5.78 ± 0.09	6.2 ± 0.38
M. incanum	8.78 ± 0.78	8.55 ± 0.35	8.39 ± 0.67	8.22 ± 0.40
R. trichotomum	7.36 ± 0.21		8.2 ± 0.21	7.53 ± 0.61
L. cinerum		11.43 ± 0.51		
L. hirsutum		10.66 ± 0.33		
Condensed Tannins				
A. haematoxylon	4.7 ± 0.33	2.32 ± 0.34	1.68 ± 0.20	4.21 ± 0.44
A. mellifera	0.91 ± 0.06	0.09 ± 0.02	0.28 ± 0.05	0.29 ± 0.10
G. flava	5.95 ± 0.27	2.37 ± 0.25	2.75 ± 0.28	6.16 ± 0.68
M. incanum	0.09 ± 0.05	0.01 ± 0.005	0.03 ± 0.01	0.02 ± 0.002
R. trichotomum	0.17 ± 0.07		0.05 ± 0.01	0.08 ± 0.01
L. cinerum		0.01 ± 0.001		
L. hirsutum		0.03 ± 0.01		

3. Seasonal nutritional gains in female black rhinoceros (*Diceros bicornis*) relative to reproductive requirements.

3.1 Abstract

Seasonal nutritional gains of female black rhinoceros at Tswalu Kalahari Reserve in South Africa were compared with estimated nutritional requirements for reproduction. This population has shown a high population growth rate since re-introduction in 1995. Leaves and twigs of seven browse species contributing 80 % of the dry mass of the diet were analysed chemically for NDF, crude protein and condensed tannins, to provide estimates of digestible organic matter and available protein.

Proportional monthly contributions of woody plant species to the diet were combined with seasonal chemical analyses to estimate gains in digestible organic matter and available protein. Overall seasonal variation in dietary content of protein and digestible organic matter was low. Although diet quality during the wet season diet was higher than the early dry, late dry or transition season, there was no marked decline in digestible organic matter or protein in the diet during the typically limiting late dry season. A semi-evergreen species, *Acacia haematoxylon*, contributed the majority of digestible organic matter and protein in the diet at this time. Despite known differences in woody plant species contribution to the estimated diet contents of individual rhinos, there was no difference in the nutritional composition of diets.

The proportional dietary content of digestible organic matter and protein required to meet maximum reproductive requirements was calculated for an estimated daily dry matter intake of 29 kg. Dietary proportions of digestible organic matter and protein in the diet exceeded estimated reproductive requirements throughout the seasonal cycle. Digestible organic matter was marginally greater than requirements, whereas protein nearly three times surplus, suggesting that energy is more likely to form the limiting resource.

These findings emphasise the importance of *A. haematoxylon* as a late dry season dietary resource for black rhino in this area and indicate that this species could be associated with the high reproductive performance of rhino at Tswalu. Increased population density and intraspecific competition for this resource would be predicted to result in density-dependence impacts and lower population growth rate. Calculating maximum productive habitat capacity for black rhino from the energy gains required for reproduction by individual female rhinos may help in maximising metapopulation growth rates, a key goal of black rhino conservation strategies.

Key words: *Browsing herbivore nutrition; Acacia haematoxylon; crude protein; energy; seasonal variation; reproductive requirements*

3.2 Introduction

An important component of black rhino conservation strategies is maintaining rapid metapopulation growth rates in existing populations of this critically endangered species, to mitigate poaching losses and allow establishment of new populations (Emslie and Brooks, 1999). The IUCN African Rhino Specialist Group (AfRSG) Continental Action Plan and all current National Strategies advocate managing for metapopulation growth rate of at least 5 % per annum and preferably higher (Emslie and Brooks, 1999; Emslie, 2001).

Inter-calving intervals of individual female black rhino have been proposed as an indicator for monitoring population performance, due to the clear inverse relationship between inter-calving intervals and growth rate (Knight, 2001). As megaherbivores (adult body mass > 1000 kg: Owen-Smith, 1988), black rhinos are characterised by long life history features with an extended 15-month gestation period (Goddard, 1966; Hall-Martin and Penzhorn, 1977). Female black rhino do not seem able conceive before 8 months after giving birth (Garnier *et al.*, 2002) though lactation has been observed to continue for up to sixteen months in captivity (Gregory *et al.*, 1965). Hence, the minimum recorded inter-calving interval for black rhino is around 2.1 years (Owen-Smith, 1988) though mean values vary in different areas (Hrabar and du Toit, 2005). Mean intervals of 2.4 years have been reported in the Great Fish River Reserve in South Africa and 3.5 years in the Waterberg Plateau Park in Namibia (Helary *et al.*, 2009). Black rhino occurring at very high density (1.2 rhinos / km^2) in Solio Game Reserve, Kenya had an inter-calving interval in excess of 3 years (Patton *et al.*, 2008). Black rhino re-introduced to Tswalu Kalahari Reserve in the Northern Cape of South Africa, have shown excellent performance rates (du Toit, 2001) with low mean inter-calving intervals (mean±SE: 2.2±0.1 years, n = 17) and high annual growth rate (13±3 %).

Breeding success as assessed by inter-calving intervals is linked to diet quality and subsequent nutritional status of individual females. In large herbivores, individuals in good condition have higher fecundity rates, allocate more resources to offspring, attain adult size and achieve reproductive maturity at earlier ages than individuals in poor condition (Bonenfant *et al*., 2009). At increased population densities, food shortages are the main factor generating such density-dependent responses upon demographic rates of large herbivores (Fowler, 1987). The breeding rates of red deer hinds on the Isle of Rum in Scotland appear related to the time required to regain peak condition following reproduction (Clutton-Brock *et al.*, 1982, Clutton-Brock and Coulson, 2002), which is dependent upon food resource availability and linked to population density. In the Pilanesberg National Park in South Africa, female black rhino had longer inter-calving intervals in periods of lower rainfall with lower food resource availability (Hrabar and du Toit, 2005). Hearn (2000) suggested that differences in reproductive performance of female black rhinos in three regions of north-western Namibia were also related to differences browse availability.

In most African savannas, diet quality for browsing herbivores varies seasonally due to the influence of rainfall patterns on plant phenology. Browse availability typically decreases during the dry season, due to leaf loss and consumption by herbivores. As a consequence of these phenological changes the chemical content and nutritional quality of the plant material also declines (Pellew, 1984; Dierenfeld *et al*, 1995). Young plant tissue is generally less lignified and more digestible than mature tissue and contains higher levels of protein (Van Soest, 1982; Pellew, 1984; Dierenfeld *et al*., 1995). Therefore, levels of indigestible fibre in browser diets tend to increase during the dry period when most of the annual forb species have died and deciduous species have shed their leaves (Pellew, 1984; Owen-Smith and Cooper, 1989; Hall-Martin *et al*., 1982). Hence, levels of crude protein and metabolizable energy in browser diets follow a similar pattern and typically decrease during the dry season (Hall-Martin *et al*., 1982; Pellew, 1984; Owen-Smith and Cooper, 1989; Atkinson, 1995). Therefore, the late dry season is the critical period for herbivores and the point at which nutritional bottlenecks are most likely to occur (Owen-Smith, 2002).

As a consequence, survival and reproduction in herbivores is dependent upon the availability of vegetation components providing adequate rates of intake of energy, protein and other essential nutrients to meet requirements at critical times of the year (Owen-Smith and Novellie, 1982; Owen-Smith and Cooper, 1989). Energy has been identified as the main limiting factor for browsers including deer species (white tailed deer and black tailed deer) in Texas and Alaska (Bryant *et al.*, 1980; Parker *et al.*, 1999), for kudu (*Tragelaphus strepsiceros*) in South Africa (Owen-Smith and Cooper, 1989) and for captive rhino fed indigenous browse in Zimbabwe (Atkinson, 1995). As crude protein contents of woody plant matter generally remains high throughout the year, protein is less likely to prove limiting for browsing herbivores, even during dry periods (Bryant *et al.*, 1980; Owen-Smith and Cooper, 1989; Atkinson, 1995; Parker *et al.*, 1999). However, the actual amount of protein available to browsing herbivores is also dependent upon the level of condensed tannins and their impacts upon protein digestibility as well as the proportion of fibre-bound nitrogen (Robbins, 1983; Dierenfeld *et al.*, 1995). Clauss *et al.*, (2006a) found that digestible organic matter can be used as an estimate of available energy for browsing rhinos.

Analysis of black rhino diet content at Tswalu showed that *Acacia haematoxylon* forms the main dietary resource for black rhino during the dry season (Chapter 2). As a semi-evergreen species, *A. haematoxylon* is unusual in the Mimosoideae subfamily for retaining mature green leaves throughout the seasonal cycle. Although there were differences in individual diet content throughout the year, this single plant species constituted over 75 % of dietary dry mass for all five adult female rhino during the late dry season. Availability of this palatable evergreen resource during the dry season means that the female black rhino in Tswalu have a high quality diet throughout the year. Hence, they are not subject to the seasonal declines in nutritional status which have been observed in browsing herbivores elsewhere.

The aim of this paper was to compare seasonal nutritional intake by black rhino at Tswalu with nutritional requirements for reproduction and discuss how these findings might relate to the high population growth rate.

Therefore, the objectives and hypothesises were;

1) To determine the seasonal nutritional content of female black rhino diet at Tswalu

H_0 Nutritional composition of the diet of the five female rhinos would not show differences in digestible organic matter or protein content between individuals.

H_0 Dietary levels of digestible organic matter and protein would be greatest during the wet season.

H_0 Dietary levels of digestible organic matter and protein would not decline from the early dry period to transition period, due to an increase in *A. haematoxylon* in rhino diet content during the late dry period.

2) To compare estimates of nutritional gain with estimates of protein and energy levels needed to meet maximum reproductive requirements

H_0 Female black rhino at Tswalu would be able to meet nutritional requirements of crude protein and energy for reproduction throughout the seasonal cycle.

H_0 Proportional digestible organic matter content in the diet would be closer to reproductive requirements than proportional dietary intake of protein.

3.3 Methods

Study site

This study was conducted at Tswalu Kalahari Reserve, a 1,080 km^2 private game reserve in the Northern Cape of South Africa (S 27°04' - 27°44' and E 22°10' - 22°36'). The predominant vegetation type in the reserve has been classified as Shrubby Kalahari Dune Bushveld (Low and Rebelo, 1996). Climate is semi-arid and rainfall is seasonal and highly variable between years. Monthly rainfall data compiled from farm records (1973-2002) and daily records maintained by staff at Tswalu (2003-2005) show a mean annual rainfall in the area of 280 ± 164 mm (mean ± SD) (Unpublished data). Rainfall was slightly below average (229 mm) during the first year of the study from January 2004 - December 2004 and above average (428 mm) during the second year from January 2005 - December 2005. The annual cycle was split into four seasons relating to woody plant phenology (defined as retention of mature green leaves); wet (January-March), early dry (April-June), late dry (July-

September) and transition period from late dry to wet season when new leaf growth was flushing (October-December). See Chapter 2 for more details on seasonal plant phenology.

Eight black rhino were re-introduced to Tswalu from Etosha National Park, Namibia in June 1995. The population had grown to 23 by December 2005 and showed a high annual growth rate with low mean inter-calving intervals. The five adult females remaining from the founder population (Bogale, Inyani, Kagale, Nantoni and Usuk) were selected as the focal animals for this study as the only reproductive females on the reserve at this time.

Data collection

Rhino diet content

Diet content data was collected using a backtracking method common in black rhino diet studies (Joubert and Eloff, 1971; Mukinya, 1977; Loutit *et al*., 1987; Hall-Martin *et al*., 1982; Oloo *et al.*, 1994; Ganqa *et al*., 2005; Helary *et al*., 2009). Rhino spoor were located in the early morning and followed to collect information on rhino browsing activity from the previous evening. This technique works well at Tswalu as rhino movements are easily detected from spoor retained in the sandy substrate. Only fresh spoor identified by an experienced tracker as less than 24 hours old were followed for data collection. See Chapter 2 for a detailed description of backtracking methodology. Over the two year data collection period, 147 feeding tracks were recorded totalling 274.5 km (daily range: 0.5 to 5.1 km) between January 2004 and December 2005 (wet: n = 30, early dry: n = 29, late dry: n = 39, transition: n = 48).

Black rhino bites can be distinguished from those of other browsers by their characteristic neatly-pruned appearance (Muya and Oguge, 2000) Browsing activity was recorded for one focal rhino each day, as the number of bites taken from each plant species along a feeding track. All severed shoots less than 5 mm thick occurring within a hypothetical circle of 5 cm of diameter were counted as one bite following Hall-Martin *et al.* (1982). Recent browsing was distinguished from older use by comparing the paler yellow-green colour of the wood at point of a fresh bite with the dry, brown colouration of older bites (Emslie and Adcock, 1994). For five days in each season, the diameter of all shoots within each bite were measured and categorised into size classes (0<1 mm, 1<3 mm, 3<6 mm) to allow bites to be converted into dry mass using a regression equation.

Dry mass

Dry mass regression equations for shoot diameter were developed for the woody plant species that contributed 80% of the diet content as shown in Chapter 2. Twenty twigs of *A. haematoxylon*, *A. mellifera*, *G. flava*, *R. trichotomum*, *M. incanum*, *L. cinerum* and *L. hirsutum* in the three diameter size classes (0≤1 mm, 1≤3 mm, 3≤6 mm) were collected in the wet season when mature leaf retention was greatest. Leaves and twigs were air-dried for two years throughout the data collection period then the dry mass of each sample was obtained on an Ohaus Precision Plus TP4000D scale calibrated to an accuracy of three decimal places.

The relationships between the twig diameter values (x) and stem and leaf dry weight (y) for each species were determined using regressions equations; $y = ax^b$ where a and b are constants (Basile and Hutchings, 1966). Mean bite mass for each plant species in each season could then be calculated from diameter size class of twigs in each bite. Leaf:twig ratio was adjusted dependent upon the proportion of mature leaves recorded as retained for each species each month. The mass of each leaf and twig fraction was also used to calculate a leaf:twig (=wet season leaf mass / wet season twig mass) wet season ratio for each plant species. Leaf retention (0, 1 - 5, 6 - 33, 34 - 66, 67 - 100%; Dekker and Smit, 1996) and leaf phenology (immature, mature, yellow and dry) were recorded along each feeding track. The total dry mass contribution for a plant species each month was the sum in each diameter class of the dry mass of stems and proportion of leaves retained (Helary *et al.*, 2009). For additional plant species which contributed the remaining 20% of the diet, dry mass data was substituted from the known species considered to have the most similar structure. Mean dry mass intake recorded per feeding track was 9.2 kg (daily range: 1.3 kg – 35.0 kg).

Plant samples

Plant species assessed were those contributing up to 80% of the diet in each season, thus; *A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum* and *R. trichotomum* in November 2004 (transition to wet season), September 2005 (late dry) and January 2006 (wet) and *A. haematoxylon*, *A. mellifera*, *G. flava*, *M. incanum*, *L. cinerum* and *L. hirsutum* in May 2005 (early dry). Chapter 2 contains details of seasonal diet content of black rhino at Tswalu. Samples from five different individual plants of each species were pruned at the observed diameter selected for each plant species by browsing rhinos. The intention being to match the leaf:twig of analysed samples with material ingested by rhino. All samples were collected prior to 10 am to prevent the effects of prolonged exposure to sunlight and leaf material was separated from twigs at the base of the petiole (Dierenfeld *et al.*, 1995). The samples were air-dried and stored in paper bags prior to being over dried where necessary in preparation for chemical analysis.

Data analysis

Chemical analysis

Leaves and twigs were analysed separately. All plant samples were ground through a 0.5 mm screen. Standard wet chemical analyses were performed on a subset of the total sample using techniques outlined by AOAC (American Organization of Analytical Chemists, 1990). Fibre constituents (NDF) were determined using procedures from ANKOM technology fibre analysis (Goering and van Soest, 1970). Nitrogen (N) was extracted using the macro-Kjeldahl procedure (AOAC, 1990). Condensed tannin analyses were performed as described in Hagerman (2002), the acid butanol assay was used with Sorghum tannin standard. For the remaining samples, N and NDF content were analysed using NIRS (Near Infra Red Spectrometry). An inductively coupled plasma-optical emission spectrometer (ICP-OES) and an ANKOM 200/220 Fibre Analyzer were used to measure the N and NDF contents in the samples from the calibration set. Wet chemistry analysis of fibre and condensed tannin content was performed by Dawood Hattas from the Botany Department of the University of Cape Town. The macro-Kjeldahl procedure for N extraction was undertaken by BEMLAB in Cape Town. NIRS analyses were conducted at the Dairy Research Institute at Irene in Pretoria.

To estimate energy availability, NDF was converted to digestible organic matter (dOM g/g) using the equation; dOM = (-NDF*0.98) + 101 for browsing rhinos taken from Clauss *et al.* (2006a). Crude protein (CP) was calculated by multiplying the nitrogen content by 6.25. Available protein (AP) was calculated using the ratio of CP – CT/2 % developed for browsing ungulates (Owen-Smith and Cooper, 1987). Although rhinos are hindgut fermenters, this approach was included to provide an approximation of the seasonal impact of condensed tannins on protein availability.

Dietary nutrient content

Mean values were calculated for the concentration of protein and digestible organic matter within samples (n = 5) of both the leaf and twig matter of each plant species in each season. The dietary content of protein or digestible organic matter each day was produced by multiplying the seasonal value for the relevant plant part with the respective dry mass ingested of each plant part on that specific day. Chemical contents of the remaining part of the diet were inferred from plant species with the most similar structure and phenology.

Nutritional requirements

Energetic requirements were estimated using the field metabolic rate (FMR), which includes energy needed for maintenance, basal metabolism, thermoregulation and activity (Nagy, 1987; Nagy, 1994): $FMR = (4.63\ M^{0.762})/1000$. For an adult female black rhino of body weight 1000 Kg (Owen-Smith, 1988), the FMR would be 173 MJ /day. The daily extra energy cost incurred by the gravid uterus prior to parturition can be estimated at 44% of the basal metabolic rate (BMR) ($BMR = (70\ M^{0.75}) \times 4.184/1000$) (Robbins, 1983) where M is the maternal weight in Kg, and (4.184/1000) is used to convert Kcal into MJ. Therefore, the daily energy requirement of a pregnant female prior to parturition was estimated as 196 MJ / day. Seasonal values for digestible organic matter in the diet were converted to energy using a gross energy value for rhino browse of 18.2 MJ/kg DM recorded by Clemens and Maloiy (1982) in East Africa. Total energy values were converted to digestible energy using a value of 0.83 (ARC, 1965 in Owen-Smith, 1989).

Following Atkinson (1995), daily protein requirements (g/day) were estimated using the standard relationship used by Foose (1982): Protein requirements = 0.912 $M^{0.75}$ where rhino body mass (M) is measured in kg. This basal measure represents endogenous requirements, determined from nitrogen excretion in the urine. However, losses of protein due to digestive and metabolic processes elevate actual protein requirements to be approximately 2 to 3 times greater (Foose, 1982). Crude protein digestibility for black rhinos in bomas fed an indigenous cut browse diet was recorded between 58% and 68% (Atkinson, 1995). Therefore, using a measure of 3 x basal requirements with a crude protein digestibility estimate of 60%, the black rhino daily protein requirement for maintenance is approximately 487 g/day for a 1000 kg animal. Daily reproductive protein is estimated as 35% of the total maternal endogenous requirements (Robbins, 1983). Hence, protein requirements for a reproductively active female were estimated at 657 g/day.

Required dietary proportions

It was not possible to measure total daily dry matter intake by the free-ranging focal rhinos as it was not known what proportion of the 24 hour period was represented by each foraging track. Therefore, it is not possible to assess directly whether dietary intake of protein and digestible organic matter or metabolizable energy would be limiting in relation to reproductive requirements during the different times of year. In order to compare estimated proportional gains with requirements, estimates were made of the dietary concentrations of crude protein and digestible organic matter required to meet maximum gestation and lactation requirements at a standard estimate of total dry matter intake.

Following Nagy (2001), daily dry matter intake by black rhino was calculated as DMI (g) = 0.323 $(M)^{0.744}$ giving a value of approximately 29 kg dry matter for a rhino of body weight 1000 kg (Atkinson, 1995). Maximum estimated intake on a feeding track of 3.2 km at Tswalu was 35 kg DM, but it is not known what proportion of a 24 hour period this represented.

Statistical analysis

Multifactor ANOVAs were used to analyse for seasonal differences in dietary content of protein and digestible organic matter. The estimated proportion of a nutrient in the diet each day was used as the response variable. Factors were five individual rhinos (Bogale, Inyani, Kagale, Nantoni and Usuk), four seasons (wet, early dry, late dry and transition) and two years of data collection (2004 and 2005). Post-hoc significant differences were tested using Tukey Honest Significance test.

All proportional dietary content data were arcsine transformed prior to analysis to conform to normality requirements (Zar, 1999). The *P*-level for rejection of the null hypothesis was <0.05. All values are reported as mean ± standard error. All analyses were performed using STATISTICA version 6 (StatSoft, Inc. 2001).

3.4 Results

Individual rhino

Despite differences in plant species contribution to individual rhino diet (Chapter 2), there was no difference in overall dietary concentrations of digestible organic matter (Bogale = 48.0 ± 0.3 %; Inyani = 48.1 ± 0.3 %; Kagale = 48.0 ± 0.4 %; Nantoni = 47.6 ± 0.4 %; Usuk = 48.0 ± 0.4 %, $F_{4, 106}$=1.790, *P*=0.136) or differences in dietary concentrations of digestible organic matter in individual rhino diet in different seasons ($F_{12, 106}$=0.858, *P*=0.591).

Proportional content of crude protein content among individual rhinos did not show individual differences (Bogale = 11.0 ± 0.2 %; Inyani = 11.0 ± 0.1 %; Kagale = 10.9 ± 0.1 %; Nantoni = 11.1 ± 0.2 %; Usuk 11.0 ± 0.2 %, $F_{4, 106}$=0.634, *P*=0.639). Nor did dietary concentrations of crude protein differ in individual rhino diet in different seasons ($F_{12, 106}$=1.6533, P=0.0880). Available protein did not differ in individual rhino diet overall (Bogale = 9.9 ± 0.2 %; Inyani = 9.6 ± 0.2 %; Kagale = 9.6 ± 0.2 %; Nantoni = 9.9 ± 0.2 %; Usuk 9.7 ± 0.2 %, $F_{4, 106}$=0.502, P=0.734) or in different seasons ($F_{12, 106}$=1.3764, P=0.189).

Diet source

During the wet season, *G. flava* contributed 34 % of the monthly digestible organic matter in the diet, *A. mellifera* 23 % and *A. haematoxylon* 25 %. *Acacia haematoxylon* provided the majority of the digestible organic matter in the diet in the early (53 %), late dry (75 %) and transition (57 %) seasons.

The source of crude protein in the diet in the wet season was distributed between *G. flava* (34 %) and *A. mellifera* (27 %) with a smaller contribution from *A. haematoxylon* (20 %). As expected, the value of *A. haematoxylon* as a source of crude protein increased during the drier seasons (early dry season 42 %, late dry season 66 %, transition season 46 %).

Nutrient contents

The magnitude of monthly variation in both digestible organic matter and protein contents of the diet throughout the year was relatively low, at approximately 20 % and 10 % respectively. Potential energy availability in the diet, measured as digestible organic matter, was marginally greater in 2004 (48.4 ± 2.0%) than 2005 (47.6 ± 1.8%) ($F_{1, 106}$=4.043, P=0.047). The seasonal pattern differed between 2004 and 2005 ($F_{3, 106}$=8.3685, P=0.00005) (Fig. 1). Levels of digestible organic matter were greater in the wet season in both years (50.5 ± 0.2%) than any other season (Tukey HSD; all P<0.001). During 2004 there was no difference in dietary digestible organic matter between the early dry and late dry seasons (early dry = 47.4 ± 0.3%: late dry = 46.8 ± 0.5%). The transition period in 2004 had higher levels of digestible organic matter than the early and late dry seasons that year (48.8 ± 0.4% Tukey HSD; early dry P=0.00012: late dry P=0.00012). The increased proportion of *R. trichotomum* at the beginning of the transition season in October 2004 caused a rise in dietary digestible organic matter at this time (Chapter 2). In 2005, the diet contained lower levels of digestible organic matter in the late dry season (45.6 ± 0.2% Tukey HSD; early dry P=0.00012, transition P=0.002) than either the early dry season (47.8 ± 0.4%) or the transition season (47.2 ± 0.2%) though there was no difference between the latter two.

Crude protein content in the diet showed a gradual and significant decline from the wet season through the late dry season as deciduous plant species lost their leaves ($F_{3,\ 106}$ = 22.975, P=0.00001). Mean levels of crude protein in the diet of 11.8 ± 0.2% in the wet season and 11.0 ± 0.1% in the early dry season were higher than the late dry and transition seasons (late dry 10.6 ± 0.1%; transition 10.7 ± 0.1%) (Fig. 2). There was no difference in total dietary crude protein ($F_{1,\ 106}$=0.007, P=0.933) between years. Dietary content of available protein also showed significant seasonal differences (Fig. 2), with lower levels in the transition season (9.4 ± 0.1%) than any other season (wet: early dry: late dry: ,$F_{3,106}$=3.3400, P=0.022) but no difference between years ($F_{1,\ 106}$=0.0987, P=0.754).

Estimated gains relative to requirements

Field metabolic requirements for black rhino females that are not pregnant were estimated at 173 MJ/day (as detailed in the methods section). The minimum digestible organic matter concentration in the diet required to meet these maintenance requirements was calculated at 39.5% (for daily dry matter intake of 29kg) (Fig. 3). For pregnant females, field metabolic requirements were estimated at 196 MJ/day meaning a minimum dietary concentration of 44.7% digestible organic matter was required.

Monthly proportions of dOM in the diet were clearly greatest during the wet season months in both years and lower during the drier months (Fig. 3). However, the lowest dietary concentration of dOM in female black rhino diet at Tswalu was 45.3% towards the end of the dry season during August 2005; hence estimated levels of digestible organic matter exceeded estimated requirements for reproduction by at least 0.6% throughout the seasonal cycle (Fig. 3). The maximum excess gain in digestible organic matter against reproductive requirements was 5.9% at during the wet season in March 2004.

For females that were not pregnant estimated protein requirements were 487 g/day and the minimum protein concentration in the diet necessary to achieve this was 4.8% (assuming daily dietary dry mass intake of 29kg) (Fig. 4). In pregnant females, protein requirements were estimated at 657 g/day and required dietary protein concentration would be approximately 5.8%.

Estimates of dietary concentration of both crude and available protein were in excess of reproductive requirements throughout the year (Fig. 4). Minimum concentration of available protein in the diet of female rhino at Tswalu was 8.9% in December 2004, therefore estimated available protein in the diet exceeded reproductive requirements by at least 3.1% throughout the seasonal cycle (Fig. 4).

3.5 Discussion

Nutritional content of female black rhino diet at Tswalu was, as predicted, greatest during the wet season. Late dry season estimates of dietary content of digestible organic matter, crude protein and available protein were roughly comparable to early dry and transition season. Estimates of potential energy showed different seasonal patterns between years, with a greater concentration in the transition season in 2004 compared to 2005, associated with increased consumption of *R. trichotomum* during the new leaf flush in this year (Chapter 2). Digestible organic matter was lower in the late dry season than the early dry or transition seasons during 2005, though the actual dietary concentration remained relatively high at 45.6 %. Crude protein content was greatest in the wet season but was significantly higher in the early dry season than either the late dry or transition season. Estimates of available protein were lowest during the transition season, due to the high condensed tannin content of new shoots at this time.

The most noteworthy aspect of these seasonal estimates of nutritional gain is the low magnitude of variation in diet quality throughout the year. Monthly variation in digestible organic matter and protein content of the diet was just 20 % and 10 %

respectively. Analysis of seasonal variation in energy and protein content of kudu at Nylsvley show declines of approximately 30 % for digestible dry matter and 40 % for protein between the wet and late dry season (from values in Owen-Smith and Cooper, 1989). Shrader *et al*. (2006) found a 40 % decline in protein intake over the dry season in grazing white rhino (*Ceratotherium simum*).

In terms of proportional diet content, the minimum digestible organic matter during the late dry season (45.6 %) is on the upper level of digestibility estimates available for free-ranging rhino. Proportion of indigestible fibre (NDF) in the dry season diet of black rhino at Waterberg Plateau Park in Namibia was 57.6 %, giving a digestible organic matter content of 44.6 % (Helary *et al.,* 2009). Rhino in bomas fed on indigenous browse during the early dry season in Zimbabwe had dry matter digestibilities between 41 % and 49 % (Atkinson, 1995 in Clauss *et al*., 2006a). However, at Great Fish River Reserve in South Africa, NDF in the dry season was 46.2 %, giving a dOM estimate of 55.7 % which was greater than estimates from Tswalu (Helary *et al.,* 2009). The late dry season dietary concentration of crude protein of 10.6 % is higher than has been observed in black rhino elsewhere. Estimates of crude protein concentration in the late dry season diet for black rhino were was 6.1 % at Waterberg Plateau Park in Namibia and 6.2 % at Great Fish River Reserve in South Africa (Helary *et al*., 2009). Crude protein levels in the diet of rhinos in bomas fed indigenous browse in Zimbabwe during the early dry season ranged between 9.6 % and 10.5 % (Atkinson, 1995 in Clauss *et al*., 2006a).

The high quality dry season diet and absence of a marked late dry season decline in energy or protein was primarily attributable to consumption of *A. haematoxylon*. As this species retained mature leaves throughout the year, shoots contained high levels of nutrients even during the late dry season (10.2 % crude protein and 46.4 % digestible organic matter: Chapter 2). Results from this chapter highlight the importance of this species during the late dry season, as the source of approximately 70 % of protein and 80 % of energy at this time.

In fact, despite overall differences in dietary contributions of other woody plant species, *A. haematoxylon* formed the major part of the early dry, late dry and transition season diet of all focal female rhino (Chapter 2). Hence, as predicted, neither energy nor protein content in the diet showed significant differences between individual rhinos. These results show that although dietary content in terms of woody plant species may differ between rhinos, there is no resultant impact upon overall nutritional status. This indicates that individual's substitute resources of similar value to ensure their requirements are met (Bolnick *et al.*, 2003).

Outputs from the estimated energy and protein balance for female black rhino at Tswalu indicated that reproductive requirements were met throughout the year. Hence, rhinos were predicted to be able to obtain sufficient nutrients for year-round breeding. This was as expected, given the high breeding rate recorded for this population. As predicted, estimated energy gains were closer to estimated requirements for reproduction compared to protein intake, which far exceeded estimated requirements throughout the year. That energy appears more likely to form the limiting resource for black rhino at Tswalu follows the pattern predicted for browsers by Owen-Smith and Novellie (1982) and supported by observations on kudu in Nyslvley Nature Reserve, South Africa (Owen-Smith and Cooper, 1989) and captive rhino in Zimbabwe (Atkinson, 1995). For black rhinos at Tswalu, available protein gains were nearly two times greater than requirements for reproduction. In contrast, digestible organic matter gains were close to requirements for reproduction during the late dry season at Tswalu. Hence, minor differences in energy gains would be anticipated to have a greater influence on future population performance, due to the surplus availability of protein throughout the year.

It is accepted that the main limitation of this paper is the assumption made regarding daily dry matter consumed by rhinos. Unfortunately, it was not possible to quantify total daily dry matter intake from the free-ranging rhinos as the proportion of total intake recorded along feeding tracks that was dry mass was not known. Therefore, a standard estimate of daily dry matter intake was produced from Nagy's (2001) equation relating dry matter intake to body mass, following the approach of Atkinson (1995). The resultant estimate of 29 kg dry matter intake used in this analysis is supported by studies which have quantified black rhino daily intake of indigenous browse in bomas (Dry mass: 25 kg (Atkinson, 1995), 30 kg (Ghebremeskel *et al.*, 1991), Wet mass 40 – 50 kg (Maddock *et al.*, 1995)). Owen-Smith and Novellie (1982) used an estimate of 3 % body mass when estimating daily dry mass intake for an adult female kudu, which would be equivalent to 30 kg for a black rhino of body mass 1000 kg (Owen-Smith, 1988). In fact, the value of 29 kg is less than the maximum calculated dry matter intake from Tswalu was 35 kg from a 3.2 km feeding track in October 2005.

The other parameter affecting estimates of energy gains is the energy value for rhino browse. The value used here was 18.2 MJ / kg from the work of Clemens and Maloiy (1982) from East Africa. Owen-Smith and Cooper (1989) used a browse energy value of 18 kJ / g from ARC (1965) to estimate kudu energy gains. This value is supported by estimates of gross energy content between 17.6 – 18.7 MJ / kg reported by Clauss *et al*. (2006a). Loutit *et al*. (1987) found a lower value of 16.3 MJ / kg for rhino browse from Namibia, but this was from analysis during just the late dry season.

The absence of nutritional restrictions on rhino reproduction at Tswalu was supported by field observations which showed rhino body condition remained high throughout the year (*pers. obs.*). Rhino body condition scores were recorded at each sighting based on the standardised monitoring system of Reuter and Adcock (1998) which makes a visual assessment of fat stores. In other areas, such as the Zambezi Valley in Zimbabwe, rhino body condition has been noted to decline due to the nutritional constraints associated with the dry season (Dierenfeld *et al*., 1995). Shrader *et al.* (2006) suggested that white rhino in Hluhluwe-iMfolozi Park, South Africa were required to mobilize fat reserves to help meet their nutritional needs during the dry season. Adult female black rhinos tend to be the first to lose condition due to nutritional demands of pregnancy and lactation (Reuter and Adcock, 1998) but this was not observed at Tswalu.

This analysis has focussed on energy and protein as the most likely nutritional factors limiting rhino reproductive success. However, dietary content of phosphorous, sodium and zinc were considered potentially marginal in black rhino browse in the Zambezi Valley in Zimbabwe (Dierenfeld *et al.*, 1995). Analysis of faecal endogenous mineral losses in black rhino has shown that sodium absorption was lower than expected (Clauss *et al.*, 2006b). It is noted that all minerals must be present in sufficient quantities in the diet or breeding rates may be affected even if energy and protein are in excess. Salt licks were provided at waterholes at Tswalu and black rhino were observed to use them occasionally (*pers. obs.*). Hence, it was not possible to link reproductive success with mineral concentrations in natural diet in this study.

In conclusion, the reproductive performance of female black rhino at Tswalu does not appear nutritionally limited due to their adaptive use of food resources, dependent upon seasonal changes in quality and availability. Hence the estimated nutritional requirements for gestation, parturition and lactation can be attained throughout the year. Pellew (1984) identified a similar link between giraffe energy balance throughout the year and their reproductive success in the Serengeti, Tanzania. At the population density recorded during this study, food availability and quality allowed female black rhino to meet the nutritional requirements for reproduction even during the typically limiting late dry season. This was primarily due to availability of *A. haematoxylon* in the dry season. As the rhino population grows, intra-specific competition for resources will increase and individual gains may no longer meet requirements. Subsequent losses in individual female body condition would be predicted to cause an increase in inter-calving intervals with an associated decline in the population growth rate (Clutton-Brock *et al.*, 1982, Clutton-Brock and Coulson, 2002). The next step will be to develop a metaphysiological model to assess the potential impact of declines in *A. haematoxylon* availability on energy balance of individual rhinos (Chapter 6). The concept of balancing individual female energy requirements to reproductive requirements offers a new approach for calculating the maximum productive density of black rhino.

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Figures

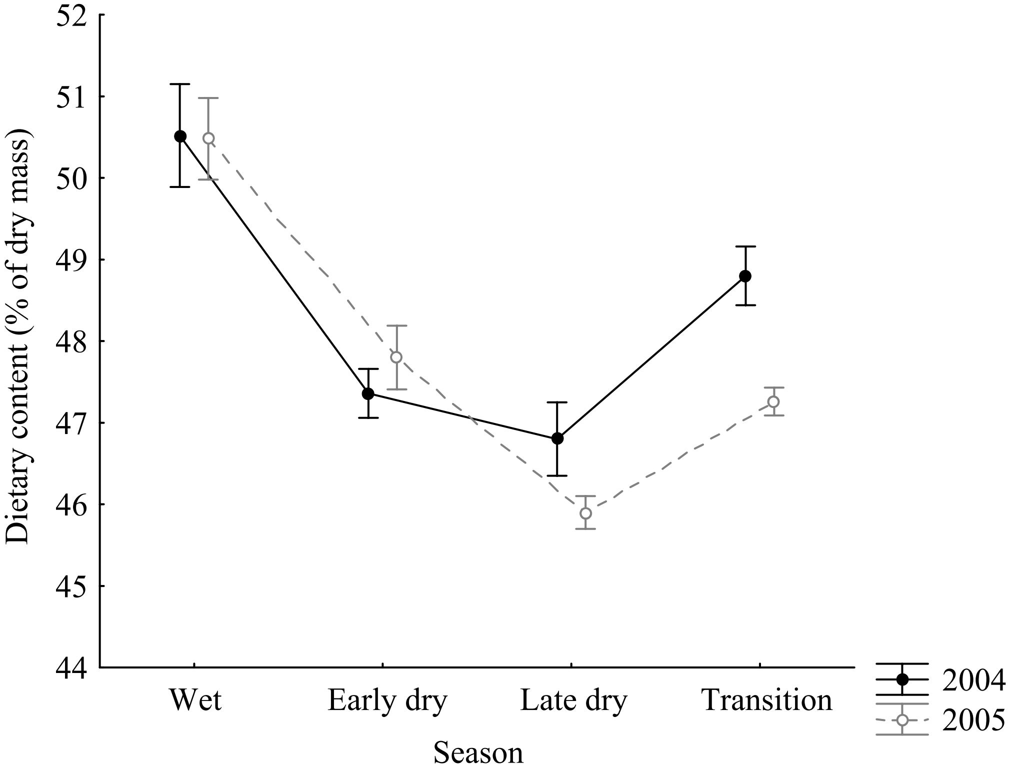

Figure 1. Mean (± SE) digestible organic matter as percentage of dietary dry mass for focal female rhino in four different seasons.

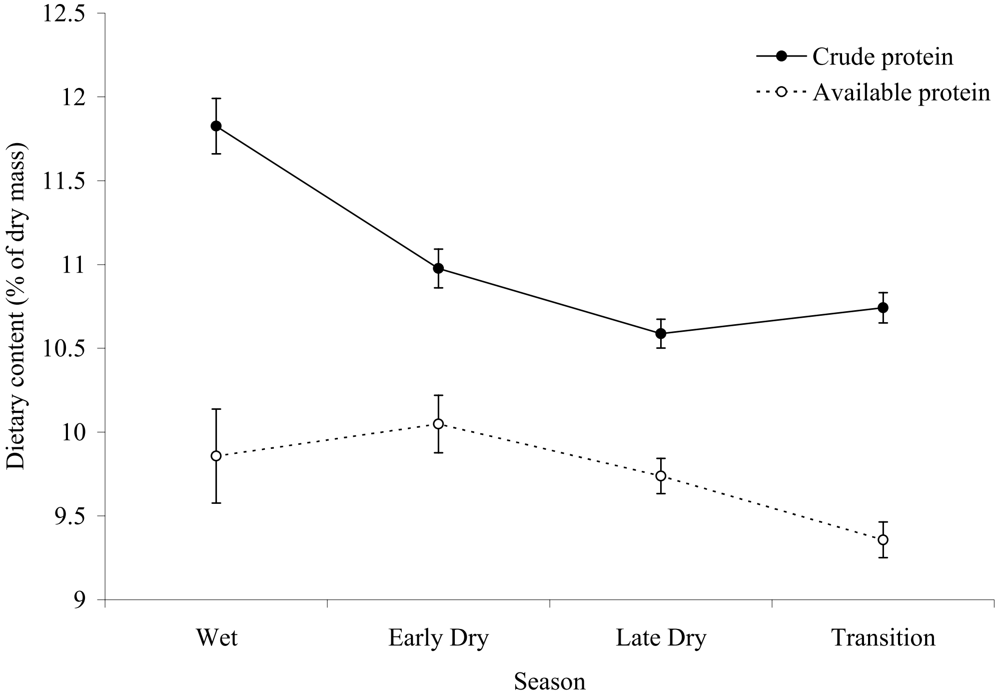

Figure 2. Mean (± SE) crude and available protein as percentage of dietary dry mass for focal female rhino in four different seasons.

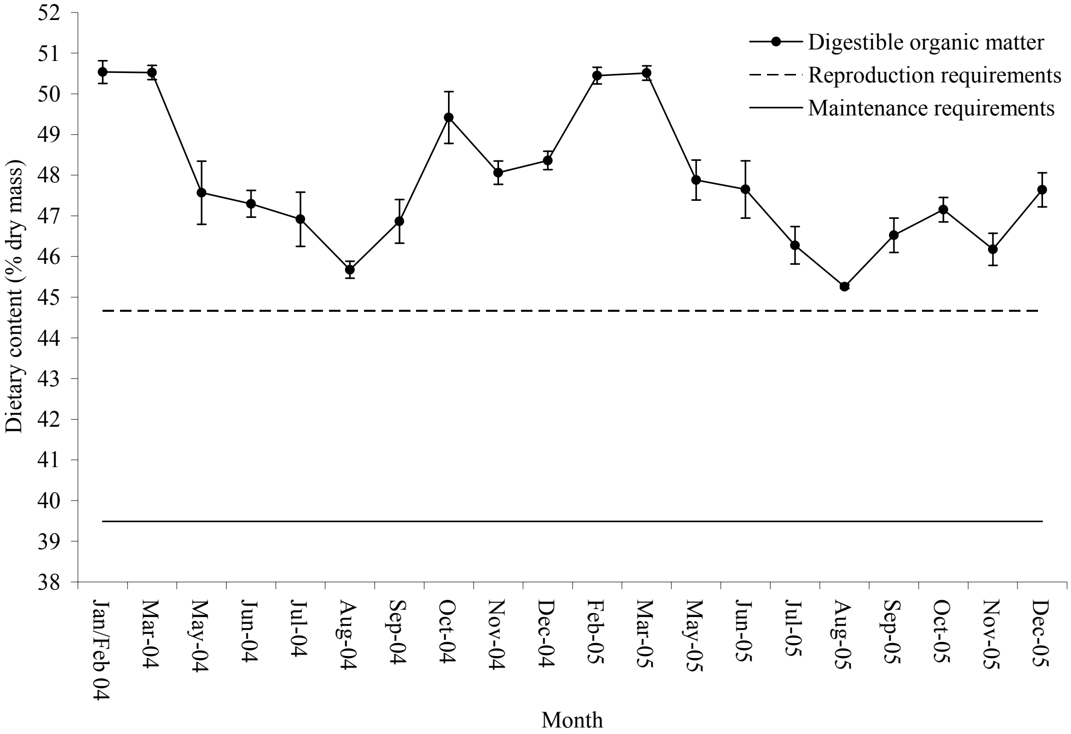

Figure 3. Mean (± SE) monthly variations in digestible organic matter concentration in the daily diets of female black rhino at Tswalu relative to estimated requirements for maintenance and reproduction.

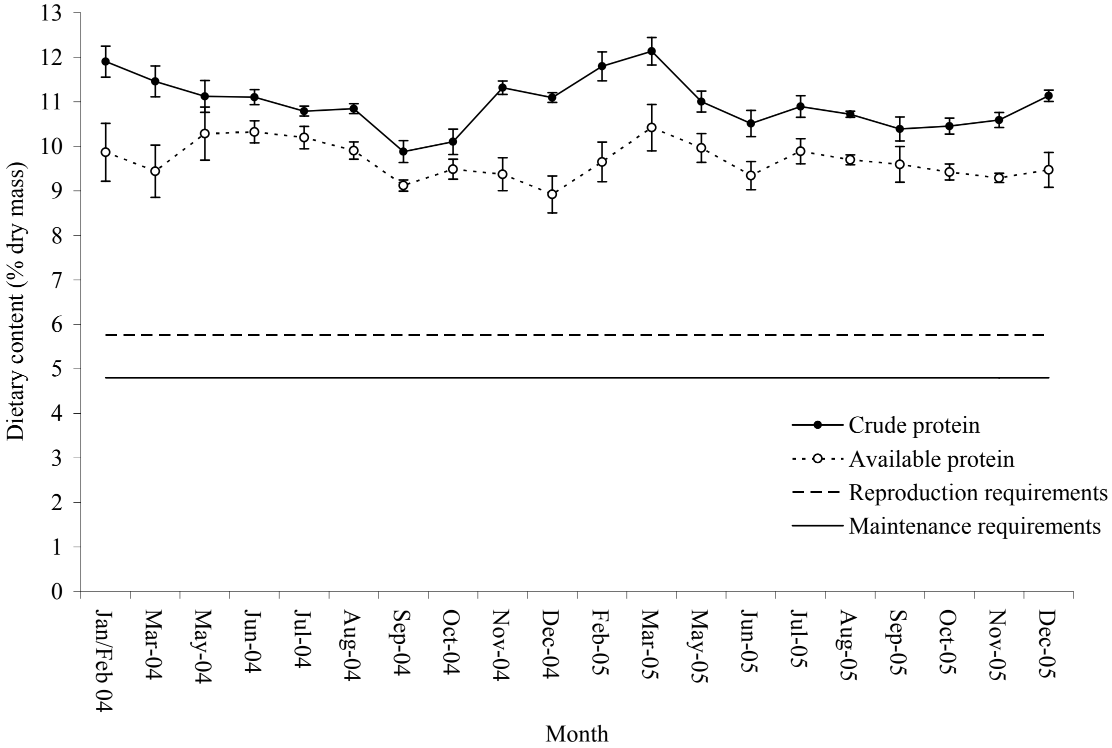

Figure 4. Mean (± SE) monthly variations in protein concentration in the daily diets of female black rhino at Tswalu relative to estimated requirements for maintenance and reproduction.

4. Growth response of *Acacia haematoxylon* to simulated black rhinoceros (*Diceros bicornis*) herbivory.

4.1 Abstract

An experiment was designed to investigate the growth response of a semi-evergreen species (*Acacia haematoxylon*) to simulated browsing impact of twig pruning by black rhinoceros (*Diceros bicornis*). *Acacia haematoxylon* forms a key reserve resource during the dry season for black rhino re-introduced in 1995 to a semi-arid fenced reserve in South Africa. There is a paucity of information in the scientific literature regarding the dynamic relationship between black rhino and their woody plant resource base.

Plants were clipped to simulate the impact of terminal twig removal at a diameter comparable to black rhino biting on this species. Treatment groups consisted of three intensities (25 %, 50 % and 75 %) of removal of shoots plus control plants which were not clipped. Clipping was performed on plants in three height (< 1m, 1 - 2.5m and > 2.5m) classes during the early wet season, late wet season and mid dry seasons in 2004 and 2005. The number and length of new annual growth shoots on one branch of each plant and all epicormic resprouts on each plant were measured after the following growth season (2005) and after second subsequent growth season (2006) for plants clipped in 2004.

Results from this experiment suggest that in the short-term *A. haematoxylon* is able to compensate for biomass removal due to simulated browsing, as has been shown for a number of other *Acacia* species in African savannas. Moderate to severe clipping caused plants to produce a greater length of regrowth the following growth season with fewer shoots than those recorded on control plants. Plants in the tallest height class produced more annual shoot regrowth per branch than smaller ones. Plants subjected to the greatest biomass removal responded by producing epicormic resprouts from quiescent buds and this response was clearest in the tallest height category.

There was no statistically significant impact of season of clipping upon resultant plant regrowth, although all growth responses measured showed a pattern of lower response on plants clipped during the early wet season. Plants did not continue to show increased growth response to clipping in the second growth season post-damage.

Findings from this first experiment assessing compensatory growth response by *A. haematoxylon* indicate that a strong positive effect was produced from both annual shoots and epicormic resprouts in the following growth season. Increased plant production following browsing can be viewed as a form of facilitation, with the potential to benefit browsing herbivores through increased food resource availability. However, the sustainability of this response under intense browsing pressure in the longer-term is not known.

Key words: *epicormic resprouts; compensatory growth; twig biting; semi-arid savanna; browse-browser dynamic*.

4.2 Introduction

The dynamic relationship between browsing mammalian herbivores and their woody plant resource base has important implications for both plant and animal population dynamics. However, this relationship is not well understood for black rhinoceros in African savannas. Literature on black rhino browsing pressure has tended to focus on impacts at a plant community level by unusually high density rhino populations within fenced reserves (Hall-Martin *et al*., 1982; Brett, 2001; Heilman *et al*., 2006; Cowling *et al*., 2009; Luske *et al*., 2009). As large-bodied herbivores that feed by pruning terminal twigs, including both leaves and stems, throughout the seasonal cycle, black rhino have potential to have a considerable influence on the growth response of their selected browse species.

Clipping or browsing of African *Acacia* trees has been reported to stimulate increased shoot regrowth in a range of simulated and natural browsing studies (Dangerfield and Modukanele, 1996; Gadd *et al*., 2001; Gowda, 1997; Pellew, 1983; Teague and Walker, 1988). Compensation was observed by *Acacia karroo*, *Acacia nilotica*, *Acacia tortilis*, *Colophospermum mopane* and *Combretum apiculatum* within a year following simulated severe browsing in the dry season (Milton 1988; Bergström *et al.* 2000; Hrabar *et al.* 2009) and in *Acacia erubescens* following simulated twig-biting during the rainy season (Dangerfield and Modukanele, 1996). Natural browsing has caused compensatory growth responses in *Acacia nigrescens* and *Acacia tortilis,* in which lightly and heavily browsed trees did not differ in net annual shoot extension (du Toit *et al.*, 1990),

By altering plant root:shoot ratio, shoot removal may lessen the competition for nutrients between shoots (McNaughton, 1983; Danell and Bergström, 1989; du Toit *et al.*, 1990). Removal of terminal meristems can also break the apical dominance and suppression of lateral meristems, altering the growth form of a plant (Aarssen, 1995). These physiological alterations to shoot morphology can influence both the plant's competitive ability and future browsing pressure. Medium or high intensity pruning in woody species, removing a major proportion of terminal meristems, has been shown to result in fewer shoots in the following growing season

(Danell *et al.*, 1994; Bergström *et al.*, 2000). This means less competition for resources between remaining shoots and hence these shoots can become larger and have higher nutrient concentrations than those on undamaged trees (Danell *et al.*, 1994; Bergström *et al.*, 2000; Rooke *et al.*, 2004; Makhabu *et al.*, 2006). The result is production of fewer but larger shoots when compared with unbrowsed control trees (Bergström and Danell, 1987; du Toit *et al.*, 1990). Although shoot growth may be increased as described under long-term browsing regimes, this may not be sustainable (Teague 1988; Hester *et al*. 2006; Guillet and Bergström, 2006; Rooke and Bergström 2007).

Following severe biomass removal, some trees respond by sprouting basal shoots or epicormic resprouts from the lower part of the stem (Bond and Midgley, 2001). This enhances the persistence of the plant via development of new ramets (Bond and Midgley, 2001, 2003). Sprouting in adult plants is seen as an expression of persistence traits developed as a response to scenarios of severe disturbance (Bond and Midgley, 2003). Roots, acting as underground storage organs of plants, protect a portion of the metabolic biomass through periods of adversity, thereby enabling the regeneration of biomass at a later point (Owen-Smith, 2008).

Plant phenological state in different seasons has been observed to influence the growth response. Milton (1988) found that *A. tortilis* trees cut in summer had significantly lower shoot mass production than control or winter pruned trees. Teague (1984) found that *A. karroo* was most affected by pruning during in early flush following the dormant dry season and during the reproductive phase normally occurring in the summer. Water, and hence nutrients, are most available when elevated soil water drives a pulse of nitrogen mineralization at the start of the wet season (Scholes and Walker, 1993) and removal of biomass produced at this time could hence leave plants less able to respond.

Acacia haematoxylon is a medium-sized tree characteristic of desert and semi-desert areas in southern Africa, often occurring on deep, red, sandy soils (van Rooyen *et al.*, 2001; Coates-Palgrave, 2002). It is a semi-evergreen species, retaining leaves throughout the year, with new foliage production coinciding with leaf shed in

September and no period of total leaf loss (*pers. obs.*). This species has been found to be the key dry season resource for black rhinos re-introduced to Tswalu Kalahari Reserve, contributing over 75 % of the dietary dry mass during the dry season (Chapter 2).

The aim of this research was to investigate how browsing by black rhinos might affect the growth response of *A. haematoxylon* at Tswalu. Fire impact is limited in the reserve which does not have a policy of controlled burns and accidental fires are extinguished. My experiment was part of a larger study assessing black rhino resource use in this area. Therefore, there were constraints on the time and logistics that could be focussed on the experimental study of *A. haematoxylon* response to simulated browsing damage. It was decided to focus on plant growth response as a key indicator of rhino browsing impact and potential future browse availability. This experiment was specifically designed around the dynamic relationship between black rhino and *A. haematoxylon* and involved manual pruning in three seasons throughout the year.

Based on the above limited understanding of savanna woody plant growth responses to herbivory, it was predicted that:

H_1 moderate to severe clipping of branches would stimulate increased regrowth during the following wet season compared to control plants;

H_2 plants in the smallest size class should produce the least regrowth in the response to clipping and those in the largest size class the most;

H_3 plants clipped in the early wet season would have a lower growth response than those clipped in the dry or late wet season;

H_4 plant regrowth in the second subsequent wet season would not be increased compared to control plants

4.3 Methods

Data collection

Study site

This experiment was conducted on a farm adjacent to the western boundary of Tswalu Kalahari Reserve, a privately-owned reserve in the Northern Cape of South Africa (Tswalu S 27°04’ - 27°44’ and E 22°10’ - 22°36’). The geology of Tswalu has been defined as predominantly aeolian sand and vegetated dunes of the Kalahari Group Formation, with some alluvium, gravel, limestone and silcrete resulting in nutrient poor soils (van Rooyen, 1999). Vegetation in this area has been classified as primarily Shrubby Kalahari Dune Bushveld (Low and Rebelo, 1996). Mean annual rainfall at Tswalu is 280 ± 164 mm (mean ± SD measured by July-June seasonal cycle from 1973-2006, Tswalu Kalahari Reserve unpublished data) and occurs mainly in the form of short thunderstorms between November and April. Rainfall was slightly below average (235 mm) in the first seasonal cycle from July 2003 - June 2004, above average (400 mm) during the second from July 2004 - June 2005 and very high (510 mm) during the last seasonal cycle from July 2005 – June 2006.

Experimental design

The study was carried out on *A. haematoxylon* plants within an approx. 3 km^2 paddock fenced to exclude browsing herbivores. The vegetation type within the paddock was akin to that described as *Hermannia burchelli* shrubveld (van Rooyen, 1999) and the main woody plant species present were *A. haematoxylon*, *Acacia erioloba*, *Acacia mellifera* and *Grewia flava*. The land had historically been used for grazing for cattle, which have been observed to consume fallen *A. haematoxylon* seed pods but do not browse upon the leaves and stems (M. Smit *pers comm.*). All domestic stock were excluded from the paddock for the duration of the experiment and there are no burning regimes in this area.

As stated, the aim of this research was to quantify the growth response of *A. haematoxylon* to herbivory. It was decided to test *A. haematoxylon* growth responses experimentally using short-term simulated herbivory rather than recording responses on plants browsed directly by rhino. Using an experimental approach allowed the intensity and frequency of biomass removal to be easily controlled with low variation of treatment intensity within experimental groups. These benefits were thought to outweigh the potential disadvantages associated with artificial browsing experiments. However, it is noted that experiments using plants subjected to artificial browsing do entail some inherent differences to those experiencing natural browsing. The impact of mammalian herbivore actions such as trampling, and perhaps more importantly urination and defecation with subsequent impacts on nutrient cycling and plant community structure (Hobbs, 1996) were absent from this trial. An assessment of the differences between artificial and natural damage to woody plants found that variation was somewhat smaller for those recording plant growth and reproduction than for those assessing plant physical and chemical resistance traits (Lehtilä and Boalt, 2004). Hence, it was assumed here that the impact of simulated browsing on plant growth would provide similar effects as natural browsing damage (Lehtilä and Boalt, 2004).

A number of recent studies have indicated that the presence of mammalian saliva could influence plant growth response. Bergman (2002) found that application of moose (*Alces alces*) saliva on torn sallow saplings (*Salix caprea*) led to more branches being produced than on saplings without saliva treatment. Rooke (2003) found that the addition of goat (*Capra hircus*) saliva to *Combretum apiculatum* shoots post-clipping caused a greater growth response. It has been suggested that the increased growth response in the presence of saliva could be due to the protective coating formed on the clipped shoot. It was not logistically feasible to replicate saliva addition in this simulated browsing experiment. However, it is noted that if saliva does enhance compensatory growth, the results from this experiment may reflect a conservative estimate of plant response.

Different browsing intensities were simulated on the *A. haematoxylon* plants by removing proportions of the number of terminal tips (categories for intensity of cut; 0, 25 %, 50 %, 75 % of branches removed). Branch tips were removed throughout the canopy of the plant by clipping branches at a diameter of 5 - 6mm.

The selected diameter of twigs for clipping was based on measurements of diameter of twigs contained in black rhino bites on this plant species (Chapter 2). Black rhino browsing twigs was this diameter is supported by measurements made by Ganqa *et al*. (2005) on a number of woody plant species in the Great Fish River Reserve, South Africa.

Plants were divided into three size classes based on maximum height of a growing part; < 1m, 1 - 2.5m, > 2.5m. As black rhino generally do not feed above 2m (Adcock, 2003) all branches clipped were below 2m. Each treatment combination of four clipping categories and three height size classes had five individual plants considered to be independent replicates (see Hurlbert, 1984). Each year, sixty plants were clipped during March (end of the wet season), July (mid dry season) and November (transition season, post new leaf flush in *A. haematoxylon*). Therefore, 180 plants were clipped during 2004 and another 180 different plants in 2005 totalling 360 individual plants. From the experimental design with four intensities of browsing, three plant height classes in three seasons over two years, the estimated minimum sample size for rejecting the false null hypothesis was 86 (Quinn and Keough, 2002). Plants used in the experiment were marked with metal tags engraved with a distinct label. GPS locations were taken for each individual plant to aid relocation for measurement.

The annual shoot growth from plants clipped during either March, July or November 2004 was measured during April/May 2005 after annual plant growth had ceased. The growth on all plants clipped during 2004 and all the plants clipped during 2005 was measured in June 2006. Plant regrowth occurred in two forms; annual shoot extension from the apical meristems and epicormic resprouting from dormant buds. Due to time constraints, it was not possible to measure all of the annual shoot extension on each plant. The number of new shoots and total length of annual growth was therefore recorded from one single branch of 10 mm diameter on each plant treated. Annual shoot extension on a branch was measured as the total length of all new shoots from apical meristems that were longer than 10 mm (an arbitrarily set limit to ease fieldwork and to exclude shoots usually of low importance for the rhinos (cf. Bergström *et al*., 2000). New growth was easily identified as pliable, pale shoots from apical meristems. The number and length of all epicormic resprouts detected on each plant was also recorded. It is noted that this study does not measure the true compensatory growth response of *A. haematoxylon* as it was not logistically feasible to weigh the biomass removed from each plant by clipping. The aim of this study was to provide comparative analysis on plant regrowth under different treatments of intensities of biomass removal on plants of different sizes in different seasons.

Data analysis

Annual shoot regrowth

Log-linear analysis was used to test the influence of four intensities of cut (C), three plant heights (H) and three seasons (S) plus the interaction between cut and height (C*H) on the number of shoots produced. Multifactor ANOVAs were used to analyse the variation in the length of new shoot growth from different treatments one year after clipping. Length of new shoot growth was tested for normality using the Kolmogorov–Smirnov test and did not require transformation. The total new shoot length on each branch were used as the response variables. Factors were two years of clipping (2004 and 2005), three months of clipping (March, July and November), three plant height categories (<1m, 1 < 2.5m and 2.5<m) and four proportions of branches clipped (0, 25 %, 50 % and 75 %). Data comparing shoot number and length measurements from 2005 (1 year post-clipping) and 2006 (2 years post-clipping) on the plants clipped during 2004 were analysed using repeated measures 3-way ANOVA with month of clipping, plant height class and proportion of branches clipped as categorical factors. The possible relationship between growth on a plant from year to year was tested using ANCOVA. The number of new shoots or total length of new shoot growth measured in 2006 was the response variable and number of new shoots or length of new shoot growth recorded in 2005 as a covariate and height class, proportion of branches clipped and month of clipping as factors. Tukey HSD test was used to test the significance of pair-wise comparisons.

Epicormic resprouts

Measurements of total length of epicormic resprouts on each plant were not normally distributed. A large number of plants, including all controls, did not produce any resprouts. Therefore data analysis was split into two; initially testing whether or not a plant responded by producing epicormic growth and which factors affected this, and then for those plants that responded with growth, assessing these effects on the quantitative amount of growth produced. A binomial classification of 0 was assigned to plants with no epicormic resprout growth and 1 to plants where epicormic growth was recorded. Logistic regression was used to estimate the probability of plant producing resprouts as a function of the three plant height classes, four proportions of branches clipped, three months in the year of clipping and two years of clipping. The relative fit of different models was assessed using AIC_c (Burnham and Anderson, 2002).

Log-linear analysis was used to test the influence of four intensities of cut (C), three plant heights (H) and three season (S) plus the interaction between cut and height (C*H) on the number of epicormic resprouts produced utilising only plants where resprouts were recorded. Multifactor ANOVA was performed utilising only plants where resprouts were recorded (epicormic growth = 1) to evaluate the impact of the four categorical factors on length of growth produced. Resprout length data were log transformed prior to analysis of variance. The relationship between the number of epicormic resprouts and total length of epicormic resprouts measured in 2005 and 2006 on plants clipped in 2004 was tested using Wilcoxon matched pairs text as this data was not normally distributed (Zar, 1999). All analyses were performed using STATISTICA (data analysis software system) version 6 (StatSoft, Inc. 2001).

4.4 Results

Number of annual shoots

Varying the proportion of branches clipped on each plant affected the number of new annual shoots recorded per branch ($x^2 = 134.59$, d.f. = 48, $P<0.0001$) (Fig. 1).

Control plants produced more shoots than those with 25 % or 75 % of branches clipped but not those with 50 % of branches clipped. Height class of plants had a positive impact on the number of annual shoots produced (x^2 = 156.19, d.f. = 2, P<0.0001). Plants in the largest height class produced more shoots (53.2 ± 19.4) per branch than those in smaller ones (42.1 ± 19.6). There was an interaction between the effects of height class of plants and intensity of clipping on the number of shoots produced (x^2 = 74.38, d.f. = 6, P<0.0001) as big trees subjected to the most severe damage produced the most shoots. Season of clipping also had an impact on the number of shoots produced the following growing season (x^2 = 21.52, d.f. = 2, P<0.0001) with the least number of shoots recorded from trees clipped in the early wet season.

Length of annual shoots

Increasing the proportion of branches clipped on each plant had a positive effect on the length of new annual shoot growth measured per branch (Fig. 2) ($F_{3, 288}$=11.987, P<.00001). Plants with 50 % and 75 % of branches clipped produced longer regrowth (2563 mm ± 134 mm and 3020 mm ± 155 mm respectively) than control plants (2168 mm ± 119 mm) or those with 25 % (2100 mm ± 129 mm) of branches clipped (Tukey HSD P<0.001). Plants in the largest height class produced more annual shoot regrowth on a branch than those in smaller ones ($F_{2, 288}$=8.913, P<0.0005: Tukey HSD P<0.005). Furthermore, the height class of plant and proportion of branches clipped had an additive effect on the total length of new shoot growth ($F_{6, 288}$=2.621, P<0.05) and the largest plants subjected to the greatest clipping intensities showed the greatest response in terms of shoot length. Plants in the height class >2.5m which had 75 % of branches removed produced 63 % more regrowth per branch than control plants in the same height class and overall more regrowth than any treatment other than plants 1-2.5m also subjected to 75 % branch removal (Tukey HSD P>0.05).

More surprisingly, month of clipping had no effect on the length of new annual shoot growth ($F_{2, 288}$=1.405, P=0.2472). Plants produced less new shoot growth two years after clipping than in the year immediately following clipping ($F_{1, 144}$=14.273, P<0.001) (Fig. 2). The length of new shoot growth measured on a plant in 2005 had no relationship with that measured from the same plant in 2006 (ANCOVA $F_{1, 143}$=1.151, P =0.285).

Epicormic resprouts

The model containing a combination of all factors - the height class of plant, proportion of branches clipped, month and year of clipping - best predicted the presence of epicormic resprouts with w_i of 0.82 (Table 1). The model excluding season as a factor was not as strongly supported.

Number of epicormic resprouts

None of the undamaged control plants produced epicormic resprouts. On plants which produced resprouts, the number of epicormic resprouts was affected by the proportion of branches clipped (x^2 = 455.86, d.f. =2, P<0.0001). Plants with 75 % of branches clipped produced more resprouts (24.3 ± 3.8) that those with 25 % (3.8 ± 0.7) or 50 % (7.4 ± 1.8) of branches cut. The height class of the plant also had an effect on the total number of resprouts produced (x^2 = 191.10, d.f. = 2, P<0.0001). Plants in the tallest height class produced more resprouts (16.1 ± 4.0) than smaller trees (1-2.5m; 7.1 ± 2.2, <1m; 3.4 ± 1.2). The interaction between height class and intensity of cut also influenced the number of resprouts (x^2 = 191.10, d.f. = 2, P<0.0001). Plants in the tallest height class subjected to the greatest intensity of clipping produced the most resprouts (44.0 ± 9.4). Season in which the plants were cut influenced the number of resprouts, with the least produced in the early wet season (x^2 = 68.67, d.f. = 2, P<0.0001).

Length of epicormic resprouts

The extent of growth response by epicormic resprouts was clearly linked to the extent of damage to the plant. The total length of epicormic resprouts per plant was greatly influenced by the proportion of branches clipped ($F_{3, 288}$=26.122, *P*<0.00001). The length of resprouts per branch on plants with 75 % (3104 mm ± 575 mm) of the branches clipped was greater than plants with 50 % (815 mm ± 235 mm) or 25 % (387 mm 815 mm ± 235 mm 107 mm) of branches clipped (Tukey HSD; *P*<0.001) (Fig. 5). The height class of the plant also affected the total length of resprouts produced ($F_{2,\,288}$=13.248, *P*<0.0001). Plants between 1-2.5m (Tukey HSD; *P*<0.01) and above 2.5m (Tukey HSD; *P*<0.001) produced greater lengths of resprouts per branch than plants below 1m. The height class of plant and proportion of branches clipped had an additive effect on the total length of epicormic resprout growth ($F_{6,\,288}$=5.666, *P*<0.00001). Total length of resprouts produced two years after clipping was lower than that produced one year after clipping (Wilcoxon matched pairs test, n=180, z=8.638, *P*<0.001).

4.5 Discussion

Acacia haematoxylon clearly showed a short-term growth increase to clipping simulating browsing by black rhino. As predicted, moderate to severe clipping of terminal shoots stimulated increased regrowth in terms of shoot length the following wet season, compared to control plants. Growth response was recorded in the form of both new annual growth and epicormic resprouts. However, the number of new annual shoots was greater on control plants. An increased shoot growth response has been observed in a number of other *Acacia* species (Dangerfield and Modukanele, 1996; Gadd *et al*., 2001; Gowda, 1997; Milton, 1988; Pellew, 1983; Teague and Walker, 1988). Clipping of up to 75 % of *A. haematoxylon* shoot terminal tips at 5-6 mm diameter represented a relatively major removal of biomass from the plant, yet increased compensatory growth was recorded, most likely due to removal of apical dominance and stimulation of lateral shoots. This is an important finding, as it suggests that in the short-term black rhino browsing can have a positive effect by stimulating a facilitatory response producing increased biomass of available *A. haematoxylon* browse in the following year.

Plants in the height class <1 m produced fewer shoots and lower length of regrowth shoots in response to clipping and those >2.5 m size class the most. This was true of both annual shoot growth and epicormic resprout production, though the pattern was clearer in the later. These plants were in a fenced exclosure and had not been subjected to previous browsing pressure and so the plants in smaller height classes were not considered to be constrained by previous browsing actions, as observed in *A. nigrescens* and *A. tortilis* subjected to long-term browsing pressure in Kruger National Park, South Africa (Fornara and du Toit, 2008). It is postulated that the greater regrowth response by plants in larger height classes could be due to the greater storage of buffer resources in taller plants (Vesk, 2006). The mechanisms promoting epicormic resprout growth are not well understood, but it is thought that resources come from stored root reserves (Bellingham and Sparrow, 2000).

There was no difference in the length of shoots produced from clipping in the early wet, late wet or mid dry season, but season did have an impact on the number of shoots produced. As expected, the results for all factors measured (number and length of new shoots and epicormic resprouts) show a consistent pattern of being lower on plants clipped during the early wet season than the rest of the year. Milton (1988) found that *A. tortilis* trees cut in summer had significantly lower shoot mass production than control or winter pruned trees. Teague (1984) found that *A. karroo* was most affected by pruning during the early flush following the dormant dry season and during the reproductive phase normally occurring in the summer. It may be that browsing during the early growing season also reduces *A. haematoxylon* capacity to produce a compensatory growth response. The contribution of *A. haematoxylon* to rhino diet declines during the early growing period, as deciduous species increase in dietary importance during the time of new leaf production (Chapter 2). Hence, browsing pressure is reduced during what appears to be the most vulnerable period for tree growth, which may aid a facilitatory relationship between black rhino and *A. haematoxylon* at Tswalu.

Annual shoot growth and epicormic resprout production were not increased in the second growing season on plants subjected to clipping when compared to the control plants from either year. This suggests that the increased growth response does not extend beyond one seasonal cycle, even when 75 % of branches had been removed. Few studies have assessed the longer-term plant responses to a short-term browsing experiment. However, Hrabar *et al.* (2009) found that *Colophospermum mopane* trees, which had been severely clipped in a manner simulating elephant browsing, continued to show a compensatory growth effect in the second growth season after clipping.

The results of this experiment suggest that in the short-term, manual clipping of terminal shoots designed to simulate twig pruning by black rhino induced a positive growth response due reduced apical control of *A. haematoxylon*. Predictions regarding future browsing pressure cannot be made without additional data on changes in chemical composition in terms of proportional increases in nutrients and anti-nutrients. However, if shoot protein content was increased and or secondary metabolite content decreased (du Toit *et al*., 1990), positive feedback could occur at high rhino browsing densities by ongoing removal of apical control and stimulation of the growth of lateral shoots as observed.

The short-term nature of this study meant the longer-term ability of *A. haematoxylon* to continue to respond to continued disruption of apical dominance were not assessed. Some studies have indicated that browsing lawns of *Acacia* species can develop, with plants producing increased palatable shoot growth under browsing pressure (du Toit *et al*., 1990; Fornara and du Toit, 2007) and that this could allow a feed-back loop analogous to a “grazing lawn” (McNaughton, 1984). Two savanna *Acacia* species (*A. nigrescens* and *A. tortilis*) subjected to severe mammalian browsing pressure in Kruger National Park, South Africa, were able to persist in a sapling form (Fornara and du Toit, 2008). However, sustained browsing pressure can have a detrimental impact, as indicated in *A. karroo,* which showed a sudden and substantial increase in mortality after three to four years of continued browsing, although browsing had initially increased plant productivity (Teague, 1988). Thus, the rhino population at Tswalu could be anticipated to benefit from increased growth stimulated by browsing in the previous year, provided rhino density does not require browsing on the same individual plants in the same or subsequent year to an extent that impedes plant persistence.

There are a number of areas, particularly from the plant physiological aspect, that could influence black rhino browsing and which warrant further investigation. These include induction of plant physical responses such as increased spinescence, internode distance and leaf area. Additionally, chemical analysis of annual shoot content, particularly crude protein, fibre and carbon-based secondary metabolite content, would allow comparison of potential palatability of shoots from plants experiencing different browsing regimes. Finally, an assessment of the impact of browsing on allocation of plant resources to reproduction, namely flower and pod production would provide an indicator of longer-term population persistence.

Feeding by high densities of black rhino caused a substantial depletion of favoured plant species at Addo Elephant National Park in South Africa (Hall-Martin *et al.*, 1982), and Solio Ranch in Kenya (Brett, 2001) where coverage of *A. drepanolobium* was steadily reduced inside the reserve. In both these places, the black rhino population had reached densities greater than 1 rhino / km^2 within fenced areas. Declines in *Acacia* species abundance due to megaherbivore browsing have been observed in fenced reserves in Kenya (Birkett, 2002; Birkett and Stevens-Wood, 2005) and South Africa (Bond and Loffell, 2001). Recent research from the Eastern Cape of South Africa has highlighted concerns regarding the sustainability of the relationship between black rhinos and another important plant species. Black rhino in this area feed extensively on tree euphorbia (*Euphorbia bothae*) (Ganqa *et al.*, 2005; Brown, 2008) and recent research suggests levels of use by re-introduced black rhino populations may not be sustainable (Heilman *et al.*, 2006; Luske *et al.*, 2009; Cowling *et al.*, 2009). However, it is noted that black rhino browsing is particularly destructive on tree euphorbia as they push the plant over to access growing tips.

Findings from the first experiment assessing compensatory growth response by *A. haematoxylon* indicate that a strong positive effect was produced from both annual shoots and epicormic resprouts in the following growth season. Increased browse production has potential benefits for black rhino in terms of food availability as described for giraffe in the Serengeti, Tanzania by Pellew (1983). However, the sustainability of the growth response under continued browsing pressure in the longer-term is not known.

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Figures and tables

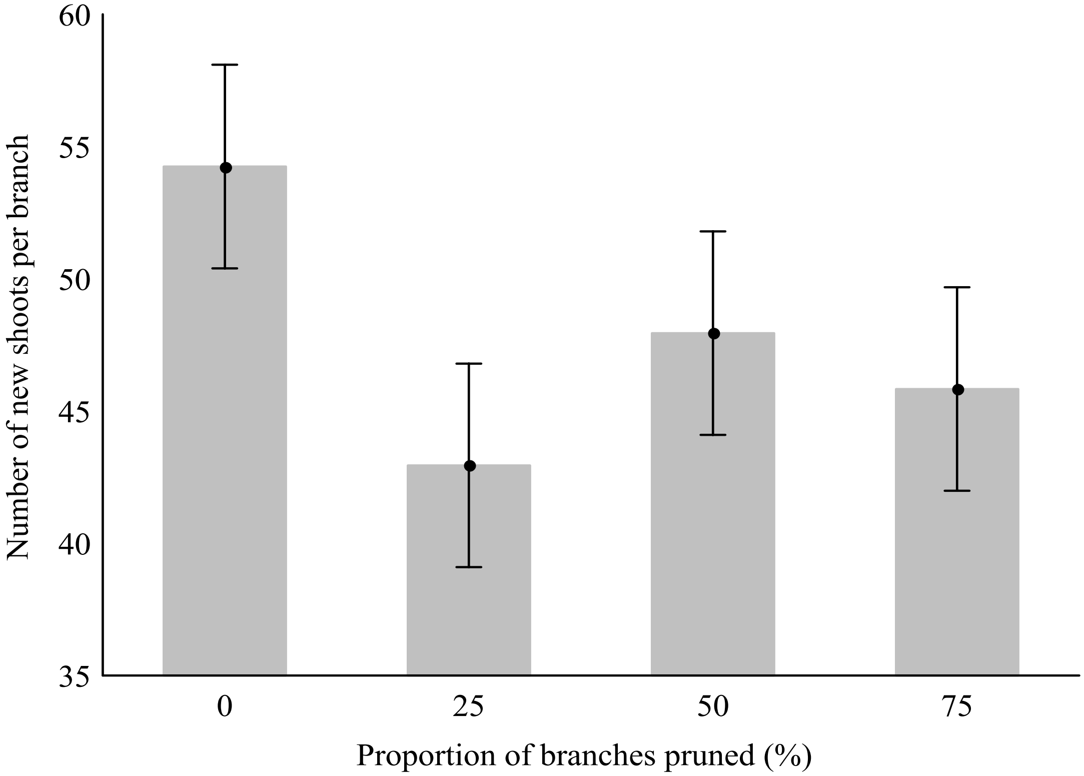

Figure 1. Mean (± SE) number of new annual shoots produced one year post clipping from one branch on each *A. haematoxylon* plant.

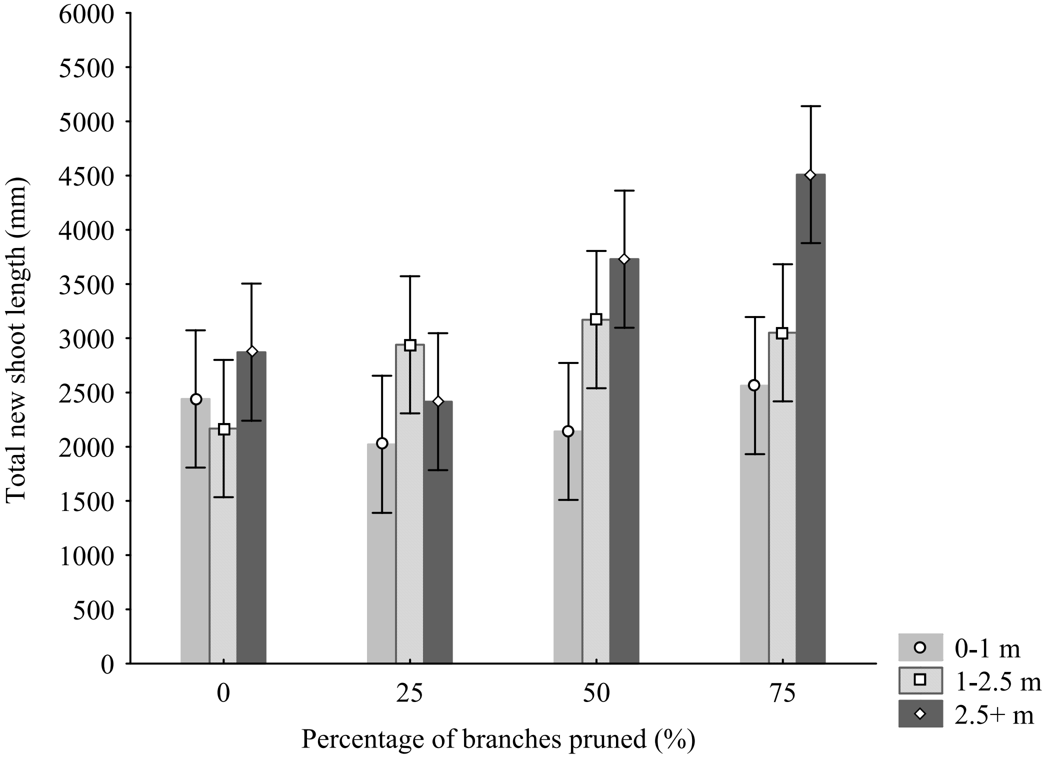

Figure 2. Mean (± SE) length of new annual shoots produced one year post clipping from one branch on each *A. haematoxylon* plant in the three different height classes.

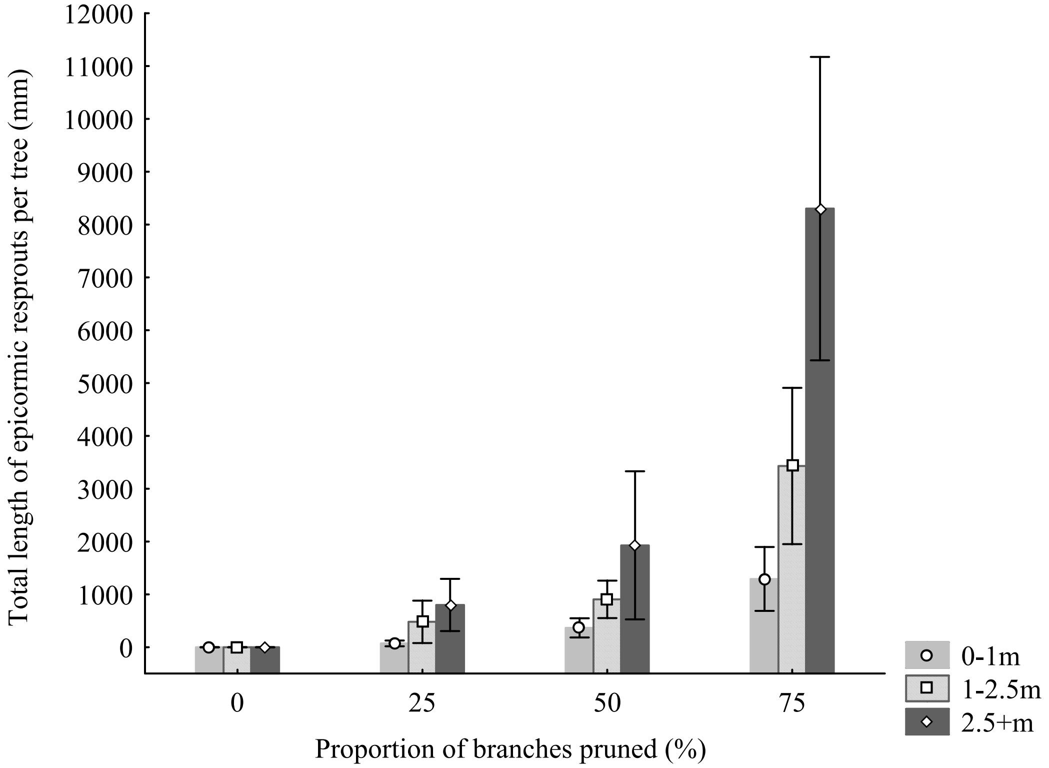

Figure 3. Mean (± SE) length of epicormic resprouts produced one year post clipping on each *A. haematoxylon* plant.

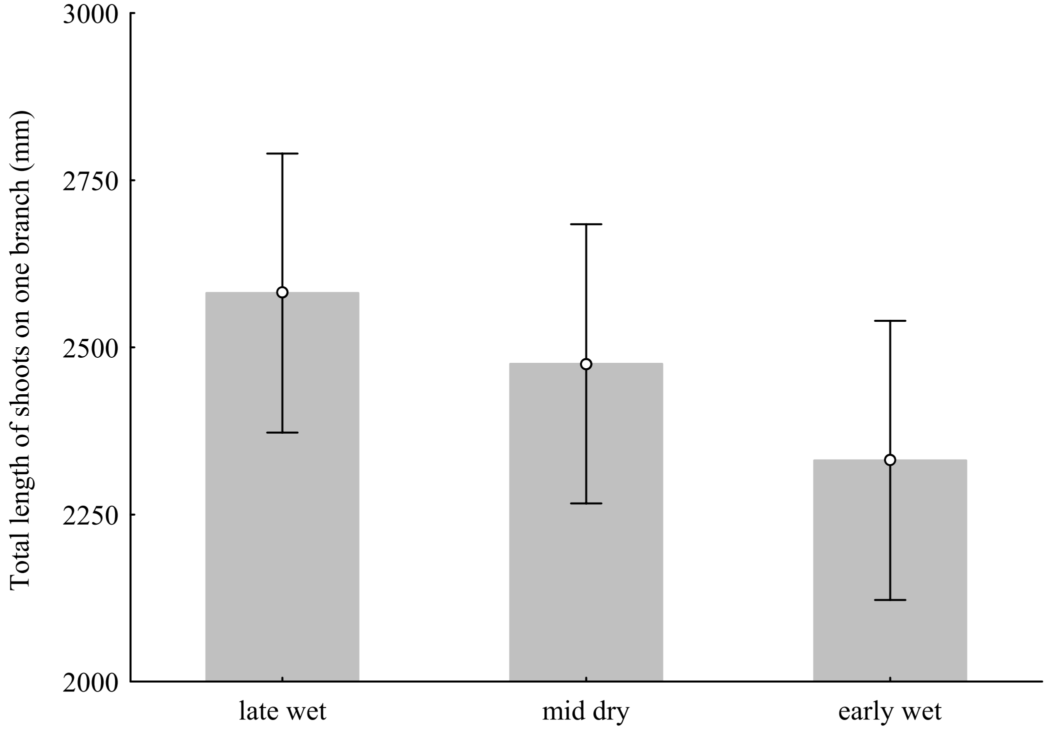

Figure 4. Mean (± SE) length of new annual shoots produced one year post clipping on each *A. haematoxylon* plant in each season.

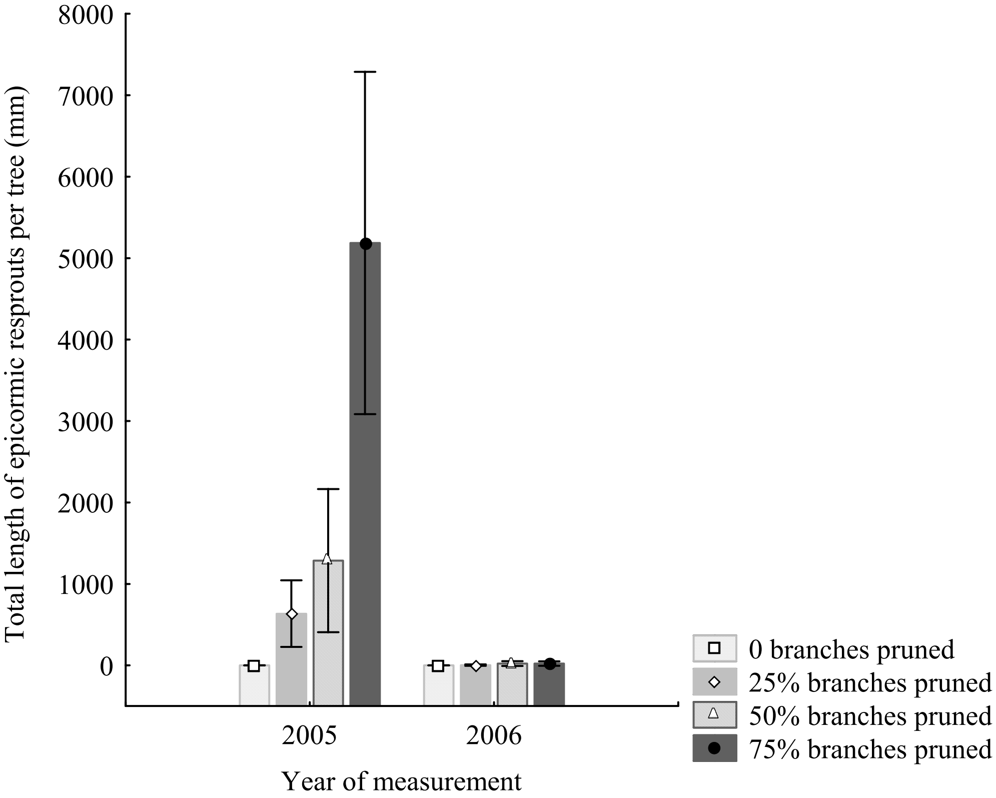

Figure 5. Mean (± SE) length of epicormic resprouts produced one year and two years post clipping on each *A. haematoxylon* plant.

Table 1. Model selection for the impact of factors of proportion branches cut, size of plant, season of clipping and year on plant regrowth after one year on one branch.

Factors	Number of parameters (K)	-2 Log likelihood	AIC$_c$	Δ*i*	exp(-Δ/2)	*wi*
cut*size*season*year	4	280.079	288.079	0	1	0.82178
cut*size*year	3	285.137	291.137	3.058	0.21675	0.17812
cut*size*season	3	300.774	306.774	18.695	8.7E-05	7.2E-05
cut*size	2	305.393	309.393	21.314	2.4E-05	1.9E-05
cut*year	2	311.995	315.995	27.916	8.7E-07	7.1E-07
cut*season	2	326.074	330.074	41.995	7.6E-10	6.2E-10
cut	1	330.286	332.286	44.207	2.5E-10	2.1E-10
size*year	2	469.73	473.73	185.651	4.9E-41	4E-41
size*season	2	478.918	482.918	194.839	4.9E-43	4E-43
size	1	481.757	483.757	195.678	3.2E-43	2.7E-43
year	1	485.376	487.376	199.297	5.3E-44	4.3E-44
season	1	494.167	496.167	208.088	6.5E-46	5.4E-46

5. Habitat selection by female black rhinoceros (*Diceros bicornis*) in relation to seasonal resource availability.

5.1 Abstract

Seasonal habitat selection at the scales of home range location and home range use was assessed in five adult female black rhinos from a growing population re-introduced to a semi-arid reserve. Analysis was based on wet and dry season home ranges created using 95 % Minimum Convex Polygons from 392 sightings recorded over three years. Seasonal patterns of habitat use were related to biomass of wet and dry season diet resources to assess the influence of changing resource availability on animal distribution.

Both individual rhinos and season were identified as factors affecting patterns of habitat use. A large proportion of the available area was not used by any of the rhinos during the data collection period. Home range locations appeared linked to availability of *Acacia haematoxylon*, a semi-evergreen species which forms the majority of the diet during the dry season in this area. Home ranges of all focal rhinos were associated with *Monechma incanum* and *Hermannia burchelli* shrubveld types, which contained higher levels of biomass of this key dry season dietary resource than the other habitat types.

During the wet season, when over 60 % of rhino's diet was formed of two widely available deciduous species, rhino sightings were not concentrated in specific habitat types within home ranges. Conversely, all rhinos focussed their dry season movements within one of the two shrubveld (*H. burchelli* or *M. incanum*) habitat types and were found to neglect those habitat types with lower availability of *A. haematoxylon*. Thus, patterns of habitat selection in the dry season reflected the seasonal decline in food availability and more heterogeneous distribution of key resources within certain habitat types.

Changes in patterns of habitat selection by individual rhinos during the dry season could provide an indication that the population is reaching habitat capacity, as usual key dry season resources have been fully consumed and animals are forced to seek alternatives. Distribution of black rhinos was found to be related to availability of the key dry season resource, which sustained the population during the most resource-limiting period of the year.

Key words: *A. haematoxylon*; key resource area; browsers; dry season; distribution

5.2 Introduction

Resource availability for browsing herbivores is subject to marked seasonal variation in both quantity and quality due to changes in woody plant phenology and chemistry. Therefore, habitat quality for herbivores cannot be estimated purely from production of palatable resources during the wet season but is dependent upon the persistence of alternate vegetation resource types throughout the seasonal cycle; those vegetation components which provide reserve resources during the resource bottleneck in the dry season are particularly important in determining habitat quality (Owen-Smith 2002). Browsers in African savannas alter their ranging patterns and reduce the size of their home ranges in the dry season to concentrate in localities with evergreen species providing important food resources during this critical time of year. Kudu (*Tragelaphus strepsiceros*), for example, foraged in open savanna habitat types during the wet season, utilising forbs in these areas, but contracted their range during the dry season to rocky hills or riparian thickets which included a higher proportion of woody species retaining foliage (Owen-Smith, 1979). Similarly, black rhinos (*Diceros bicornis*) in Ngorongoro Crater in Tanzania, ranged widely during the wet season to feed on legumes in grassland areas, but restricted their movements to riverine areas in the dry season (Goddard, 1967). Riverine areas where woody plant species retain mature green leaves into the dry season have also been identified as important seasonal resources for black rhinos elsewhere (Emslie and Adcock, 1994).

Black rhino home ranges may additionally be influenced by social factors (Adcock *et al*., 1998; Lent and Fike, 2003; Linklater *et al*., 2010). Male black rhinos are widely accepted to maintain mutually exclusive territories after reaching sexual maturity at around eight to ten years (Adcock, 1994; Adcock *et al*., 1998; Lent and Fike, 2003). Younger males behave as subordinate or satellite males, overlapping with older territorial bulls (Adcock, 1994; Adcock *et al*., 1998; Lent and Fike, 2003). However, female black rhinos are not territorial and extensive overlapping of adult female home ranges with both adult males and other females has been recorded (Klingel and Klingel, 1966; Goddard, 1967; Schenkel and Schenkel-Hulliger, 1969; Joubert and Eloff, 1971; Frame, 1980; Conway and Goodman, 1989; Kiwia, 1989;

Tatman *et al*., 2000; Lent and Fike, 2003; Göttert *et al*., 2010; Linklater and Hutcheson, 2010). Subadults and young adults may form loose associations with adult females (Klingel and Klingel, 1966; Goddard, 1967; Schenkel and Schenkel-Hulliger, 1969; Lent and Fike, 2003; Göttert *et al*., 2010). However, the degree of compression and expansion of black rhino's home ranges over time with changing population density is not well understood (Lent and Fike, 2003) and there is limited understanding of social influences on spatial organisation (Linklater, 2003). Black rhinos are known to be slow to colonize uninhabited areas of reserves (Lent and Fike, 2003) and re-colonization after harvest may be delayed by the disruption of long-standing intersexual relationships (Linklater and Hutcheson, 2010).

There have been recent discussions in the scientific literature regarding the relationships between black rhino's home range size, habitat selection, habitat quality and carrying capacity (Reid *et al*., 2007; Linklater *et al*., 2010; Morgan *et al*., 2009; Slotow *et al*., 2010). Reid *et al.* (2007) suggested that the increased home range sizes of black rhinos in Hluhluwe-Umfolozi Park, South Africa recorded from 1991-2001 compared to those recorded during the 1980s were indicative of negative changes in vegetation structure that required rhinos to maintain larger ranges to meet their nutritional requirements. The direct link between variations in home range size and habitat quality was queried by Linklater *et al*. (2010), arguing that changes in animal density alone could allow larger range sizes in an asocial species where overlap of males ranges is governed by intrasexual competition. Moreover, Linklater *et al*., (2010) criticised the analysis of Reid *et al*. (2007) noting that increased home range size was probably due to the different methods of data collection and analysis and periods of data used. Morgan *et al*. (2009) questioned the applicability of *a priori* estimates of carrying capacity for black rhinos, as habitat selection by black rhinos at three spatial scales in Mun-ya-Wana Game Reserve, KwaZulu-Natal, South Africa was not found to be related to carrying capacity estimates based on measures of total black rhino browse availability (Adcock, 2006).

However, the above analyses did not explicitly consider the potential influence of seasonal variation in resource availability on patterns of habitat selection and ultimately habitat capacity for black rhinos. To test whether habitat use and selection of different habitat types may be influenced by seasonal resource availability, habitat selection in the wet and dry seasons was assessed at two scales for five adult female black rhinos. The focal animals were part of a founder population re-introduced in 1995 to a large (479 km^2) fenced section of Tswalu Kalahari Reserve (Tswalu) a private game reserve in the Northern Cape of South Africa. Patterns of habitat selection were assessed in relation to distributions of woody plant species which were known to form the majority of black rhino's diet in different seasons at Tswalu (Chapter 2).

The proportion of habitat types within the established home ranges of individual rhinos was related to the proportion of habitat types in the total area potentially available to them as a measure of second order selection as defined by Johnson (1980; or Design II, Thomas and Taylor, 2006). Subsequently, the proportion of use of different habitat types within each individual rhino's home range was compared to the relative extent of habitat types in the home range bounds; this is third order selection (Johnson, 1980; or Design III, Thomas and Taylor, 2006). As this analysis focussed on female black rhinos, intraspecific social issues such as territorial behaviour were not considered to have a strong influence on individual habitat use. It is acknowledged that competitive and affiliative relationships may exist between individual female rhinos (Lent and Fike, 2003; Linklater and Hutcheson, 2010) but this was not considered likely to have a major impact on habitat selection. The study area contained no large predators or elephants and was supplied with a network of man-made waterholes, negating confounding impacts of these factors potentially influencing habitat use. Following Aebischer *et al*. (1993), individual animals were used as the basis of this analysis and were all mature adults of similar age (Table 1) and as part of the founder population, all had the same residence time in the area.

The aim of this study was to assess whether habitat selection by female black rhinos at Tswalu was influenced by seasonal availability of food resources.

The specific objectives and hypothesises of this chapter were:

1. To relate habitat types within the seasonal home range areas of focal female rhinos to total available area of habitat types within the Korannaberg section
2. To determine factors determining habitat use by focal female rhinos in different seasons;

H_1 During the wet season rhino's habitat selection will be related to availability of wet season diet resources.

H_2 During the dry season rhino's habitat selection will be related to availability of the key dry season resource, *A. haematoxylon*

5.3 Methods

Study site

This study was conducted at Tswalu Kalahari Reserve (Tswalu), a 1,080 km^2 private game reserve in the Northern Cape of South Africa (S 27°04' - 27°44' and E 22°10' - 22°36'). The Korannaberg section of the reserve, a fenced unit of 479 km^2 formed the site of this analysis. The geology of this area is predominantly aeolian sand and vegetated dunes of the Kalahari Group Formation, with some alluvium, gravel, limestone and silcrete (van Rooyen *et al.*, 1999). Topography within the Korannaberg section consists of the Korannaberg mountains in the north and east with extensive sandy plains interspersed with parallel dunes to the west and south. The Korannaberg section contained 23 artificial waterholes distributed such that no part of the section was more than 5km from water. Waterholes were located regularly throughout the reserve and were not biased towards any particular habitat type.

Mean annual rainfall at Tswalu is 280 ± 164 mm (mean ± SD measured by July-June seasonal cycle from 1973-2006, Tswalu Kalahari Reserve unpublished data) and occurs mainly in the form of short thunderstorms between November and April. The predominant vegetation type has been classified as Shrubby Kalahari Dune Bushveld (Low and Rebelo, 1996) which has a relatively open structure. Van Rooyen (1999) produced an ArcView 3.2a vegetation map using aerial photos and based on vegetation structure and plant species distribution. The resultant vegetation map distinguished 12 vegetation types; bushy valleys and plains, disturbed areas, dunes, dune crests, dune streets, dune valleys and plains, *H. burchelli* shrubveld, *M. incanum* shrubveld, open shrubveld, plains, panveld and hills and mountains (van Rooyen, 1999) (Fig. 1, 2 and 8). As the ultimate aim of this thesis was to estimate habitat capacity based on known vegetation types, these vegetation units were considered an appropriate distinction of habitat types for this analysis.

Study animals

Eight black rhinoceroses were translocated to Tswalu from Etosha National Park in Namibia in June 1995. This founder population consisted of six adult females (age range: eight to twenty years) and two adult males (age seven and eight years). Of these founders, one adult female and one adult male were sold in 1998. As the only adult females (aged > 5 years) in the population, the remaining five females formed the focal animals for this assessment of habitat use. There was only one adult male present for much of the data collection period, hence male home range use was not considered. As the spatial extent of adult male home ranges is additionally affected by social factors relating to territorial behaviour, this could confound the influence of seasonal resource availability (Owen-Smith, 1988; Adcock, 1994). The sub-adult animals in this area were assumed not to have established permanent individual ranges (Lent and Fike, 2003) and so were not included in analysis. Hence, it is assumed that social factors did not influence habitat use by the focal animals and all animals were equal competitors (Fretwell and Lucas, 1970).

Data collection

Rhino sightings

Rhinos were located from footprints (spoor) detected on the tight network of sandy roads and at waterholes as part of the data collection method to determine rhino’s diet by following their feeding tracks (duration: January 2004 -December 2005 see Chapter 2 for more details). Initially, when spoor was detected individuals were tracked until they were sighted and could be identified by their unique ear-notch patterns. For each sighting, the date, time, GPS location within 20 m, body condition and behaviour was recorded following the procedure of Sandwith (1990). When additional sightings of other focal animals were observed during feeding track data collection or whilst driving on the reserve, locations were recorded in the same manner. These points were categorised as “sightings”. With time it was possible to differentiate individual females indirectly using the ratio of female and calf spoor diameter and marks left by distinctive cracks on the soles of the feet (*pers. obs.*). Spoor size in subadult black rhinos has been shown to be related to age and weight (Purchase, 2007). To increase sample size, locations of spoor along feeding tracks of known animals were also used as records of habitat use. Where spoor was used to mark rhino’s presence, the GPS position for the first identified bite along a feeding track was utilised. Records for individual rhinos collected using this approach were categorised as “feeding track” locations.

Further locations were collated from the monthly records of the game scout team, who aimed to locate and identify each of the rhinos at least once per month for monitoring and security purposes (January 2004 - December 2006). Individuals were detected from spoor, which was followed until the rhino was located. Information was recorded following the standardised monitoring procedure of Sandwith (1990) identifying the individual based on earnotches and recording date, time, GPS location within 20 m, body condition and behaviour during the sighting. Locations of focal rhinos taken from monthly monitoring data were categorised as “monitoring team” data points. As the role of the game scouts was to monitor all rare species on the reserve, their activities covered the entire Korannaberg area and were not biased specifically towards the areas used by black rhinos. Tswalu has an extensive network of sandy tracks forming a tight road network, which cover habitat types within the reserve approximately equally (Fig. 1 and 2). Hence, data collection effort was considered sufficiently representative of all habitat types.

Only the first recording of an individual rhino from any of these sources was utilised each day to prevent pseudoreplication (Aebischer *et al*., 1993). Given the sandy substrate and relatively open nature of all habitat types at Tswalu, differences in detection or visibility of individuals in different areas was not considered a significant issue (Garshelis, 2000). There were 392 sightings of the five focal animals (individual range = 71 to 87) throughout the data collection period (wet season = 159; dry season = 233) (see Table 1). The source of rhino's location records was distributed as sightings = 109; feeding tracks = 119; monitoring team = 164. Sighting records over the three years were combined for analysis as Lent and Fike (2003) recommended use of sample sizes of 35 or more when calculating black rhino home range sizes. Number of wet season sightings were slightly lower than the recommended sample size (minimum 29 for Inyani, Table 1), so it is acknowledged that these samples were less adequate.

Vegetation biomass

Woody plant species biomass in each habitat type was taken from earlier work by Beck (2001) who recorded total browse availability at Tswalu between April 2001 and June 2001 using the belt transect method of Smit (1989a) (Fig. 8). This was based upon 86 transects of 100 m by 2 m throughout the study area where all woody plant species were counted and identified. Tree canopy diameter measurements were taken and used in conjunction with the Biomass Estimates of Canopy Volume computer programme (BECVOL; Smit,1989b) to give a measure of total browse volume (Beck, 2001). Transects were combined within each habitat type and extrapolated over the entire area (Beck, 2001). As the majority of black rhino browsing occurs below 2 m (Adcock, 2003), only biomass below this height was included as an estimate of available browse in each habitat type.

Woody plant biomass was divided into seasonal resource categories. The two deciduous species, *Grewia flava* and *Acacia mellifera* which were identified as forming the main wet season diet content (Chapter 2) were combined to form a staple resource category (Fig. 8). *Acacia haematoxylon* formed a single category as the main reserve resource (Chapter 2) in the dry season (Fig. 8). Biomass of all additional woody plant species in each habitat type were combined into a single "other" category.

Data analysis

Home range analysis

Analysis was based on the vegetation map of Tswalu produced by van Rooyen in 1999 from aerial photos and measurements of vegetation structure and plant species distribution. The original map distinguished twelve vegetation types; four minor areas (those forming less than 5 % of the total area) were pooled with the most similar habitat types in terms of plant species availability and spatial distribution to produce eight habitat type categories. The habitat amalgamations were as follows; dunes, dune crests and dune streets were all combined into dunes habitat type, panveld was combined with *H. burchelli* shrubveld type and disturbed areas were combined with dune valleys and plains. The map was uploaded into ArcGIS 9.1 and intersected with the Korannaberg section boundary fenceline. Proportional availability of the eight habitat types within the Korannaberg section were calculated as proportion of a habitat type = habitat type area / total Korannaberg section area.

Sightings records for each focal individual were plotted on the vegetation map as indicators of habitat use. Sightings were classified as either wet season (October – March) or dry season (April - September). These points were projected in the ArcGIS 9.1 map and used to create 95% minimum convex polygons (MCP) wet and dry season home ranges for each individual rhinos using Hawth's Analysis Tools for ESRI ArcGIS (v3.25). Where MCP home ranges overlapped the border of the reserve they were clipped with the fenceline boundary. The proportion of different habitat types in individual MCP home ranges were then calculated by intersecting each home range with the vegetation map (van Rooyen, 1999), where proportion of a habitat type = habitat type area / total home range area.

As locations of the rhinos were generally a consequence of tracking spoor from roads or waterholes, it was not valid to utilise the Adaptive Kernel technique due to biases in sample distributions. Minimum Convex Polygons have been widely utilised in studies of animal home range use including those of black rhinos (Hearn, 1999; Lent and Fike, 2003) despite acknowledged limitations (see Anderson, 1982; Alldredge *et al*., 1998) so were considered an appropriate technique for this study.

Statistical analysis

Log-linear analysis was used to assess the influence of habitat types, individual rhino, season and method of data collection on rhino sightings records. Initially, two-way interactions were used to test whether the data source had a significant influence on which habitat type individual rhino were sighting in during the different seasons (Table 2). To provide sufficiently large sample sizes of rhino's locations in each habitat type for analysis, habitat types were reduced to five by combining dune valleys and plains, plains, and bushy plains and valleys habitat types into a single "low use" category.

The saturated model consisted of five different habitat types (low use, dunes habitat type, *H. burchelli* shrubveld, *M. incanum* shrubveld and open shrubveld), two seasons (wet and dry) and five individual rhinos (Bogale, Inyani, Kagale, Nantoni and Usuk). Interactions between habitat type (response variable) and season, rhino and season*rhino were removed from the full model to determine the likelihood ratio chi-square (G^2) and the degrees of freedom of the model without the removed factor or interaction of factors (Quinn and Keough 2002). Log-linear analyses were performed using SYSTAT version 11 (SYSTAT Software, Inc. 2004).

Differences in third order selection in relation to availability for all eight habitat types by individual rhinos in both seasons were assessed using chi-square likelihood ratio test ($P<0.05$) and Bonferroni confidence intervals (Neu *et al*., 1974; Teng *et al*., 2004):

$$\overline{P}_i - Z_{a/2k}\sqrt{\overline{P}_i(1-\overline{P}_i)/n} \le P_i \le \overline{P}_i \le Z_{a/2k}\sqrt{\overline{P}_i(1-\overline{P}_i)/n}$$

where, P_i is the proportional usage of a habitat category i and n is the total number of used observations; $Z_{a/2k}$ is the upper standard normal table value corresponding to a probability tail area of $a/2k$, a is the level of significance (0.05) and k is the number of categories (habitat types) tested. The expected proportional usage of habitat types within an individual's seasonal home range (P_e) was calculated as $P_e = N_i * P_a$ where

N_i is the total number of sightings of an individual in a season and P_a is the proportional area of the habitat type making up the seasonal home ranges of an individual rhino.

5.4 Results

Factors influencing habitat type use

The source of data (feeding track, sightings or monitoring team) did not have a significant influence on sightings of individual rhinos in different habitat types in different seasons (Table 2). The three-way model combining the interactive effect of individual rhino and season was the best model to explain differences in use of habitat types (season*rhino*habitat type $G^2 = 35.04$, df = 16, $P = 0.0039$). Thus, individual rhinos were found to have different seasonal patterns in the way they used the different habitat types.

Home range location

Both wet and dry season home ranges of all rhinos were located towards the west of the Korannaberg section (Fig. 1 and Fig. 2). All home ranges in both seasons contained more than 10 % of the two shrubveld habitat types, *M. incanum* and *H. burchelli* shrubveld (Figs. 3a-b to Figs. 7a-b). Dune valleys and plains, plains, and the bushy plains and valleys habitat types towards the east of the Korannaberg section were largely excluded from all home ranges (Fig. 1 and Fig. 2). The hills and mountains habitat type on the eastern edge of the Korannaberg section was not included in any of the home ranges at second order selection.

Home range use

In the wet season none of the rhinos were selecting or neglecting any of the habitat types within their home ranges (Table 3). During the dry season, all the rhinos were focussed within one of two shrubveld habitats (*M. incanum* or *H. burchelli*) within their home ranges (Table 4). These were the habitat types with greatest *A. haematoxylon* biomass (Fig. 8). *Acacia haematoxylon* biomass was 121 g/m^2 in *M. incanum* shrubveld (27 % of total biomass), 83 g/m^2 (32 % total biomass) in *H. burchelli* shrubveld, 35 g/m^2 (15 % total biomass) in dunes habitat type but less than 22 g/m^2 or 10 % total biomass in all other habitat types (Fig. 8). Two habitat types with lower availability of *A. haematoxylon* were avoided during the dry season (Table 4); two rhinos (Nantoni and Usuk) neglected the open shrubveld habitat and Inyani neglected the dune valleys and plains habitat type during the dry season. More surprisingly, all rhinos were found to avoid the dunes habitat type during the dry season (Table 4).

5.5 Discussion

A large proportion of the Korannaberg section at Tswalu was not used by the five focal rhinos. They were absent from much of the central and eastern region encompassing the hills and mountains habitat type, bushy valleys and plains habitat and the dune valley and plains habitat type. Home ranges were concentrated in the west of the reserve and were found to be primarily associated with *H. burchelli* and *M. incanum* shrubveld habitat types. Although this analysis focussed on the adult females in the population, observations on the wider population during the data collection period indicated that these patterns of habitat use were true for the population as a whole (*pers. obs.*). Patterns of habitat use by black rhinos at Tswalu thus appeared linked to availability of *A. haematoxylon*, which was greater in *M. incanum* and *H. burchelli* shrubveld than in the other habitat types.

Assessment of third order habitat selection in different seasons corroborated the influence of *A. haematoxylon* availability on ranging patterns, particularly during the dry season. In the wet season, there was no indication that any of the focal rhinos were focussing on any of the different habitat types. Two deciduous woody plant species, *Grewia flava* and *Acacia mellifera* contributed more than 60 % of rhino's diet at this time (Chapter 2). These two plant species thus formed the staple resource in the wet season and were relatively evenly distributed and widely available throughout the different habitat types (Fig. 8). *Acacia haematoxylon* also formed approximately 20 % of rhino's diet in the wet season. Hence, it was to be expected that rhinos would be more evenly dispersed throughout habitat types during the wet season when food availability was greater and more homogenously distributed.

In the dry season, when deciduous species lost their leaves *A. haematoxylon* was found to form the key diet resource, contributing over 75 % of the monthly diet in the late dry season (Chapter 2). Patterns of habitat selection by black rhinos in this season were found to reflect the overall decline in food availability and the more heterogeneous distribution of key resources within certain habitat types at this time. All rhinos focussed their movements within one of the two shrubveld (*H. burchelli* or *M. incanum*) habitat types, which had the greatest availability of *A. haematoxylon*. Habitat types with lower *A. haematoxylon* biomass, such as open shrubveld and dune valleys and plains, were neglected within individual rhino's home ranges during the dry season.

All of the focal animals also neglected using the dunes habitat type during the late dry season, despite this vegetation type having relatively high availability of *A. haematoxylon*. Low use of the dunes habitat within home ranges could be linked to topography, as negotiating the steep, sandy dunes would place additional energetic demands on the rhinos. Wall *et al*. (2006) found that elephants in northern Kenya avoided steep slopes and showed that the energetic costs of even minor hills could be barriers to use for heavy animals such as elephants and rhinos. Cromhout (2007) noted that movement by buffalo (*Syncerus caffer*) was also restricted in dune habitat at Tswalu and suggested this was most likely in relation to energy costs associated with the deep sandy soil. Nutritional gains from the greater available biomass of deciduous species in dunes habitat type during the wet season may mitigate energetic demands that could not be met using solely *A. haematoxylon* during the dry season. However, this habitat type could provide a spatial buffer (Owen-Smith, 2002) during lower rainfall years, particularly as rhino density increases (Hobbs and Hanley, 1990).

Seasonal patterns from studies in East Africa and Namibia found that black rhinos tend to range more widely onto open grassland areas to utilise forbs present during the wet season and have more restricted ranges near woody vegetation retaining green foliage in hilly regions or in riverine areas during the critical dry season (Goddard, 1967; Joubert and Eloff, 1971; Kiwia, 1989; Loutit *et al*., 1987; Mukinya, 1973; Emslie and Adcock, 1994; Oloo *et al*., 1994; Göttert *et al*., 2010). Forbs were not widely available and did not contribute greatly to black rhino's diet at Tswalu (Chapter 2); however, the use of key resource areas observed during the dry season supported findings from this analysis. Shrubveld habitat types with greater availability of the semi-evergreen *A. haematoxylon* formed the key resource areas where rhinos were focussed during the critical dry season at Tswalu.

There have been recent efforts to use home range size as an indicator of changes in habitat quality and subsequently habitat capacity for black rhinos. Reid *et al*. (2007) suggested that increases in black rhino's home range sizes over time in Hluhluwe-iMfolozi Game Reserve in South Africa were due to rhinos ranging further to meet nutritional requirements and indicated a decline in carrying capacity due to changes in vegetation composition (see also Slotow *et al*., 2010). However, black rhino populations are structured by intra-sexual competition between males as well as affiliative relationships amongst some females and inter-sexual associations (Linklater and Hutcheson, 2010). Hence, increased individual home range sizes could simply be due to lower animal density and are not necessarily an indication of deterioration in habitat quality and reduction in carrying capacity (Linklater *et al*., 2010).

Findings from Tswalu suggest that longer-term analyses of patterns of habitat selection by individual rhinos during the dry season may provide a more effective method to identify whether a population is reaching, or has exceeded, habitat capacity. This approach could detect changes in individual's habitat use, signifying that usual key dry season resources have been depleted and animals are forced to investigate alternatives. Preference of individuals for habitat types are known to change as population density increases (Hobbs and Hanley, 1990). Furthermore, a correlation between patterns of habitat selection by black rhinos and estimates of carrying capacity within different habitat types at Mun-ya-Wana Game Reserve (Morgan *et al*., 2009) may have been detected if seasonal variation in resource availability had been included as a factor in habitat selection and carrying capacity analyses.

Since habitat use changes with population density (Hobbs and Hanley, 1990), it is not possible to extrapolate results from the data collection period to assess the relative potential of habitat types to support increased densities of rhinos in the future. In Chapter 6, a metaphysiological model is developed to estimate maximum productive habitat capacity for black rhinos, based on energy gains in relation to reproductive requirements. The model projects quantitative outputs to support qualitative results from this chapter, indicating that some habitat types were less suitable for black rhinos.

Tswalu provided a relatively simple system in which to assess the relationship between seasonal resource availability and black rhino's habitat selection, given the marked dependence on *A. haematoxylon* during the dry season. Consideration of seasonal changes in resource availability, with particular reference to the resource types providing key reserves during the critical dry season, may provide greater understanding of patterns of black rhino's habitat use, habitat selection and habitat capacity in other areas. Black rhinos distribution was found to be related to spatial availability of the key dry season resource, which sustained the population during the most resource-limiting period of the year.

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Figures and Tables

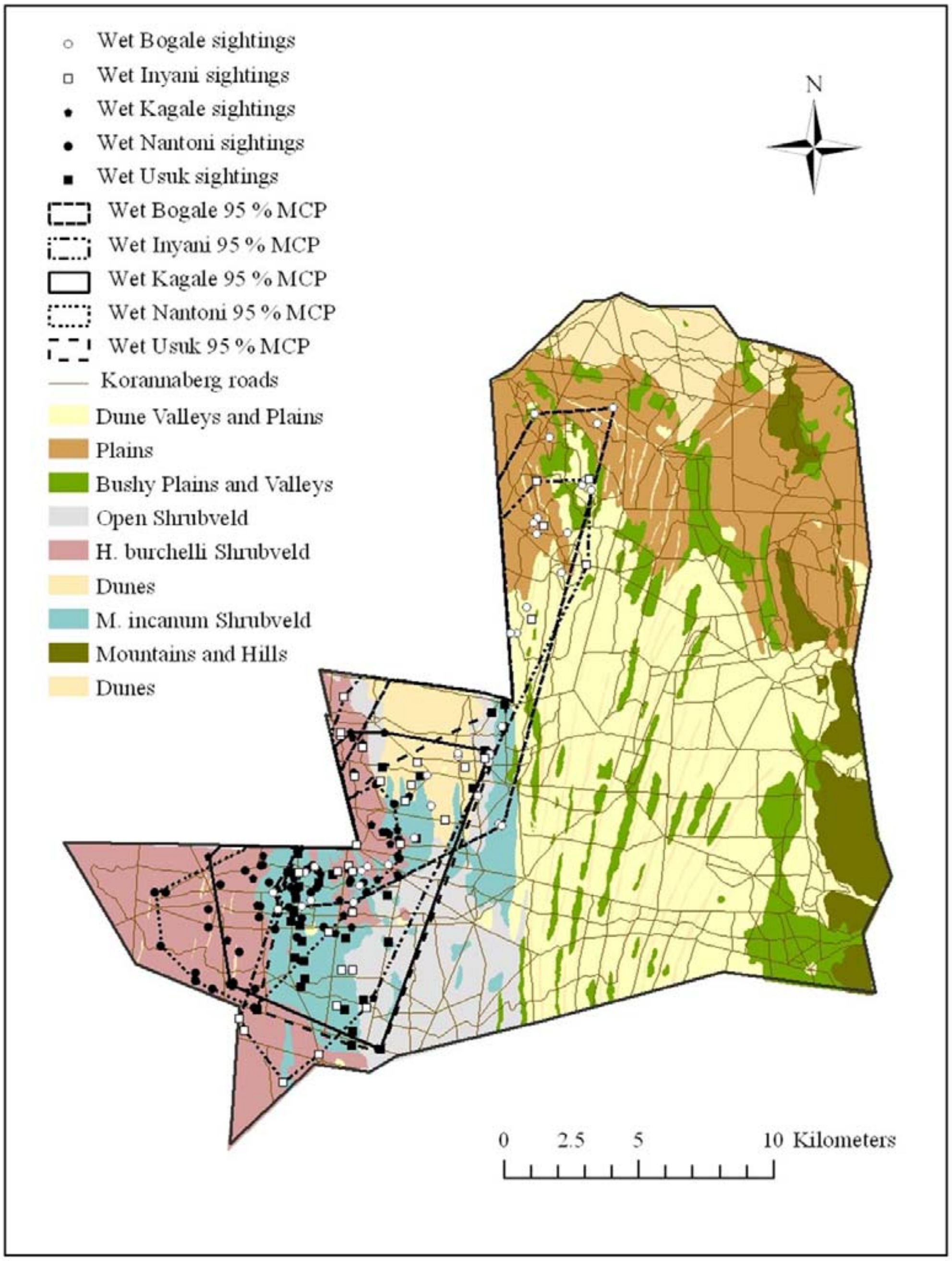


Figure 1. Map of the 479km^2 fenced Korannaberg section at Tswalu showing the eight habitat types from van Rooyen (1999) and sighting records from the wet season used to create 95% MCP home ranges for the five female black rhinos.

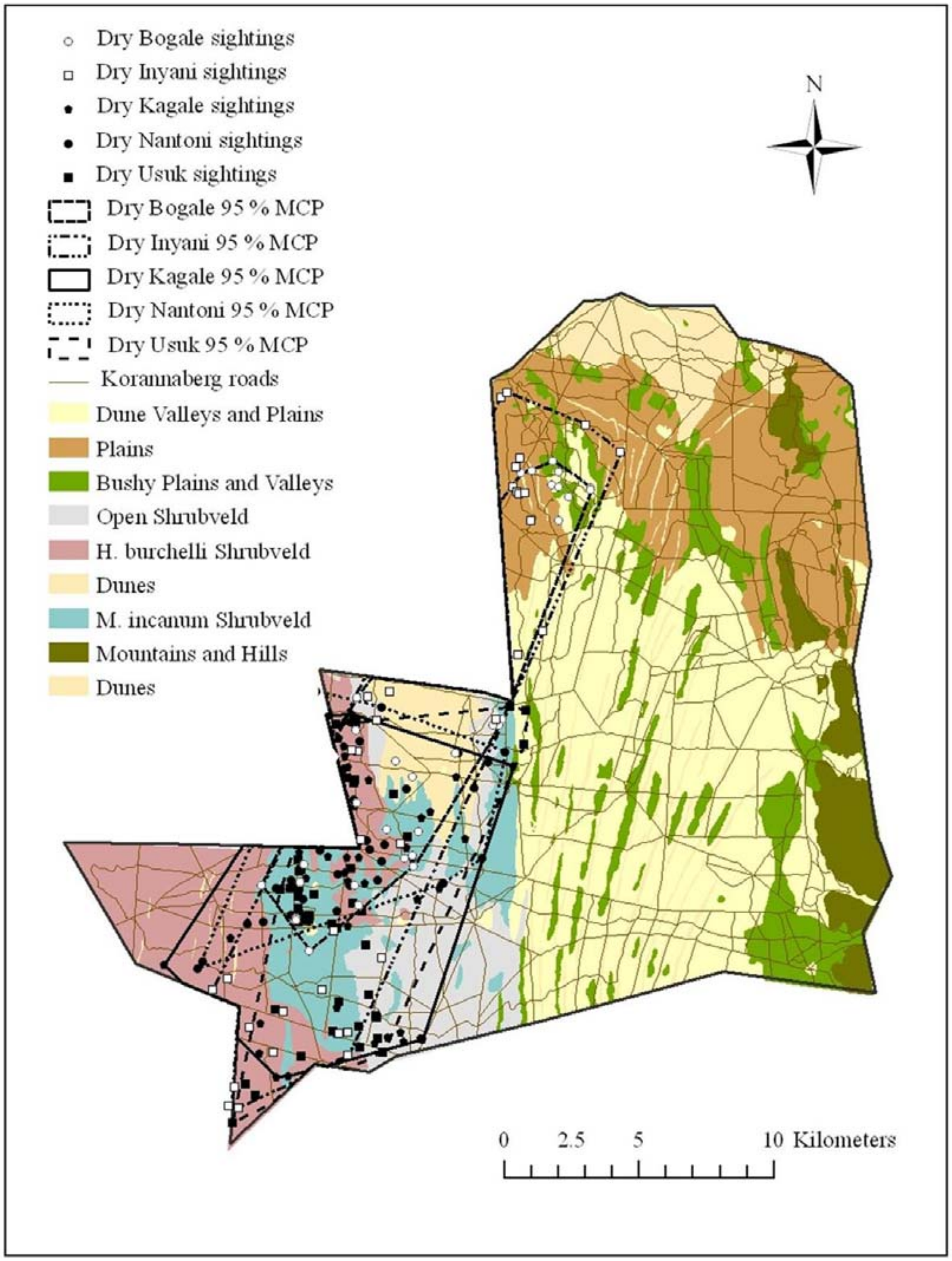
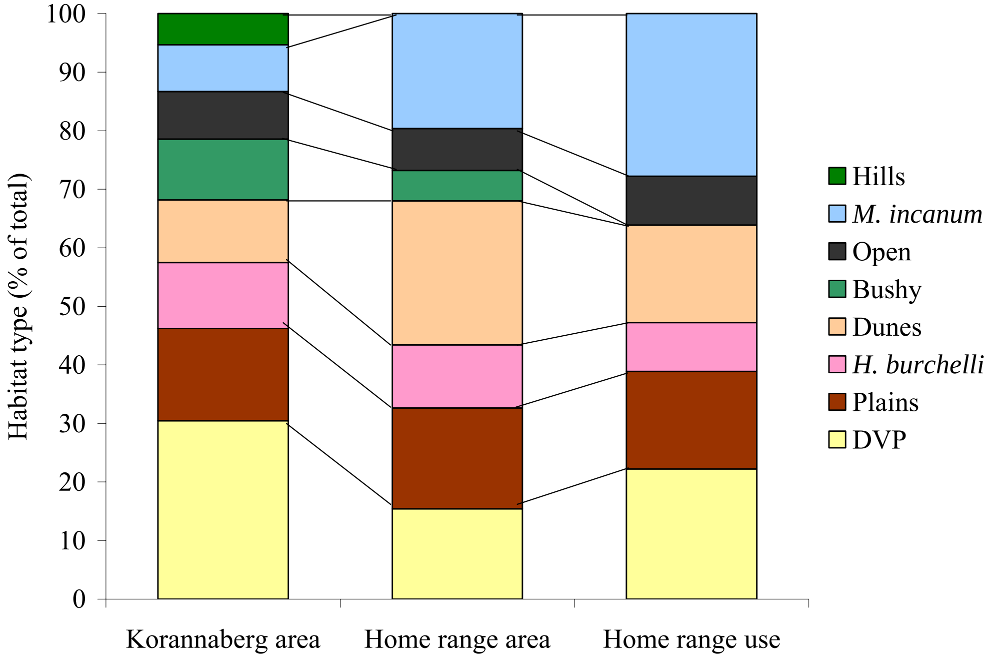


Figure 2. Map of the 479km^2 fenced Korannaberg section at Tswalu showing the eight habitat types from van Rooyen (1999) and sighting records from the dry season used to create 95% MCP home ranges for the five female black rhinos.

a. Wet season



b. Dry season

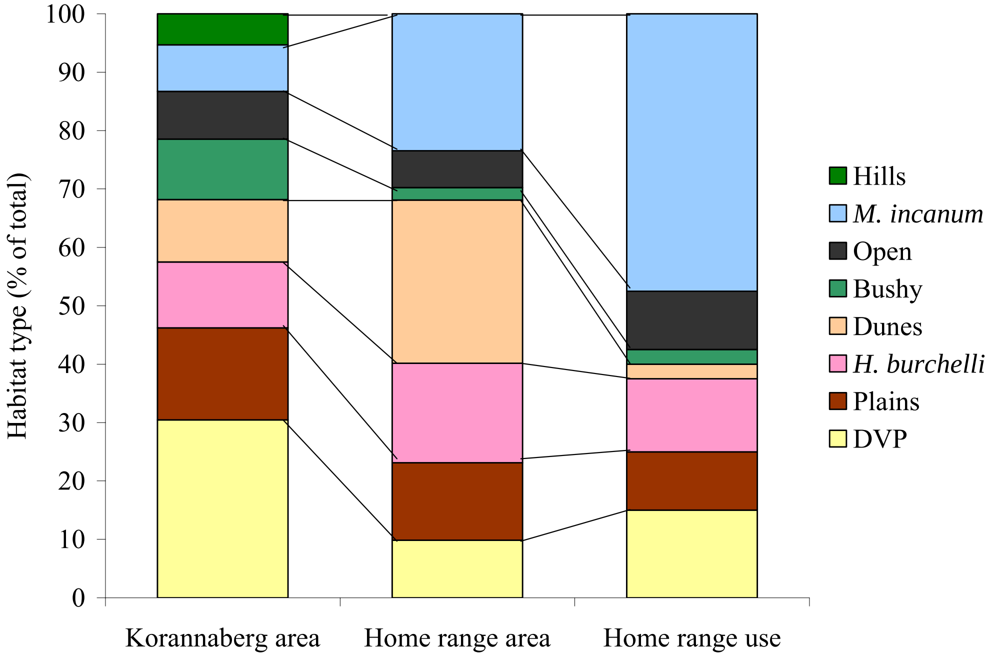
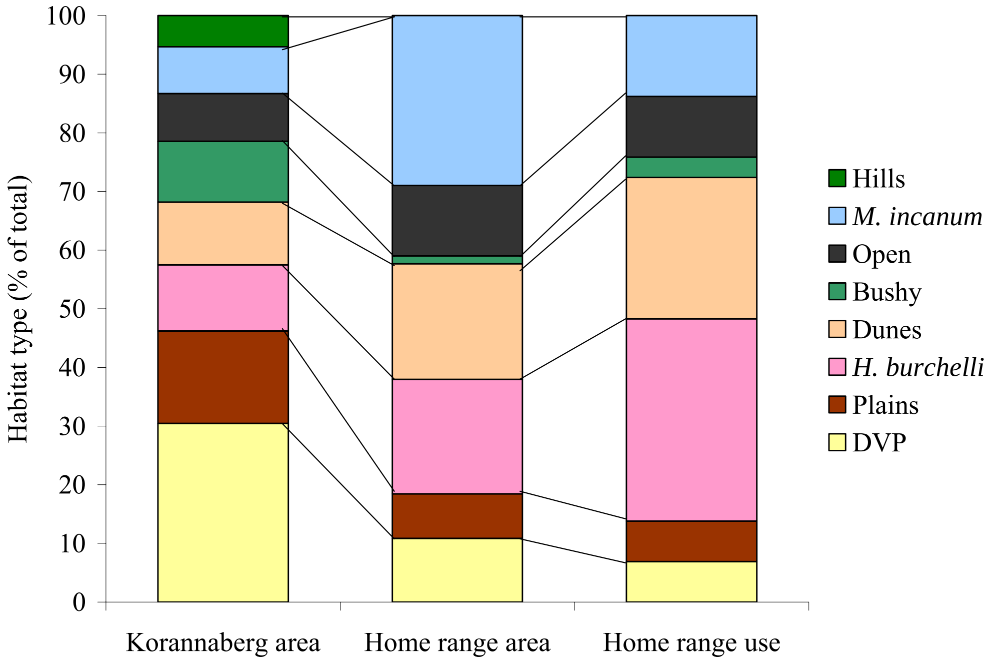


Figure 3. Percentage of habitat types within total fenced Korannaberg area, Bogale seasonal home ranges and Bogale habitat locations.

a. Wet season



b. Dry season

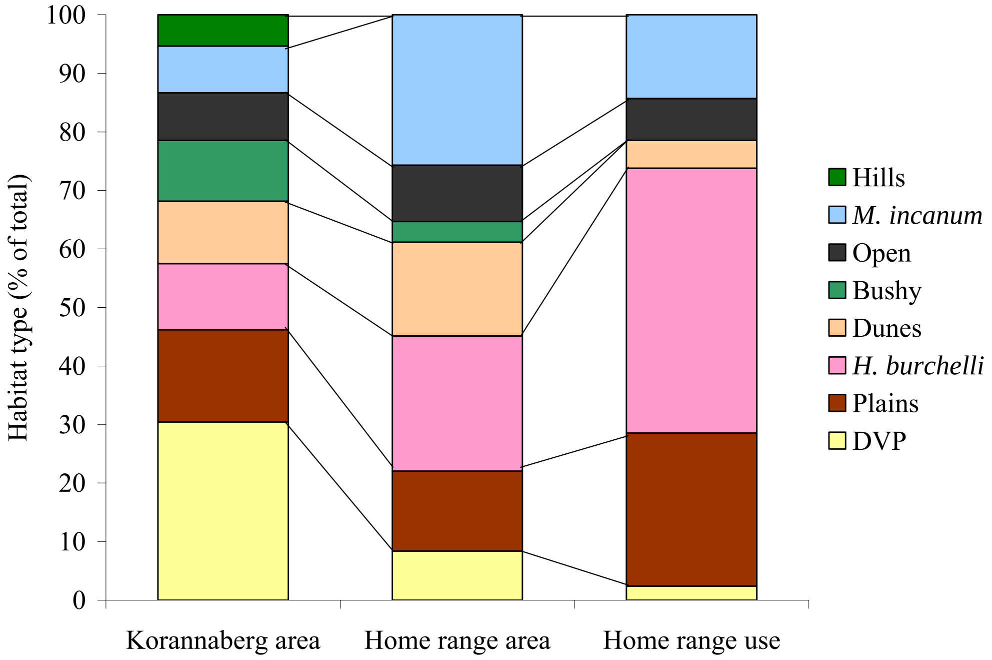
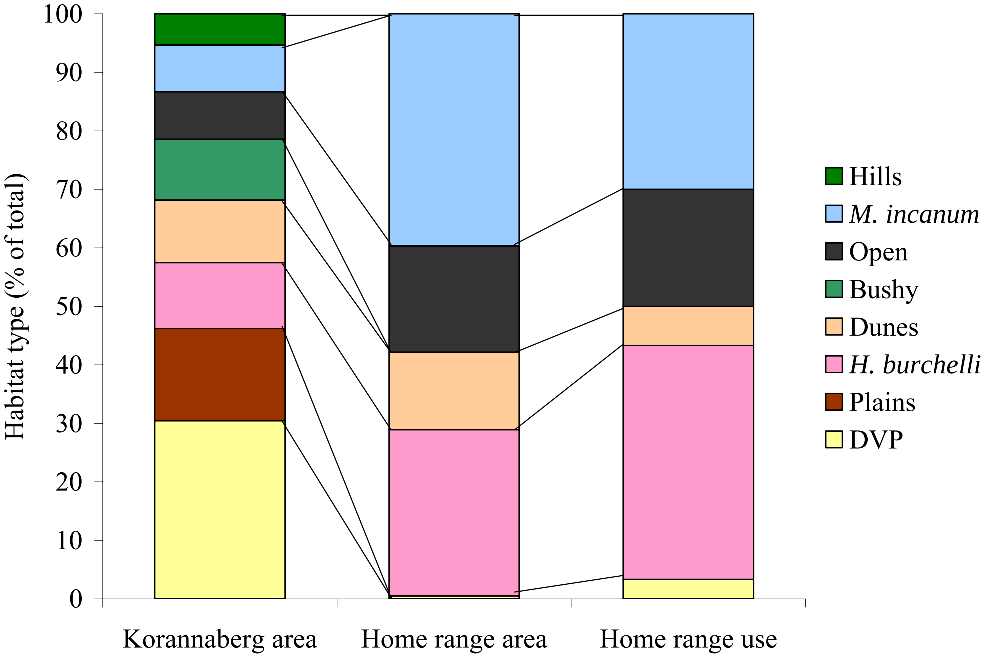


Figure 4. Percentage of habitat types within total fenced Korannaberg area, Inyani seasonal home ranges and Inyani habitat locations.

a. Wet season



b. Dry season

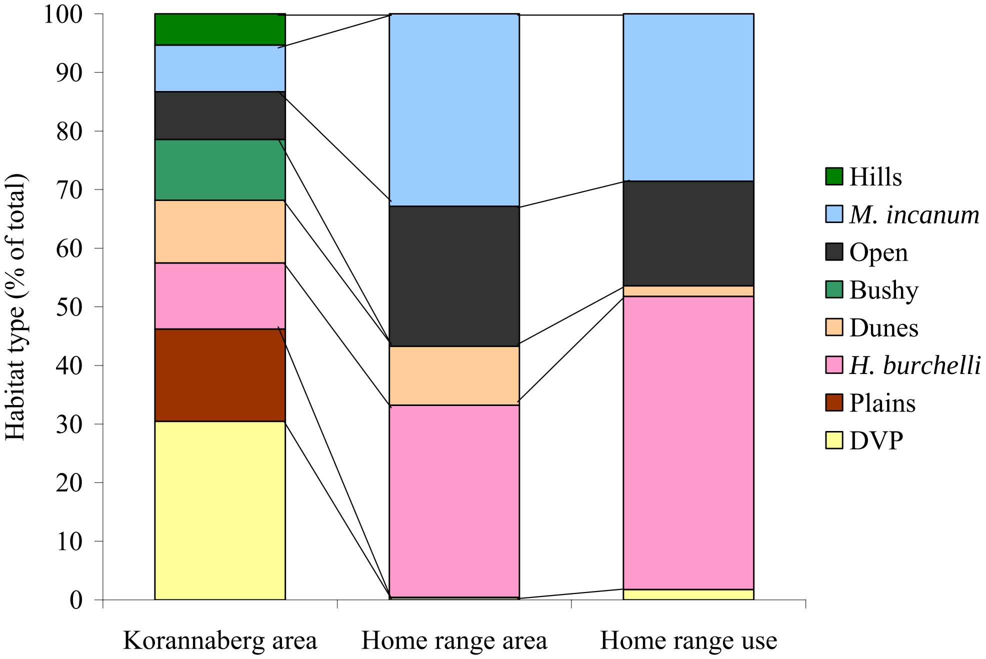
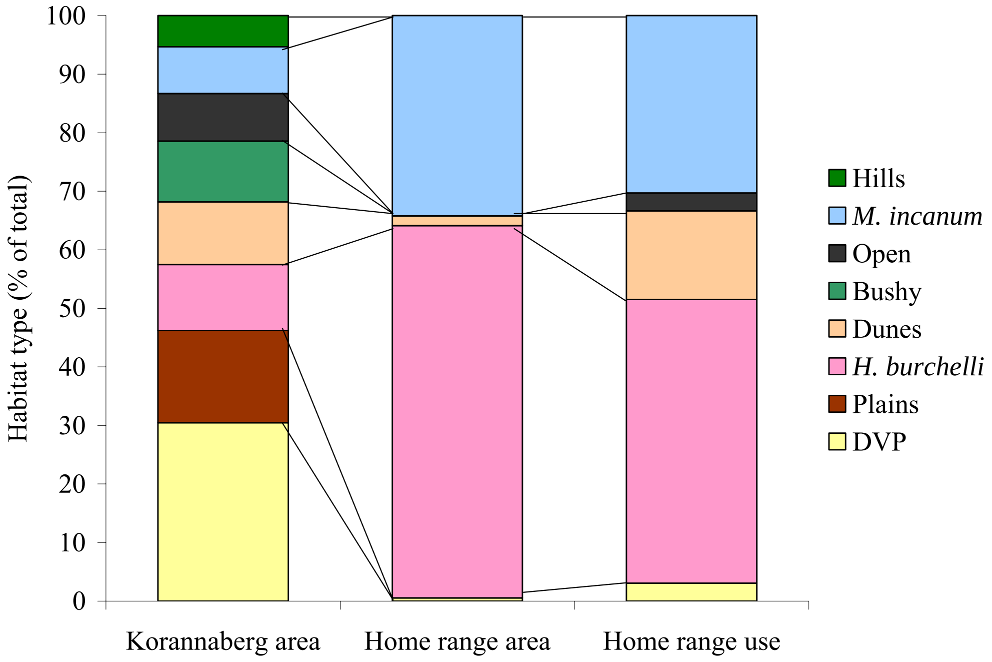


Figure 5. Percentage of habitat types within total fenced Korannaberg area, Kagale seasonal home ranges and Kagale habitat locations.

a. Wet season



b. Dry season

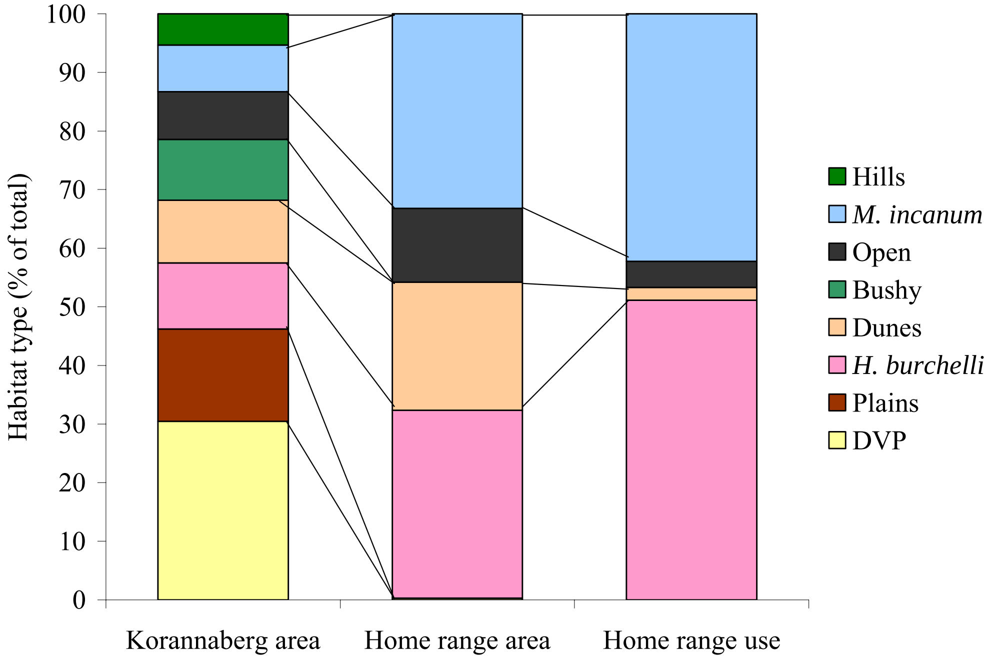
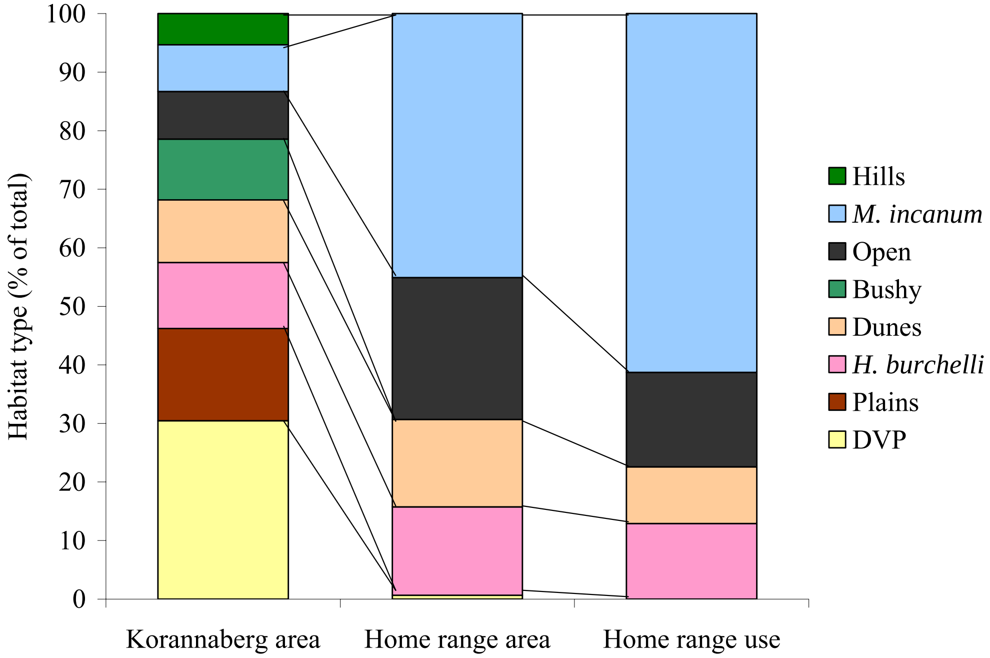


Figure 6. Percentage of habitat types within total fenced Korannaberg area, Nantoni seasonal home ranges and Nantoni habitat locations.

a. Wet season



b. Dry season

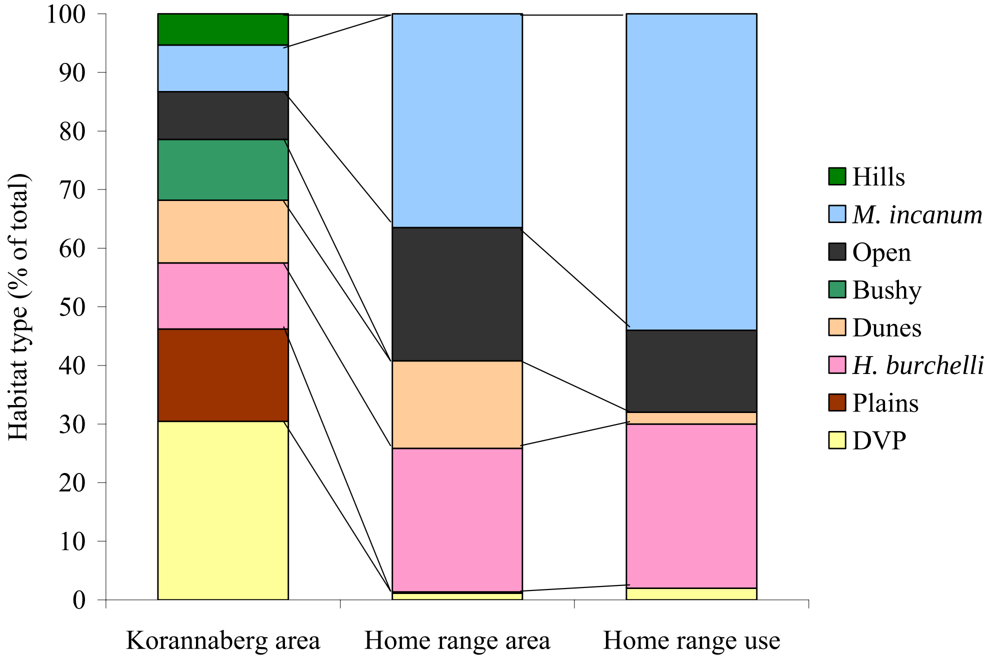


Figure 7. Percentage of habitat types within total fenced Korannaberg area, Usuk seasonal home ranges and Usuk habitat locations.

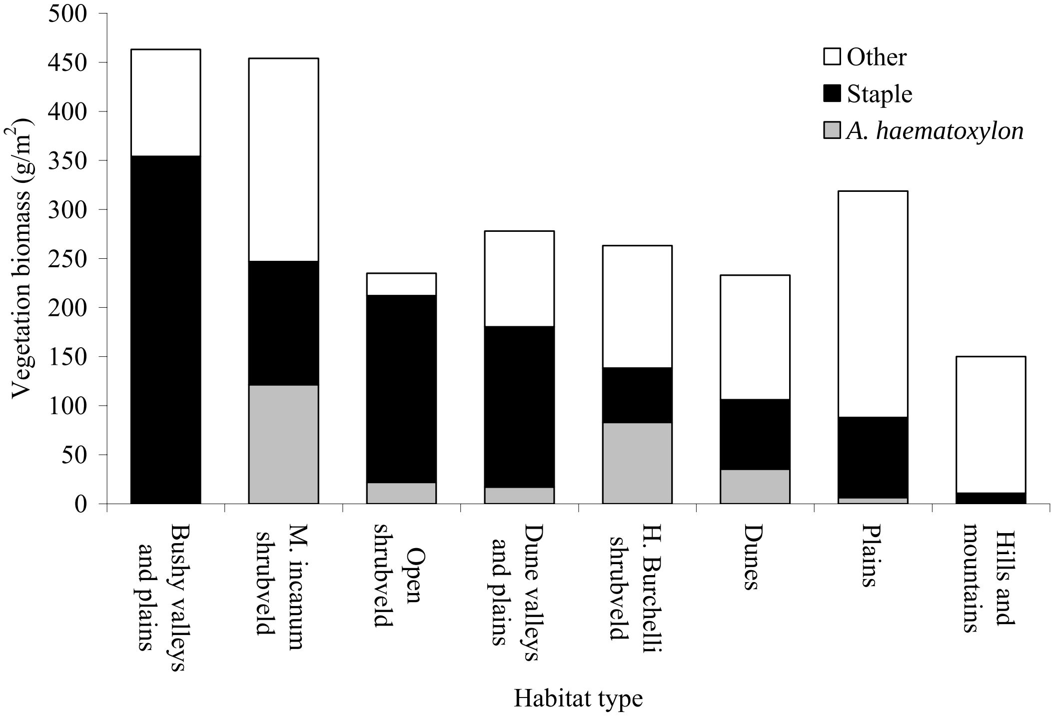


Figure 8. Total available vegetation biomass (g/m^2) of black rhino browse categories.

Table 1. Wet season home range size as estimated by 95% MCP and number of sightings used for these estimates for five adult female black rhinos.

Rhino	Estimated age at 31/12/05	Annual home range (km^2)	Total no. sightings	Wet season home range (km^2)	No. wet season sightings	Dry season home range (km^2)	No. dry season sightings
Bogale	31	74.8	76	70.6	36	55.9	40
Inyani	19	119.3	71	87.0	29	105.8	42
Kagale	24	99.6	87	66.4	30	94.6	56
Nantoni	26	63.7	77	35.6	33	50.5	45
Usuk	26	84.4	81	55.5	31	81.0	50

Table 2. Comparison of models incorporating different two-way interactions of factors influencing sightings of focal female rhino at Tswalu.

Model	G^2	df	*P*
habitat type*rhino	138.79	16	<0.001
habitat type*season	27.03	4	<0.001
habitat type*source	13.78	8	0.088
rhino*source	10.01	8	0.264
rhino*season	2.29	4	0.683
season*source	0.72	2	0.698

Table 3. Third order habitat selection during the wet season by individual female black rhino, as revealed by proportion of observed sightings in different habitat types with Bonferroni confidence intervals showing predicted variation and expected proportion of sightings based on proportion of home range area.

Habitat type	Rhino	Observed no. sightings	Expected no. sightings	Expected proportion used (*Pe*)	Actual proportion used (*Pi*)	Bonferroni interval for *Pi*	*Pi* / *Pe*
H. burchelli							
shrubveld	Bogale	3	4	0.108	0.083	0.000 ≤ Pi ≤ 0.205	0.77
	Inyani	10	6	0.195	0.38	0.141 ≤ Pi ≤ 0.619	1.95
	Kagale	12	9	0.284	0.4	0.176 ≤ Pi ≤ 0.624	1.41
	Nantoni	16	21	0.636	0.485	0.267 ≤ Pi ≤ 0.702	0.76
	Usuk	4	5	0.151	0.129	0.000 ≤ Pi ≤ 0.280	0.85
M. incanum							
shrubveld	Bogale	10	7	0.196	0.083	0.000 ≤ Pi ≤ 0.205	0.42
	Inyani	4	8	0.29	0.138	0.000 ≤ Pi ≤ 0.308	0.48
	Kagale	9	12	0.397	0.3	0.091 ≤ Pi ≤ 0.509	0.76
	Nantoni	10	11	0.342	0.303	0.103 ≤ Pi ≤ 0.503	0.89
	Usuk	19	14	0.451	0.613	0.394 ≤ Pi ≤ 0.832	1.36
Open							
shrubveld	Bogale	3	3	0.071	0.083	0.000 ≤ Pi ≤ 0.205	1.17
	Inyani	3	3	0.12	0.103	0.000 ≤ Pi ≤ 0.253	0.86
	Kagale	6	5	0.181	0.2	0.017 ≤ Pi ≤ 0.383	1.1
	Nantoni	1	0	0	0.03	0.000 ≤ Pi ≤ 0.105	0
	Usuk	5	8	0.242	0.161	0.000 ≤ Pi ≤ 0.326	0.67
Dunes	Bogale	6	9	0.246	0.167	0.002 ≤ Pi ≤ 0.331	0.68
	Inyani	7	6	0.197	0.241	0.031 ≤ Pi ≤ 0.452	1.22
	Kagale	2	4	0.133	0.067	0.000 ≤ Pi ≤ 0.181	0.5
	Nantoni	5	1	0.05	0.152	0.000 ≤ Pi ≤ 0.308	3.04
	Usuk	3	5	0.149	0.097	0.000 ≤ Pi ≤ 0.230	0.65

Dune Valleys and Plains	Bogale	8	6	0.154	0.222	0.039 ≤ Pi ≤ 0.406	1.44
	Inyani	2	3	0.108	0.07	0.000 ≤ Pi ≤ 0.196	0.65
Plains	Bogale	6	6	0.172	0.167	0.002 ≤ Pi ≤ 0.331	0.97
	Inyani	2	2	0.076	0.07	0.000 ≤ Pi ≤ 0.196	0.92
Bushy	Bogale	0	2	0.052	0	0 ≤ Pi ≤ 0	0

Table 4. Third order habitat selection during the dry season by individual female black rhino, as revealed by proportion of observed sightings in different habitat types with Bonferroni confidence intervals showing predicted variation and expected proportion of sightings based on proportion of home range area. Differences between observed and expected proportions are marked in boldface.

Habitat type	Rhino	Observed no. sightings	Expected no. sightings	Expected proportion used *(Pe)*	Actual proportion used *(Pi)*	Bonferroni interval for *Pi*	*Pi / Pe*
***H. burchelli* shrubveld**	Bogale	5	7	0.17	0.125	0.000 ≤ Pi ≤ 0.264	0.74
	Inyani	**19**	**10**	**0.193**	**0.452**	**0.248 ≤ Pi ≤ 0.656**	**2.34**
	Kagale	**28**	**18**	**0.328**	**0.5**	**0.334 ≤ Pi ≤ 0.666**	**1.52**
	Nantoni	**23**	**14**	**0.321**	**0.511**	**0.325 ≤ Pi ≤ 0.697**	**1.59**
	Usuk	14	12	0.245	0.28	0.121 ≤ Pi ≤ 0.439	1.14
***M. incanum* shrubveld**	**Bogale**	**19**	**9**	**0.235**	**0.475**	**0.266 ≤ Pi ≤ 0.684**	**2.02**
	Inyani	6	11	0.246	0.143	0.000 ≤ Pi ≤ 0.286	0.58
	Kagale	16	18	0.324	0.286	0.136 ≤ Pi ≤ 0.435	0.88
	Nantoni	19	15	0.332	0.422	0.238 ≤ Pi ≤ 0.606	1.27
	Usuk	**29**	**18**	**0.365**	**0.58**	**0.380 ≤ Pi ≤ 0.780**	**1.59**
Open shrubveld	Bogale	4	3	0.063	0.1	0.000 ≤ Pi ≤ 0.226	1.59
	Inyani	3	4	0.123	0.071	0.000 ≤ Pi ≤ 0.176	0.58
	Kagale	10	13	0.243	0.179	0.052 ≤ Pi ≤ 0.305	0.74
	Nantoni	**2**	**6**	**0.126**	**0.044**	**0.000 ≤ Pi ≤ 0.121**	**0.35**
	Usuk	**5**	**11**	**0.227**	**0.1**	**0.000 ≤ Pi ≤ 0.206**	**0.44**
Dunes	**Bogale**	**1**	**11**	**0.28**	**0.025**	**0.000 ≤ Pi ≤ 0.090**	**0.09**
	Inyani	**2**	**7**	**0.158**	**0.048**	**0.000 ≤ Pi ≤ 0.135**	**0.3**
	Kagale	**1**	**6**	**0.108**	**0.018**	**0.000 ≤ Pi ≤ 0.062**	**0.17**
	Nantoni	**1**	**10**	**0.219**	**0.022**	**0.000 ≤ Pi ≤ 0.077**	**0.1**

	Usuk	**1**	**7**	**0.149**	**0.02**	**0.000 ≤ Pi ≤ 0.069**	**0.13**
Dune Valleys and Plains	Bogale	6	4	0.098	0.15	0.000 ≤ Pi ≤ 0.300	1.53
	Inyani	**1**	**4**	**0.088**	**0.024**	**0.000 ≤ Pi ≤ 0.087**	**0.27**
	Kagale	1	0	0.01	0.018	0.000 ≤ Pi ≤ 0.062	1.8
	Usuk	1	1	0.011	0.02	0.000 ≤ Pi ≤ 0.069	1.82
Plains	Bogale	4	5	0.133	0.1	0.000 ≤ Pi ≤ 0.226	0.75
	Inyani	11	6	0.158	0.262	0.082 ≤ Pi ≤ 0.442	1.66
Bushy Plains and Valleys	Bogale	1	1	0.021	0.025	0.000 ≤ Pi ≤ 0.090	1.19

6. Maximum productive habitat capacity for black rhinos (*Diceros bicornis*) at Tswalu Kalahari Reserve

6.1 Abstract

Maximum productive habitat capacity for black rhino in eight different habitat types at Tswalu Kalahari Reserve was assessed using an adaptive resource use approach, which considered seasonal variation in food availability. Black rhino at Tswalu have shown high population growth rates since re-introduction in 1995. Projections of recommended rhino density for maximum population growth were based on the highest population density at which female rhino could attain energetic requirements for reproduction throughout the year.

Model projections were based on biomass of the five woody plant species known to form 70 % of rhino diet plus an additional buffer resource category, which provided submaintenance nutritional gains. Model simulations ran over 52 weeks incorporating seasonal changes in plant phenology and chemistry. Each week, the model selected the plant species providing the greatest energy intake, derived from available plant biomass, eating rate and digestible organic matter content of each species. Model output consisted of digestible organic matter gains each week, which were related to biomass of digestible organic matter required to meet reproductive requirements. Simulations were run using foraging times of eight, ten and twelve hours for simulated rhino densities between 0.01 – 0.25 rhinos/km^2.

Recommended rhino density projections for the two shrubveld habitat types used by black rhino at Tswalu were between approximately 0.10 and 0.16 rhinos/km^2. This suggests density in these areas could potentially be elevated by about one third above those during the study period, assuming no change in habitat conditions. Two additional habitat types were projected to support fewer than 0.02 rhinos/ km^2. The four remaining habitat types appeared unsuitable to support a maximally breeding population.

Model simulations reducing availability of *A. haematoxylon* by 50 %, reduced recommended rhino density projections by approximately 60 %. Total removal of *A.*

haematoxylon in preferred habitat types meant rhino were not able to meet energy requirements for reproduction in the dry season as other plant species did not provide compensatory gains.

Available biomass of *A. haematoxylon* at the end of the late dry season was identified as a simple indicator of actual rhino density in relation to maximum productivity habitat capacity at Tswalu. Identifying key resources used during the late dry period and managing rhino density accordingly could help maximise reproductive rates in other populations. This chapter demonstrates a new conceptual approach to addressing habitat capacity for black rhino, which may aid in achieving the goal of maximising metapopulation growth rates of this critically endangered species.

Key words: *metaphysiological modelling*; *adaptive resource use*; *seasonal*; *key resource*; *reproductive success*; *density dependence; inter-calving intervals*

6.2 Introduction

Producing estimates of carrying capacity for browsing mammalian herbivores in African savannas is challenging due to the differences in nutritional value of woody plant species as well as the effects of seasonal leaf loss. However, it is necessary for wildlife managers to have an understanding of the capacity of the vegetation in an area to support a specific herbivore species in order to ensure appropriate stocking rates. This is particularly important for management of a critically endangered species such as black rhino (Freidman and Daly, 2004). One of the main strategies advocated for successful rhino conservation is to manage existing meta-populations for maximum productivity to minimise loss of remaining genetic diversity and mitigate poaching losses (Emslie and Brooks, 1999; Emslie, 2001). To achieve this, density-dependent effects on reproduction must be considered, particularly when developing conservation strategies for rhinos confined to fenced reserves (Rachlow and Berger, 1998; Okita-Ouma *et al*., 2010).

Understanding the maximum productive carrying capacity (MPCC) or maximum sustainable yield (Caughley, 1976) of an area for black rhino is therefore a fundamental aspect of successful metapopulation management (Emslie and Brooks, 1999; Emslie, 2001; Owen-Smith, 2001; Linklater, 2003; Emslie *et al.*, 2009; Morgan *et al*., 2009; Okita-Ouma *et al*., 2010). The IUCN African Rhino Specialist Group (AfRSG) provisionally adopted the figure of 75 % of Ecological Carrying Capacity (ECC), i.e. 75 % of the density for zero growth, as an estimate of MPCC (Emslie and Brooks, 1999) and recommends rhino populations are stocked at this density. Large mammals are regulated largely by direct effects of food limitations on survival and reproduction (Fowler, 1987). For megaherbivores, with adult body mass in excess of 1000 kg, the major regulatory responses operate through decreasing fecundity (Owen-Smith, 1988). Observed demographic responses by black rhinos to nutritional restrictions are increases in inter-calving intervals and a delay in the age at which females first reproduce (Hitchins and Anderson, 1983; Hrabar and du Toit, 2005). Hence, above MPCC it is anticipated that black rhino inter-calving intervals would lengthen as nutritional restrictions compel individual females to take longer to recover body reserves before breeding again, as observed in red deer (Clutton-Brock *et al.*, 1982; Clutton-Brock and Coulson, 2002).

This chapter demonstrates a new conceptual approach to determining maximum productive habitat capacity for black rhino, based on the energetic requirements for reproduction of individual female rhino. The crux of this approach is to estimate the highest population density at which each female rhino could attain maximum energetic gains for reproduction throughout the entire seasonal cycle. Since these projected gains exceed reproductive requirements, there should be no loss in body condition and inter-calving intervals should be minimised (Rachlow and Berger, 1998). Thus, this approach could assist in achieving the conservation goal of maximising black rhino metapopulation growth rates (Emslie and Brooks, 1998; Emslie, 2001).

The modelling format selected for this exercise is a growth, metabolism and mortality (GMM) model (Owen-Smith, 2002; Owen-Smith, 2007). Owen-Smith (2002) developed the GMM, based on the metaphysiological modelling methodology of Getz (1991, 1993), as a model to investigate the adaptive resource use concepts. The adaptive resource use approach to assessing habitat suitability (Owen-Smith, 2002) was created from the understanding that in seasonal environments distinct vegetation components are required under different conditions during the seasonal cycle (Owen-Smith and Cooper, 1989). The adaptive resource use approach therefore incorporates seasonal variability in vegetation growth, quality and quantity as well as the adaptive responses of herbivores to this variability (Owen-Smith, 2002). A GMM model for habitat suitability calculates the aggregated herbivore population biomass that can be supported by vegetation biomass. Animal population growth is dependent upon the difference between rates of uptake and conversion of resources into biomass, and losses of biomass to metabolism and mortality (Owen-Smith, 2002; Owen-Smith, 2005; Owen-Smith, 2007). Projections of herbivore density are thus based on animal biomass that can be gained by consuming available plant biomass, relative to physiological attrition and mortality losses and subject to seasonal variation in the vegetation resource base (Owen-Smith, 2002; Owen-Smith, 2005; Owen-Smith, 2007).

The black rhino maximum productivity (BRMP) habitat capacity model of this chapter is based on a GMM programme developed for habitat suitability assessments for greater kudu (*Tragelaphus strepsiceros*). The scenario addressed in the current modelling exercise is a black rhino population at Tswalu Kalahari Reserve, a large private game reserve in the Northern Cape of South Africa. Eight black rhinos were re-located to Tswalu in 1995 from Etosha National Park in Namibia. This population has since shown indicators of excellent performance (du Toit, 2001) with low mean inter-calving intervals (ICI) (2.2 years ± 0.1, n = 17) and early age at first calving (6.1 years, n =3), hence remaining below habitat capacity with no indication of density dependence impacts on demographic rates (Fowler, 1987; Bonenfant *et al*., 2009).

Focal animals at Tswalu were the subject of a two year study assessing diet content and nutritional status. Hence, detailed information was available on rhino feeding behaviour and plant species phenology and chemical contents, with which to parameterise the model. Since simulation models provide an opportunity to examine the potential outcome of future events (Starfield and Bleloch, 1991), here the GMM model could also be used to evaluate the impacts of declines in availability of *A. haematoxylon*, identified as the key resource for rhino in this area (Chapter 2 and 3), in a way that was not possible by experimentation. Model projections are thus intended to provide an estimate of the extent to which rhino population density could increase in the different habitat types before an impact on reproductive capacity would be anticipated. Above the recommended threshold density projections it is anticipated that inter-calving intervals would lengthen as nutritional restrictions mean individual females must recover body reserves before breeding again (Clutton-Brock *et al*., 1982; Clutton-Brock and Coulson, 2002).

The aim of this paper was to develop a model including seasonal variation in resource availability to produce projections of maximum productive habitat capacity for black rhino in different habitat types. The purpose was to provide management at Tswalu with guidelines for stocking densities for maximum population growth.

The specific questions addressed were;

1. What is the threshold rhino density above which reproductive performance would be predicted to decline in each habitat type?
2. How do model projections of rhino density relate to patterns of population density in different habitat types during the study period?
3. Can other plant species compensate for a decline in availability of *A. haematoxylon*?

6.3 Methods

Model structure

The maximum productive habitat capacity for black rhino model (BRMP: Appendix I) was adapted from the habitat suitability model for kudu (Owen-Smith, 2007: HABPOPUL). Model format is True Basic Bronze Edition programming language (True Basic © 1998). The crux of this approach was to produce an estimate of the maximum density of rhino that could meet energy requirements for reproduction throughout the seasonal cycle, defined here as the maximum productive habitat capacity. Recommended density was thus determined by comparing projected weekly energy gains against energy requirements for reproduction at increasing rhino population density.

The foundation of the model was the amount of plant biomass available to rhino within the eight different habitat types at Tswalu (Fig. 1). Six different resource categories were used, representing the five major woody plant species in rhino diet at Tswalu plus an additional category containing biomass of all additional species, designed to represent the buffer resource type in Owen-Smith's (2002) categories. The additional resource category hence provided submaintenance nutritional gains. The first step was to calculate which of the six available resources would provide the greatest intake of digestible organic matter each week. Intake gains were based on proportional digestible organic matter (dOM), eating rates, availability of food for consumption and rhino search rates. Rhino diet each week was formed of the plant species with the highest dOM gain, following a maximising approach. Daily dry matter intake of the selected species was calculated for three scenarios using foraging times of 8, 10 or 12 hours. Weekly dOM gains were compared to reproductive requirements.

Fundamental to this approach is the recognition that as simulated rhino population density increased, available vegetation biomass was consumed more quickly. Hence, during the early and late dry seasons, each week vegetation biomass was reduced by the dry mass of the plant species consumed the previous week. Vegetation biomass was not reduced during the wet and transition seasons, to allow for plant growth replacing consumed biomass at this time of year. For deciduous species, leaf fall was simulated in the model during the early dry season as a reduction in available plant biomass and digestible organic matter content. This represented loss of leaf matter and availability of twigs as a possible resource.

Model calculations ran on a weekly iteration over 52 weeks to represent the annual cycle. Initial rhino density was set at 0.01 rhinos/km^2 and increased by 0.01 over 25 increments to 0.25 rhinos/km^2 which was considered the maximum potential density based on records from other arid savanna areas (Buk and Knight, 2010).

Plant biomass intake

The basis of this model is the functional response based on the Michaelis-Menten or Holling Type II equation, where intake rates increase with food availability until a plateau is reached where food handling time limits search time for new food items (Holling, 1959; Owen-Smith, 2002; Owen-Smith, 2007). The relative rate of dry matter biomass gain (G_P) was dependent upon biomass of vegetation available as browse (F), eating rate for plant species or type (I_P), acceptance coefficient or fraction of available food consumed (a) and search rate (s);

$$G_P = saF/(1+saF/I_P).$$

Gain of total dry mass (G_P) was converted to gain of digestible organic matter (dOM) intake (D_P) using the appropriate seasonal dOM content (C_P) for each plant species;

$$D_P = G_P * C_P$$

Digestible organic matter gains (D_P) each week were multiplied by the relevant value of foraging time each day (t_F) to produce a value of daily digestible organic matter gain (W_P);

$$W_P = D_P * t_F.$$

Plant species were ranked according to daily digestible organic matter gain (W_P). The species providing the greatest gain was selected to form the diet in that weekly iteration following the HABPOPUL model for kudu habitat suitability assessment (Owen-Smith, 2002).

Plant biomass reduction

For weeks 13 to 25, during the early dry season, weekly leaf attrition due to seasonal leaf loss in deciduous species reduced remaining biomass eventually to just that of twigs, where leaf loss of a plant species each week (E_P) was dependent upon the total original plant species biomass (O_P), the proportional leaf biomass (L_P) and the weekly rate of attrition (A_P) (Table 1);

$$E_P = (O_P * L_P) * A_P$$

For weeks 13 to 39 representing the early dry and late dry seasons, available biomass of a plant species was reduced by the biomass consumed during the previous week. This was calculated for each plant species as;

$$B_{P(week+1)} = B_{P(week)} - (mBp_{(week)}\ d/10000)*7$$

where, B is the available biomass of the resource type ($_p$) in a certain week, which decreases dependent upon the mass (kg) eaten per day per rhino (m) relative to the rhino population density (d). Thus, as the simulated population density increased, the available biomass of resources was consumed more quickly. In simulations where the energetic intake exceeded the energetic requirements, the daily vegetation biomass offtake of a plant species was capped at the level required to meet maximum reproductive energetic requirements. The purpose of this was to prevent the model over-estimating the rate of consumption of vegetation biomass. Daily biomass intake was stopped at 35 kg / day, considered the best estimate of the upper limit of browse biomass intake by free-ranging black rhino (Marcus Clauss *pers. comm.*).

Study site

The model scenario was based on black rhino diet content and foraging behaviour recorded at Tswalu Kalahari Reserve (Tswalu) a 1,080 km^2 private game reserve in the Northern Cape of South Africa (Tswalu S 27°04’ - 27°44’ and E 22°10’ - 22°36’). Black rhino were re-introduced to the reserve in 1995 and at the end of the study period in December 2005 continued to show high annual growth rates of 13 ± 0.3 %. The exceptionally high annual growth rate was due in part to the adult female bias in population structure. This analysis focussed on the 17 rhino fenced within the 450 km^2 Korannaberg section of the reserve.

The predominant vegetation type at Tswalu has been classified as Shrubby Kalahari Dune Bushveld (Low and Rebelo, 1996) which has a relatively open structure. Abundant tree and shrub species in the area include *A. haematoxylon*, *Acacia erioloba, Acacia mellifera*, *Boscia albutrunca*, *Grewia flava* and *Terminalia sericea* (van Rooyen, 1999). Eight habitat types were identified based upon the vegetation map of van Rooyen (1999); bushy plains and valleys, dunes habitat type, plains habitat type, dune valleys and plains, hills and mountains, *H. burchelli* shrubveld, *M. incanum* shrubveld and open shrubveld (Fig. 2) (see Chapter 5 for more details).

Rhino density data

Sightings of the five adult females in the population were used to derive 95 % MCP home ranges as described in Chapter 5. Sightings of the twelve additional rhino in the Korannaberg section (three subadult females; seven subadult males; two adult males) between January 2004 to December 2005 (total sightings: 943, individual range: 8-55) were used to construct 95 % MCP home ranges for all individuals using Hawth's Analysis Tools for ESRI ArcGIS (v3.25) in ArcGIS 9.1. Each individual's home range was intersected with the vegetation map to calculate the proportion of individual home range in each habitat type. Total proportional rhino number in each habitat type was divided by the area of each habitat to produce an estimate of the actual density of rhino (rhino/km^2) during the data collection period (Table 1).

Model parameters

Rhino diet data

The woody plant species contributing over 70 % of diet throughout the year were *A. haematoxylon*, *Acacia mellifera*, *Grewia flava*, *Monechma incanum* and *Rhigozum trichotomum* (Table 2). Seasonal dietary contribution in relation to availability was quantified by backtracking along feeding tracks (Chapter 2). Acceptance coefficient (*a*) was set at 0.15, being the mean acceptability index (AI) recorded when including all available plant species (see Chapter 2). The number of bites recorded from each plant species was converted to dry mass using diameter regression equations (see Chapter 2 for details).

As food resource availability declined during the year, due to consumption by increased densities of rhino, foraging theory predicts that additional species would be added to the diet (Owen-Smith and Novellie, 1982; Stephens and Krebs, 1986; Owen-Smith, 2002). Based on plant species availability at Tswalu this would likely be *A. erioloba, Acacia hebeclada, B. albutrunca* or *T. sericea*. As these species were not utilised during the study period, they would be expected to provide a less nutritious alternative to those selected within the diet. These species were considered to represent buffer resources, providing sub-maintenance energy gains (Owen-Smith (2002), to allow a conservative estimate of potential energy gains. The additional deciduous buffer resource type was based on analysis of NDF content of leaf and twig material of *T. sericea* from a larger study including chemical analysis of rejected plant species at Tswalu (Keryn Adcock *pers. comm.*) (Table 2). Intake rate for the buffer species was based on that of *R. trichotomum* to create a resource that would provide energy gains below maintenance requirements.

Vegetation biomass

The majority of rhino browsing occurs below 2 m (Adcock, 2003). Data on available vegetation biomass below 2 m was taken from an assessment of vegetation biomass in different habitat types by Beck (2001). Total browse volume in different habitat types was recorded using the belt transect method of Smit (1989a) (Fig. 2). Records were based upon 86 transects of 100 m by 2 m throughout the study area. All woody plant species were counted and identified. Tree canopy diameter measurements were taken and used in conjunction with the Biomass Estimates of Canopy Volume computer programme (BECVOL; Smit,1989b) to give a measure of total browse volume (Beck, 2001). Transects were combined within each habitat type and extrapolated over the entire area (Beck, 2001). Biomass of the five plant species contributing 70 % of annual diet represented the estimate of available browse of preferred species in each habitat type (kg/km^2). Available biomass of all additional woody plant species in each habitat type was assigned to the buffer resource type category (Fig. 2).

Green leaf retention on woody plant species was recorded along feeding tracks throughout the year using a 5 point scale (0, 1-5, 6-33, 34-66 and 67-100 %: Dekker and Smit, 1996). The week in which leaf fall commenced was determined for the deciduous plant species as the first week in which retention fell below 66 % and the end of leaf fall was the first week in which retention was recorded as 0. Mean weekly leaf attrition (A) in deciduous species was thus calculated as 1/number of weeks of leaf fall.

Plant chemical content

Due to the large number of plant samples, it was possible to utilise Near Infrared Reflectance Spectroscopy (NIRS) calibrated from wet chemistry data on the initial sub sample to assess fibre (See Chapter 2 for details of plant sample collection and wet chemistry analyses). . Inductively coupled plasma-optical emission spectrometer (ICP-OES) and an ANKOM 200/220 Fibre Analyzer were used to measure NDF contents in the samples from the calibration set. The proportion of non-digestible fibre NDF for each plant species in each season was converted to digestible organic matter (dOM g/g) using the equation; dOM = (-NDF*0.98) + 101 for browsing rhino taken from Clauss *et al*. (2006a).

Rhino physiology

Approximate body weight for adult female black rhino (BM = 1000 kg) was taken from Owen-Smith (1988). Foraging time (t_F) was initially set at eight hours a day to replicate likely activity patterns of black rhino (Goddard, 1967). It was not possible to record information on nocturnal activities by rhino during the data collection period, so exact foraging times were not known. Hence, simulations were also run for foraging times of ten hours and twelve hours, twelve hours being the maximum time that white rhinos were observed foraging (Owen-Smith, 1988).

The value for rhino search rate (s = 92 m^2/min) was based on the equation from Owen-Smith (2002): $s = 0.9M^{0.67}$. Eating rates for the five plant species (I_P g/min; Table 2) were related to mean bite mass for each species from dry mass regressions of twig diameter and mean bite rates for each species estimated from video recordings taken during fieldwork at Tswalu (Appendix II).

Energy requirements

The basic field metabolic rate (FMR) for an adult female without a calf was calculated as FMR = $[4.63\ M^{0.762}] / 1000$ = 173MJ / day (from Nagy (1982) following Atkinson, 1995). The daily extra energy cost incurred by the gravid uterus prior to parturition can be estimated at 44% of the basal metabolic rate (BMR) (BMR = (70 $M^{0.75}$) x 4.184/1000) (Robbins, 1983) where M is the maternal weight in Kg, and (4.184/1000) is used to convert Kcal into MJ. Therefore, the daily energy requirement of a pregnant female prior to parturition was estimated as 196 MJ / day. Seasonal values for digestible organic matter in the diet were converted to energy using a gross energy value for rhino browse of 18.2 MJ/kg DM recorded by Clemens and Maloiy (1982) in East Africa. Total energy values were converted to digestible energy using a value of 0.83 (ARC, 1965 in Owen-Smith and Cooper, 1989).

Hence, the minimum daily intake of digestible organic matter required to meet reproductive energy demands was 13.0 kg and daily digestible organic matter gains were compared against this value. Where foraging times were increased to 10 or 12 hours, it was assumed there was a concurrent increase in energy requirements due to changed energy budgets. Metabolic rate whilst feeding was assumed at 1.2 of resting value following Owen-Smith and Cooper, (1989). Hence, maintenance energy requirements for t_F = 10 hours were increased for the two additional active hours by 1.2 to 13.2 kg total and by 1.2 for 4 hours for t_F = 12 hours, giving13.4 kg total.

Model scenarios

Maximum productive capacity in each habitat was projected as rhino density at which energy gains exceeded requirements for reproduction through the seasonal cycle. Scenarios were produced for foraging times of eight, ten and twelve hours. Results for each habitat type were compared with estimates of actual rhino density in each habitat type. The intention being to provide some validation for projections by relating patterns of model output to real world findings (Starfield and Bleloch, 1991).

Within preferred habitat types (*M. incanum* and *H. burchelli* shrubveld (Chapter 5)) the weekly energy balance at threshold rhino densities was assessed throughout the year. Weekly outputs from these original scenarios were compared with those simulating 50% reduction and 100% removal of *A. haematoxylon* biomass. These seasonal analyses were performed using a standard foraging time of eight hours (Goddard, 1967).

6.4 Results

Projected maximum productive capacity in different habitat types

For all three scenarios of foraging time, there was a clear distinction between rhino densities projected for two shrubveld habitat types (*M. incanum* and *H. burchelli*) and densities for the six remaining habitat types (Fig. 3a, b and c). For eight hours foraging time (Fig. 3a), projected threshold densities were 0.16 rhinos/km^2 for *M. incanum* shrubveld and 0.10 rhinos/km^2 for *H. burchelli* shrubveld. The only other habitat type projected to enable rhinos to achieve reproductive energy requirements was the dunes habitat type, at a lower density of 0.02 rhinos/km^2 (Fig. 3a). Increasing foraging time to ten hours raised projections for recommended rhino density to 0.19 rhinos/km^2 in *M. incanum* shrubveld and 0.13 in *H. burchelli* shrubveld (Fig. 3b). Recommended density in dunes habitat type also increased to 0.04 rhinos/km^2 (Fig. 3b). Rhino were also able to meet reproductive requirements in two additional habitat types; specifically, open shrubveld and dune valleys and plains habitat type, albeit at a low density of 0.01 rhinos/km^2.

Increased energy expenditure associated with the maximum foraging time of twelve hours limited rhino densities in the different habitat types. This was due to the limit on daily biomass intake of 35 kg. Maximum productive habitat capacity in *H. burchelli* shrubveld was 0.12 rhinos/km^2 (Fig. 3c). In *M. incanum* shrubveld, projected rhino density was 0.17 rhinos/km^2, but energy gains remained close to estimated requirements (0.997) in excess of 0.25 rhinos / km^2. These high density projections were associated with the high availability (117 g/m^2) of *M. incanum* in this habitat type. Model projections suggested that rhinos foraging for twelve hours may be able to meet maximum reproductive requirements from this small semi-evergreen shrub, even when *A. haematoxylon* was consumed. Threshold rhino density remained at 0.04 rhinos / km^2 in the dunes habitat type and increased to 0.02 rhinos/km^2 in open shrubveld. Dune valleys and plains habitat type was projected to support of very low density of rhino (0.01 rhinos/km^2). Energy gains did not meet maximum reproductive requirements in the three remaining habitat types, even with extended foraging time of twelve hours. Hence, the basic outcome of these scenarios was the recognition that increased foraging time did not greatly alter the relative suitability of habitat types.

As predicted from findings in earlier chapters, there was a clear association between *A. haematoxylon* biomass and maximum productive capacity projections. *Acacia haematoxylon* biomass was 121 g/m^2 in *M. incanum* shrubveld (27 % of total biomass) and 83 g/m^2 (32 % total biomass) in *H. burchelli* shrubveld, but less than 36 g/m^2 in all other habitat types.

Comparison with population density estimated from 95 % MCP home ranges.

Model projections followed the same general ranking as density estimates from individual home ranges (Table 1), with the notable exception of open shrubveld. Density of 0.075 rhinos/km^2 was estimated from 95 % MCPs in open shrubveld, but model projections were only 0.01 rhinos/km^2 at extended foraging time of ten hours. Model projections for dunes habitat type (0.02 rhinos/km^2 at eight hours foraging time) were also slightly below actual densities from MCPs, estimated as 0.047 rhinos/km^2.

Model projections for eight hours foraging time were approximately 30 % higher in *M. incanum* shrubveld and 37 % higher in *H. burchelli* than densities recorded during the study period. Recommended rhino densities from model projections for other habitat types were not greater than observed densities (Table 1). Dune valleys and plains habitat type covers 30 % of the reserve, but had very low rhino density and model projections showed that energetic requirements could only be met by a very low density of rhinos (0.01 rhinos/km^2) with an extended foraging period of ten hours. Plains, bushy valleys and plains, and hills and mountains habitat types were very infrequently used or never used by rhino during the study period (Chapter 5 and Table 1) and were not projected to meet requirements for reproduction from model output (Figs. 3a, 3b and 3c).

Impact of decline in availability of key resource

As expected, the end of the late dry season formed the most limiting period of energy gains (Fig. 4a and 5a). As simulated rhino density increased, this was the period at which gains failed to meet requirements for reproduction. Assessment of model output showed that this was due to almost complete utilisation of available *A. haematoxylon*.

Reducing available biomass of *A. haematoxylon* in preferred shrubveld habitats by 50 % caused late dry season energy gains to fall below reproductive requirements at lower population densities and earlier in the late dry season than the scenario with 100 % *A. haematoxylon* (Fig. 4a and 4b). Removal of 50 % of *A. haematoxylon* biomass lead to a decline of approximately 60 % in maximum productive habitat capacity in *M. incanum* shrubveld (0.16 to 0.06 rhinos/km^2) and in *H. burchelli* shrubveld (0.10 to 0.04 rhinos/km^2) (Figs. 4b and 5b). Total removal of *A. haematoxylon* prevented rhinos from meeting energetic requirements for reproduction (with a foraging time of eight hours) during the early dry, late dry and transition seasons (Fig. 4c and Fig. 5c). Thus, model projections indicated that other plant species were not able compensate for a decline in availability of *A. haematoxylon*.

6.5 Discussion

This chapter describes a new conceptual approach to addressing maximum productive habitat capacity for black rhino, based on maximising individual female reproductive output. The GMM model (BRMP model) developed from this concept was used to project recommended rhino densities for Tswalu Kalahari Reserve. As with most modelling exercises, the value was not only in the quantitative projections made, but the enhanced understanding of the question being investigated. This was primarily confirmation that maximum productive habitat capacity was governed by availability and quality of key resources in the late dry season. Hence at Tswalu, biomass of *A. haematoxylon* was the principal determinant of maximum productive rhino density, thus confirming findings from earlier chapters in this thesis. The modelling process also emphasised the impact on habitat capacity projections of the quality and availability of plant species eaten when *A. haematoxylon* is fully consumed. The implications of the limited information available regarding these plant species are discussed further below.

Rhino density projections for Tswalu

.Overall recorded density of rhino in the Korannaberg section at Tswalu during the study period was 0.035 rhinos/km^2. Mean rhino density for all habitat types was therefore lower than black rhino population densities reported in similar arid areas in South Africa, specifically Augrabies Falls National Park with 0.08 rhinos/km^2 and in Karoo and Vaalbos National Parks with 0.06 rhinos/km^2 (Buk and Knight, 2010). However, maximum rhino density estimated from overlapping MCP home ranges at Tswalu was 0.12 rhinos/km^2 within *M. incanum* shrubveld and there was marked variation in actual rhino density within habitat types (Table 1 and Chapter 5).

Recommended rhino density projections for different habitat types could be split into three categories; two shrubveld habitat types (*M. incanum* and *H. burchelli* shrubveld) with relatively high density projections (greater than 0.10 rhinos/ km^2), three (dunes, open shrubveld, and dune valleys and plains) which had potential to support a lower rhino density (less than 0.04 rhinos/ km^2 and generally only occurring in increased foraging time simulations) and additional three habitat types which appeared fundamentally unsuitable to support a maximally breeding population (plains, bushy valleys and plains, and hills and mountains) as gains did not meet reproductive requirements, even for twelve hours foraging time.

Accordingly, model projections of maximum rhino density followed a similar pattern to rhino habitat selection and actual density in different habitat types at Tswalu (Table 1 and Chapter 5) and these findings provide some validation for the model output. The exception was open shrubveld habitat type, with observed density of approximately 0.075 rhinos/km^2, yet model projected density of just 0.02 rhinos/km^2, even with an extended foraging period of twelve hours. As open shrubveld habitat type occurs in close proximity to the other preferred shrubveld habitat types this finding may be a constraint associated with the 95 % MCP home range analysis used to produce actual rhino density estimates (Anderson, 1982).

Model projections of maximum productive capacity for eight hours foraging time were 0.16 rhinos/km^2 in *M. incanum* shrubveld and 0.10 rhinos/km^2 in *H. burchelli* shrubveld, indicating potential for rhino densities within the two preferred shrubveld habitat types to increase by approximately 33 %. That model projections showed rhino to be below capacity in these shrubveld habitat types was to be expected as estimates of female energy gains exceeded reproductive requirements during the data collection period (Chapter 3).

In contrast, the largest habitat type, dune valleys and plains, had low observed densities and was only projected to support 0.01 rhinos/km^2 at an extended twelve hour foraging period. Additionally, three habitat types were never projected to meet maximum energy requirements for reproduction. These four habitat types covered 62 % of the Korannaberg section and 50 % of the entire reserve area. All these habitat types were neglected by rhino in the Korannaberg section during the study period (Chapter 5).

Key resource type

Model outputs clearly indicated that, as expected, the late dry season was the period when rhino attained the lowest energy gains. Consequently, as rhino population density increases to the extent that food shortages occur, this is the period during which females would be anticipated to lose body condition. Dierenfeld *et al*., (1995) observed that rhino in the Zambezi Valley, Zimbabwe lost body condition during the late dry season. Hence, it is the period of time required to replenish reserves lost during this time which would be anticipated to impact inter-calving intervals and hence population growth rate (Clutton-Brock *et al*., 1982; Clutton-Brock and Coulson, 2002).

Both seasonal patterns and comparative density projections from different habitat types confirmed that maximum productive habitat capacity for black rhino at

Tswalu is dependent upon *A. haematoxylon* biomass. No other plant species provided equivalent energy gains to *A. haematoxylon* in the late dry season at Tswalu; hence, energy gains were generally insufficient to meet energy requirements for reproduction during the late dry season in the absence of this species. The exception was in *M. incanum* shrubveld, where high availability of semi-evergreen *M. incanum* shrub meant rhino were almost able to meet reproductive requirements using this species at the extended foraging time of twelve hours. However, it would not be recommended to attempt maintain rhino densities long-term under a scenario representing such extreme physiological demands. Regardless, these outputs illustrate how quality and availability and hence energy gains from individual woody plant species can impact habitat capacity estimates and population success. Hence, an acknowledged limitation in this exercise is regarding the potential energy gains from additional plant species which would be added to future rhino diet.

Model assumptions

As with all modelling exercises it was necessary to make a number of justifiable assumptions to simplify the process (Starfield and Bleloch, 1991; Owen-Smith, 2007). Energy was selected as the most appropriate "currency" for the BRMP model based on results from Chapter 3 and other studies on browsers (Owen-Smith and Cooper, 1989; Atkinson, 1995). However, it is noted that all dietary requirements must be met or breeding rates could be affected even if energy and protein are in excess. Sodium in particular has been identified as potentially limiting in black rhino due to absorption rates (Clauss *et al*., 2006b).

Total daily dry mass intake was capped at a maximum of 35 kg (Marcus Clauss *pers. comm.*). Hence, daily biomass intake exceeded the values of 1.5-2 % body mass from the work of Foose (1982) and Owen-Smith (1988) but was in line with dry mass intake of approximately 25-30 kg indigenous browse recorded from bomas (Ghebremeskel *et al.*, 1991; Atkinson, 1995; Maddock *et al*., 1995). Recent findings support the concept of a daily biomass limit, as rhino were not found to compensate for a declining diet quality with increasing food intake (Meyer *et al*., 2010) as had previously been suggested for hindgut fermenters (Janis, 1976).

As noted by Meyer *et al*. (2010) fat storage could provide an additional energy source during nutritionally limiting periods, as observed in white rhinos (Shrader *et al*., 2006). This would have particular relevance in areas with availability of high quality resources such as forbs during the wet season. Fat storage was excluded from the BRMP model for simplicity, given the low proportion of high quality resources in rhino diet at Tswalu and high availability of *A. haematoxylon* as a dry season resource.

Weekly diet selection by rhino was based on a simple ranking system, following the kudu habitat suitability model HABPOPUL (Owen-Smith, 2007). This was considered sufficiently representative of seasonal black rhino diet selection for the purpose of habitat capacity projections. Total foraging time could not be recorded at Tswalu as much of black rhino feeding occurs at night (Goddard, 1967). In reality, foraging time is likely to be adapted throughout the seasonal cycle in response to changes in food quality and availability (Owen-Smith and Cooper, 1989). However, this parameter was not found to greatly affect the fundamental suitability of different habitat types.

Rhino density projections are based on available vegetation biomass measurements made by Beck in 2001. These formed the most recent comprehensive data set available for all the different habitat types; however, it is possible that changes in vegetation composition and structure may have occurred over the intervening years. The browsing impact of other herbivores on available vegetation biomass was not included in the model. Competition for *A. haematoxylon* would be the main inter-specific factor influencing the rhino population. However, bites from other browsing herbivores species were infrequently detected on *A. haematoxylon* during data collection (*pers. obs.*). More in-depth analysis of browsing herbivore specificity for woody plant resources in relation to chemical and physical defences would form an interesting topic for further research at Tswalu.

Fixed estimates of carrying capacity for herbivores, particularly in semi-arid environments where there is great variation in annual rainfall, have been rightly criticised for their inaccurate assumption of a persistent equilibrium between annual vegetation production and herbivore consumption (MacLeod, 1997). The BRMP model is based on the adaptive resource use approach, in line with the argument of Illius and O'Connor (2000), that animal numbers are regulated in a density-dependent manner by the limited resources which are utilized in the dry season. However, it is noted that the influence of stochastic changes in rainfall patterns on deciduous leaf retention during the early dry season could alter habitat capacity between years. Reduced availability of leaf matter on deciduous species in the early dry season in low rainfall years could result in earlier consumption of *A. haematoxylon*.

Hence, it is emphasised that recommended rhino density projections are to be viewed as thresholds for potential concern, rather than a fixed long-term measure of "ideal" animal numbers. Additionally, it is noted that increased intra-specific aggression could still occur below the projected densities for nutritional restrictions due to social pressures (Adcock, 1994; Linklater *et al*., 2010). The complex relationship between black rhino habitat capacity, home range size and social influences is not well understood (Lent and Fike, 2003; Reid *et al*., 2007; Linklater and Hutcheson, 2010; Linklater *et al*., 2010; Slotow *et al*., 2010).

Conclusions

The catalyst for this exercise was to provide managers at Tswalu with information to guide decisions about management of the rhino population. Recommended density projections have been produced to achieve this, under the caveats detailed above. Perhaps the most important finding is that a large proportion of the reserve was identified as unlikely to support maximum rates of reproduction. However, a mean density of around 0.13 rhinos/km^2 was projected by the model for *M. incanum* and *H. burchelli* shrubveld, indicating there is still some room for population growth above 0.09 rhinos/km^2 recorded during the data collection period.

An adaptive management approach could be used to test the real-world accuracy of model outputs. If the rhino population is allowed to continue to increase, density dependence effects should be observed just above the recommended rhino densities as nutritional limitations begin to impact breeding performance. To maintain a maximally-breeding population, management should then intervene and remove animals (Okita-Ouma *et al*., 2007; Patton *et al*., 2008). Individual female inter-calving intervals should be monitored to allow detection of density dependence impacts (Knight, 2001) in case this occurs below the projected rhino densities.

Managers can test the recommended densities produced by the BRMP model by comparing the biomass of *A. haematoxylon* left at end of each dry season with the projected model biomass remaining. Limited availability of *A. haematoxylon* biomass at the end of the dry season indicates that the rhino population is reaching capacity. Establishing an annual monitoring programme to assess the amount of *A. haematoxylon* biomass remaining at the end of the dry season could thus provide a simple vegetation-based indication of rhino numbers reaching maximum productive capacity.

The novel concept originating from this research is the idea of managing black rhino population densities to maximise individual female reproductive performance, considering spatial and temporal availability of key resources. The scenario at Tswalu, with a single semi-evergreen *Acacia* species forming the key resource, is acknowledged as unusually simplistic. However, conceptual findings from this modelling exercise can be extrapolated for rhino populations in other areas. Female reproductive output may be maximised by managing population densities around individual energy requirements from key resources during the critical late dry season. Hence, a rapid technique to assess the suitability of new areas for re-introductions could be to gauge the potential key dry season resources. Consideration of seasonal restrictions in temporal and spatial resource availability when managing black rhino numbers may aid their conservation by maximising metapopulation growth rates.

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Figures and Tables

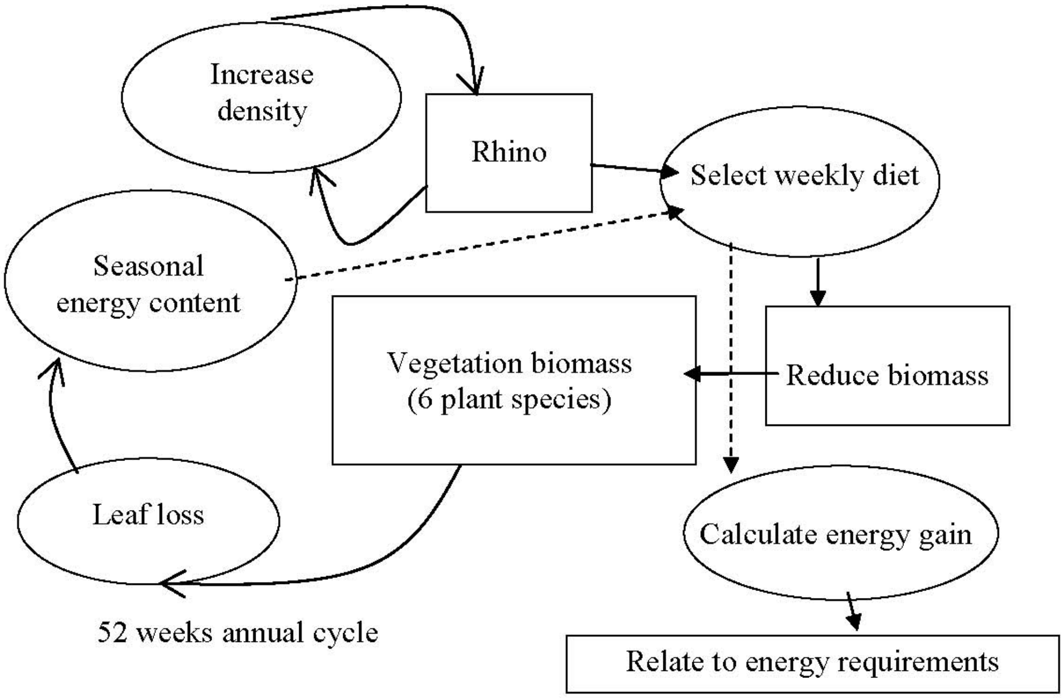


Figure 1. Diagrammatic representation of the structure of the GMM model developed to estimate habitat capacity for maximum productivity of black rhino populations (BRMP model).

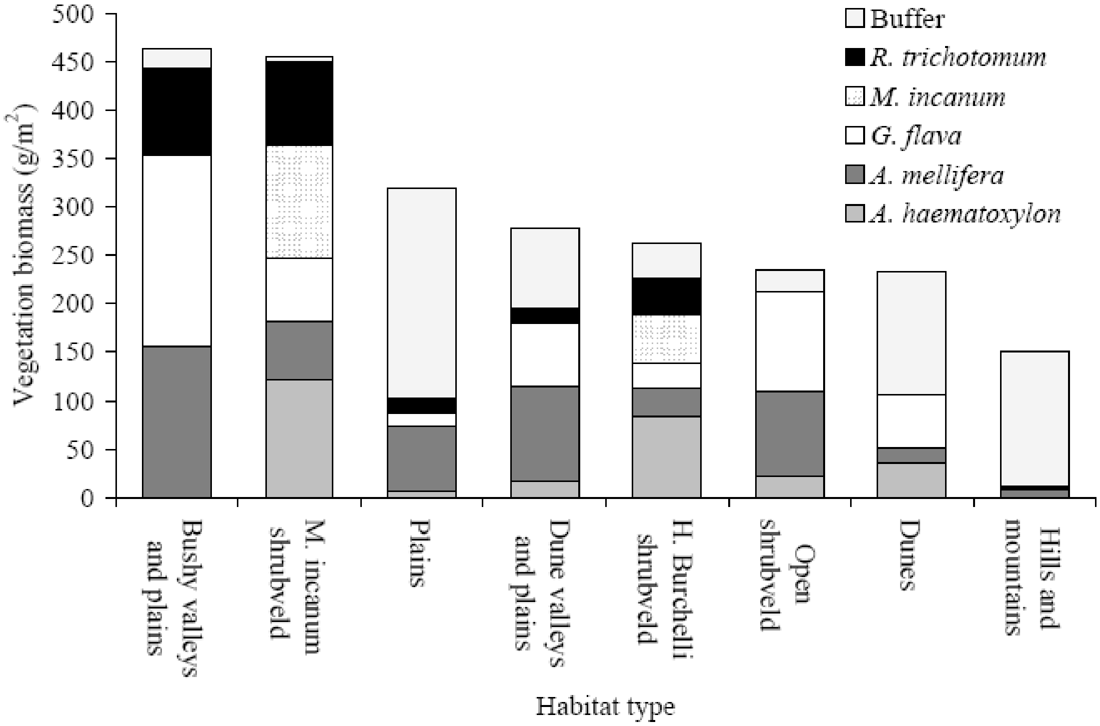
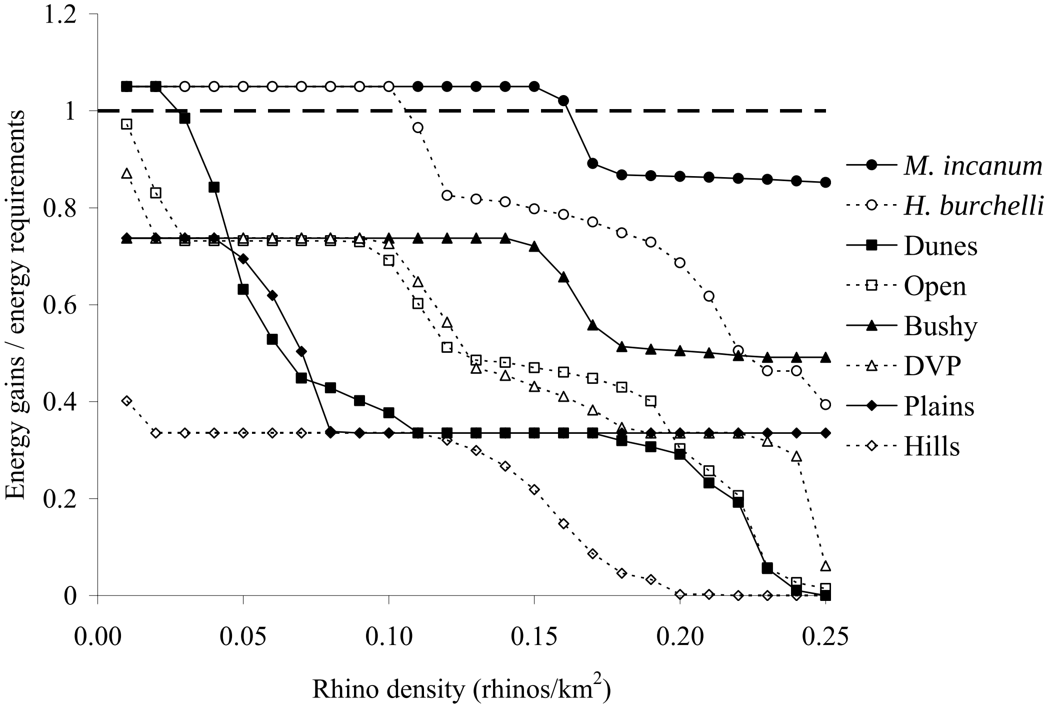
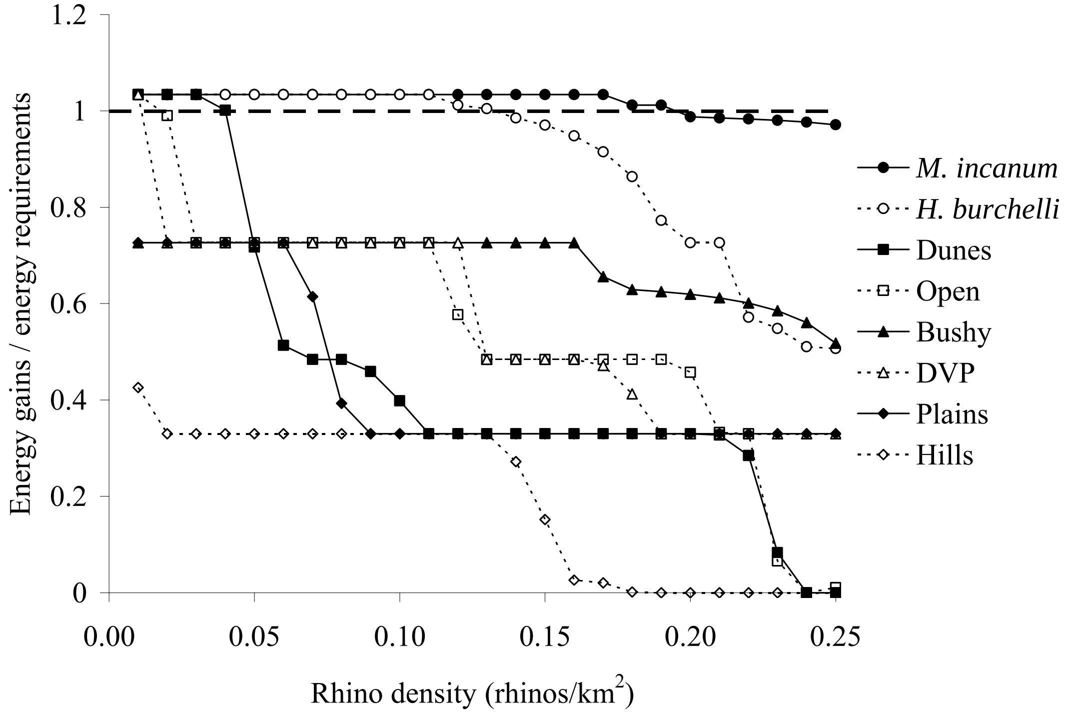


Figure 2. Biomass of the different plant species in the eight habitat types available to black rhinos at Tswalu.

a. Foraging time of eight hours



b. Foraging time of ten hours



c. Foraging time of twelve hours

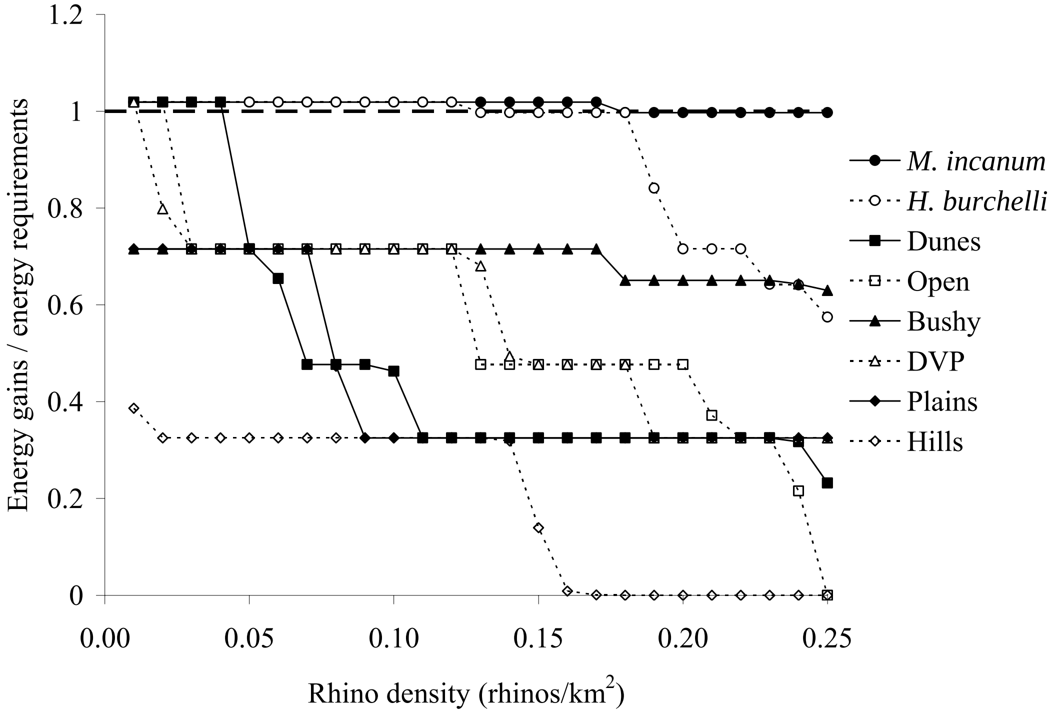
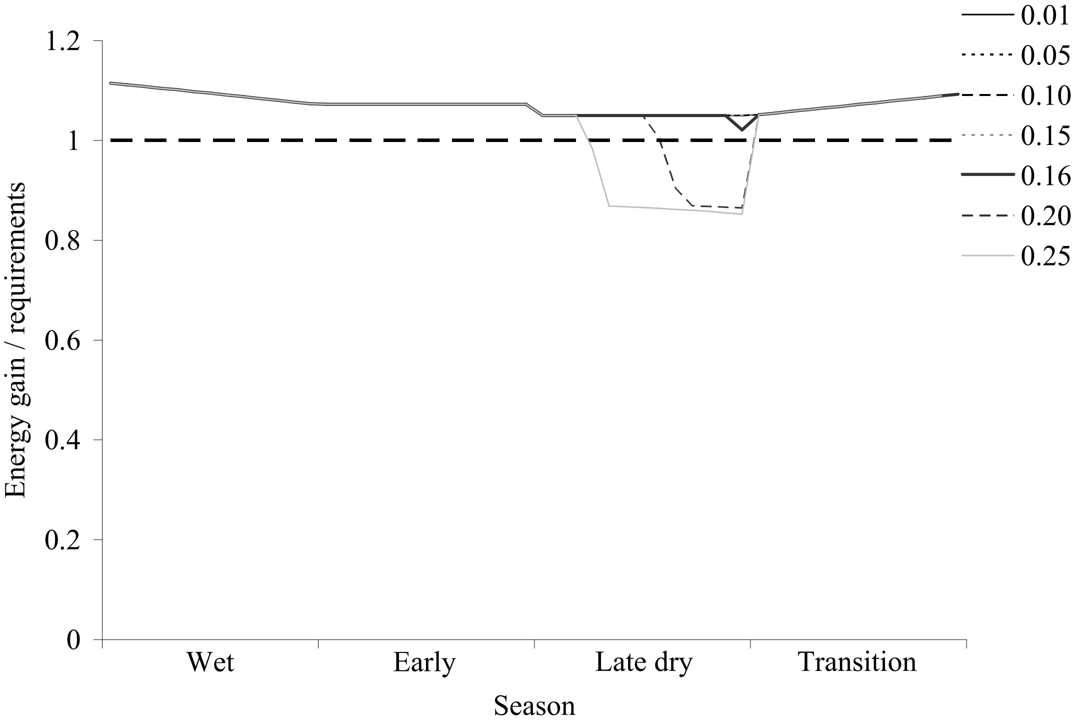
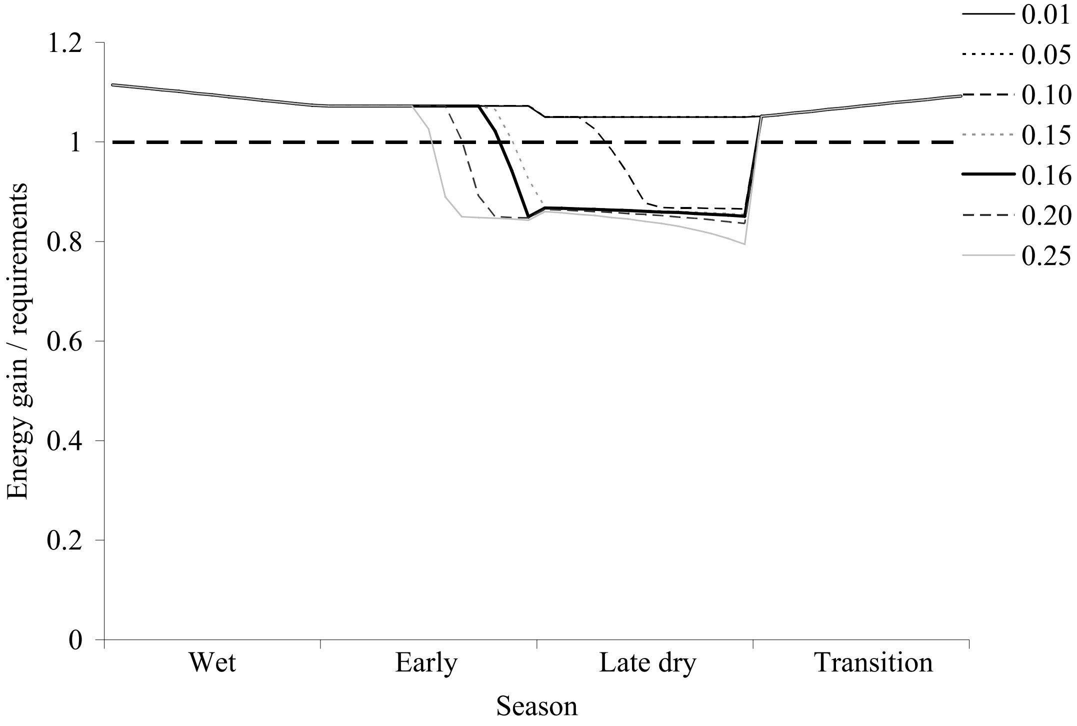


Figure 3. Relative growth potential (projected energetic gains again maximum reproductive requirements) for rhino population densities between 0.01 – 0.25 rhinos/km^2 within eight habitat types.

a. *M. incanum* shrubveld



b. *M. incanum* shrubveld with 50 % *A. haematoxylon* removal.



c. *M. incanum* shrubveld with 100 % *A. haematoxylon* removal.

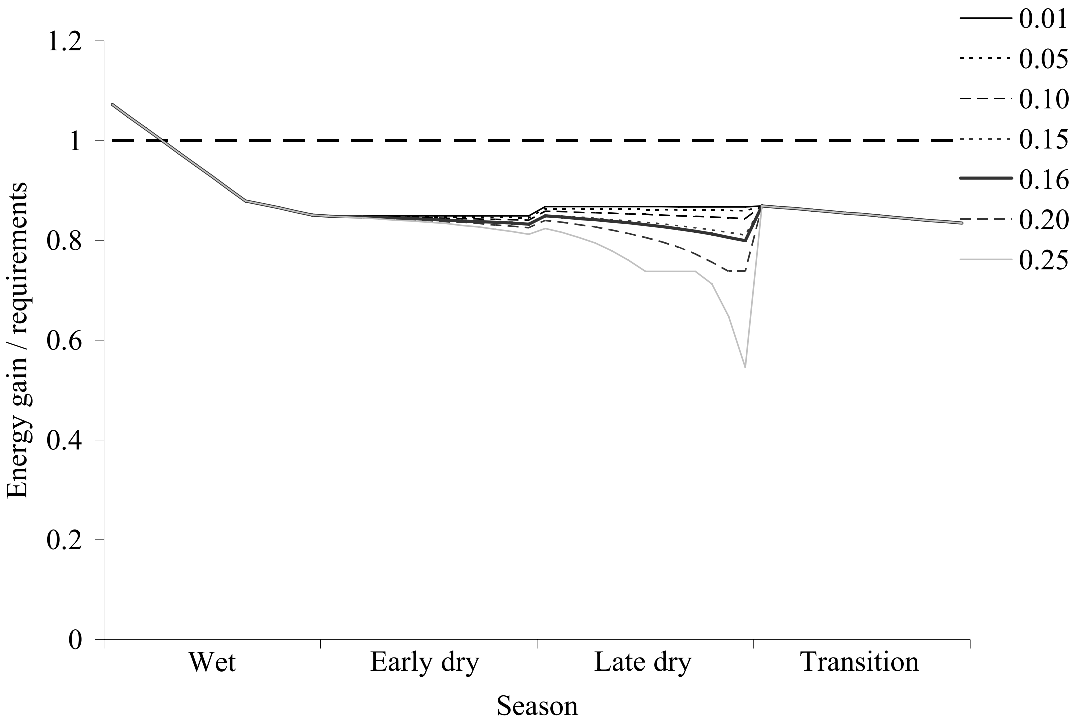
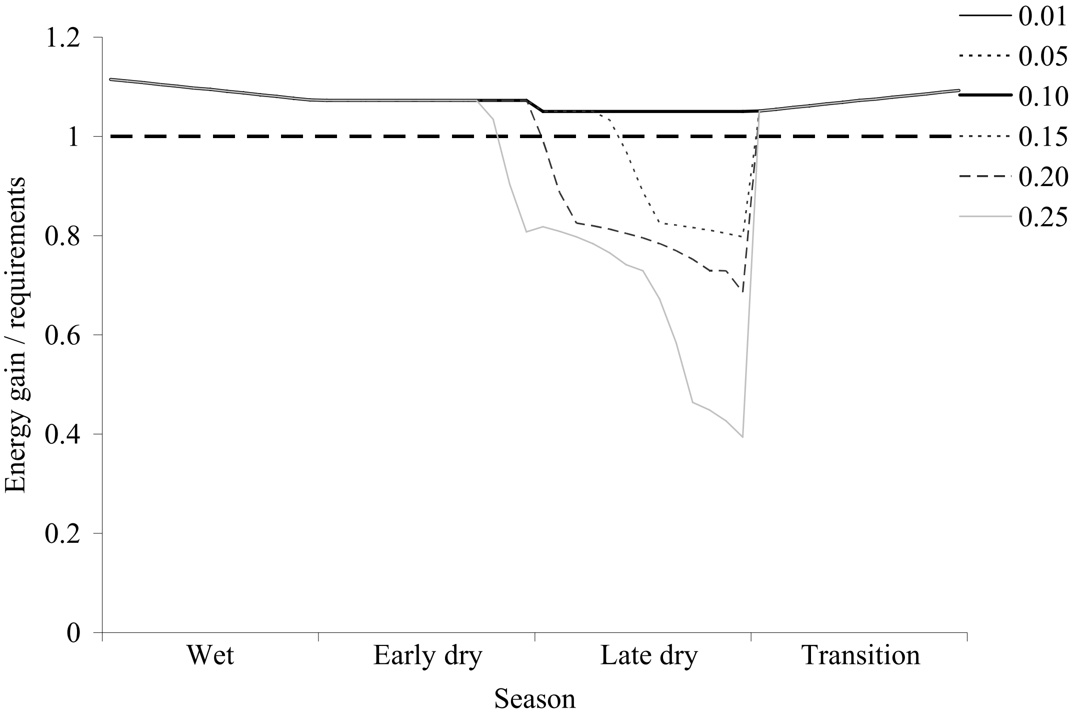
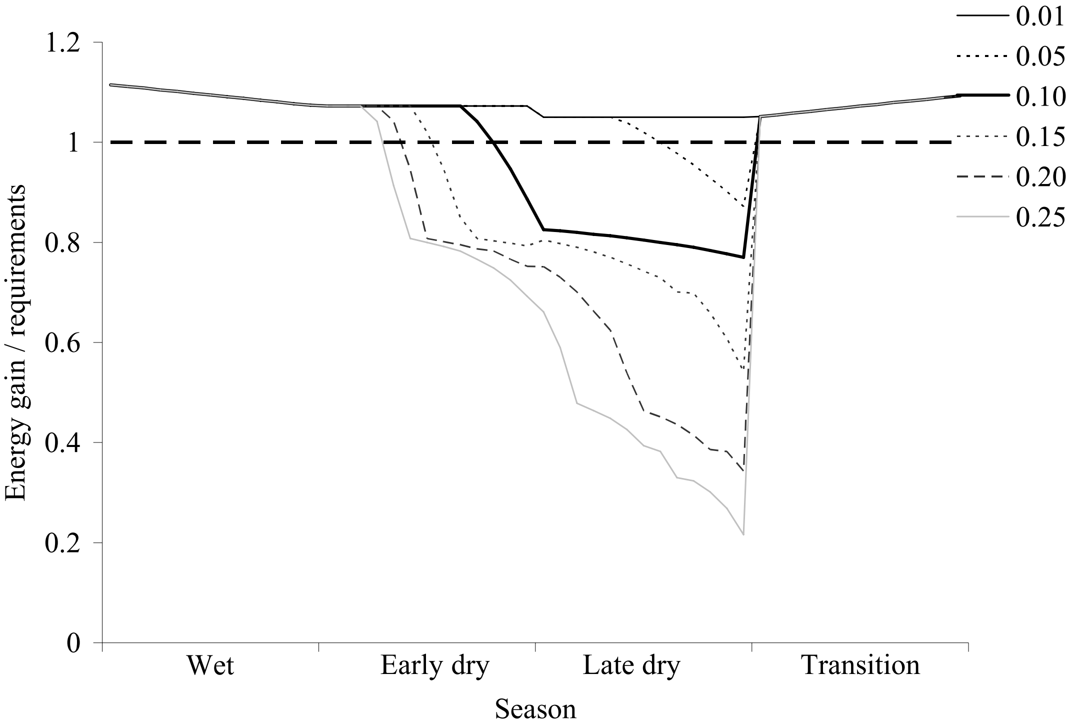


Figure 4. Weekly energy balance for rhino population densities between 0.01 – 0.25 rhinos/km^2 in *M. incanum* shrubveld with different scenarios of *A. haematoxylon* availability. Projected maximum productivity capacity in this habitat type was 0.16 rhinos/km^2.

a. *H. burchelli* shrubveld



b. *H. burchelli* shrubveld with 50 % *A. haematoxylon* removal.



c. *H. burchelli* shrubveld with 100 % *A. haematoxylon* removal.

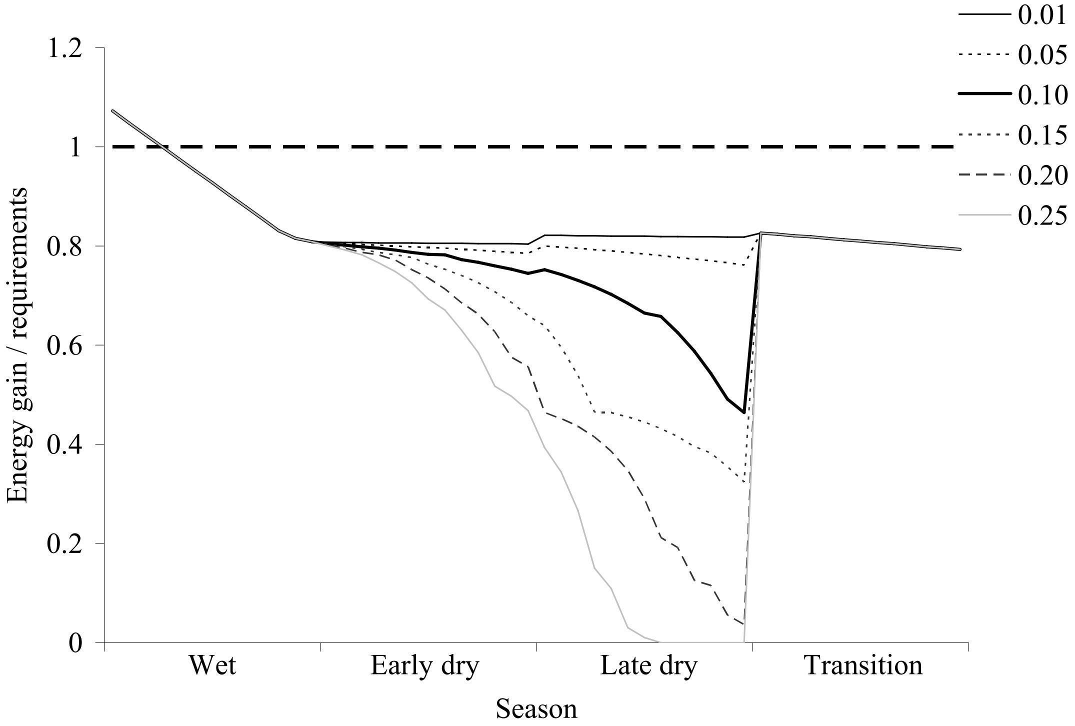


Figure 5. Weekly energy balance for rhino population densities between 0.01 – 0.25 rhinos/km^2 in *H. burchelli* shrubveld with different scenarios of *A. haematoxylon* availability. Projected maximum productivity capacity in this habitat type was 0.10 rhinos/km^2.

Table 1. Black rhino density within the Korannaberg section of Tswalu from January 2004-December 2005 calculated as individual 95% MCP home ranges intersected with habitat types from the vegetation map of van Rooyen (1999).

Habitat type	No. of rhinos	Area (km^2)	Rhino density (Rhinos/km2)
M. incanum shrubveld	4.7	38.5	0.123
Open shrubveld (Open)	2.9	39.2	0.075
H. burchelli shrubveld	4.0	54.2	0.073
Dunes	2.4	51.4	0.047
Plains	1.3	74.4	0.017
Dune valleys and plains (DVP)	1.4	146.7	0.009
Bushy plains and valleys (Bushy)	0.3	49.8	0.006
Hills and mountains (Hills)	0.0	25.6	0.000
Mean *M. incanum* and *H. burchelli* shrubveld	8.7	92.7	0.094
Mean other	8.3	387.2	0.021
Mean all	17.0	479.9	0.035

Table 2. Food type parameters for the five plant species observed at Tswalu and an additional buffer resource.

	G. flava	*A. mellifera*	*A. haematoxylon*	*M. incanum*	*R. trichotomum*	Buffer
dOM Conc$_{\text{(wet)}}$	0.49	0.49	0.50	0.50	0.43	0.30
dOM Conc$_{\text{(early dry)}}$	0.32	0.35	0.47	0.45	0.33	0.30
dOM Conc$_{\text{(late dry)}}$	0.22	0.33	0.48	0.46	0.30	0.15
dOM Conc$_{\text{(transition)}}$	0.31	0.34	0.49	0.44	0.27	0.20
I_P Eating rate (g/min)	81	94	99	64	60	90
Leaf attrition rate (week)	0.07	0.07	0	0	0.07	0.07
Onset of leaf fall (week)	12	12	0	0	20	12
Leaf:twig	0.45	0.25	0	0	0.34	0.33

7. CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Conclusions

The purpose of this research project was to increase understanding of factors affecting habitat capacity for black rhino, so as to guide management for maximum meta-population growth rates and facilitate species recovery. Hence, the overall aim was to gather data to develop a conceptual model of how seasonally adaptive resource use could influence maximum productive habitat capacity. The underlying premise was that it is the quality and quantity of key resources available in the late dry season which determines the population size of black rhino at which the reproductive output is maximized.

Maximum productive habitat capacity was conceptualised as the highest population density where nutritional quality of the diet allowed females to meet reproductive requirements throughout the entire seasonal cycle. This provides an alternate approach to the set estimate for Maximum Productive Carrying Capacity as 75 % of Ecological Carrying Capacity recommended to date (Emslie and Brooks, 1999; Emslie, 2001).

Hence, the specific objectives of the field research component of this project were;

1. To document the seasonal changes in plant species contribution to the diet and relate black rhino diet selection to plant phenology and chemistry.
2. To determine resultant seasonal changes in the nutritional gains of female black rhinos and compare with estimated nutritional requirements for reproduction.
3. To quantify the growth response of the main dry season resource, *Acacia haematoxylon*, to simulated browsing by black rhinos.
4. To establish seasonal habitat selection and use in relation to the distribution of seasonal dietary resources.

Results from chapter 2 highlight the low number of woody plant species forming black rhino diet and found that, in common with other rhino diet studies, *Acacia* and *Grewia* species composed the majority of the diet (Goddard, 1968;

Joubert and Eloff, 1971; Mukinya, 1977; Kotze and Zacharias, 1993; Emslie and Adcock, 1994; Oloo *et al.*, 1994; Bhima and Dudley, 1996; von Holdt, 1999; Muya and Oguge, 2000; Ganqa *et al*., 2005; Ndlovu and Mundy, 2009). More importantly, this chapter emphasizes the value of *Acacia haematoxylon* as a dry season dietary resource for black rhino at Tswalu. Rhino diet contained over 70 % *A. haematoxylon* during the late dry season in both years. Although the proportional contribution of woody plant species in individual rhino diet varied, the acceptance indices of main dietary species were high for *A. haematoxylon* for all individuals in the early dry, late dry and transition seasons. *Acacia haematoxylon* was thus identified as the key resource for black rhino at Tswalu. Earlier studies on black rhino diet did not agree on the most influential factors influencing plant species selection (Hall-Martin *et al*., 1982; Loutit *et al*., 1987; Dierenfeld *et al.* 1995; Ganqa *et al*., 2005; Muya and Oguge, 2000; Kipchumba, 2002; Buk and Knight, 2010). Results from Tswalu suggest that phenology is a strong determinant factor as semi-evergreen *A. haematoxylon* retains mature leaves throughout the seasonal cycle. Therefore, shoots of this species are higher in digestible organic matter and protein than those of deciduous species during the late dry season. What could not be identified during the data collection period, is the plant species which would form dry season diet in a scenario with lower availability of *A. haematoxylon* to individual rhinos.

Chapter 3 builds on the above information about seasonal proportions of different woody plant species in rhino diet to estimate energy and protein gains at different times of year. Findings confirm the dependence on *A. haematoxylon* as the key resource during the late dry season, based on the major contributions this single species made to energy and protein gains. Consumption of *A. haematoxylon* meant that there was a relatively small decline in diet quality during the dry season in comparison with wet season gains. Furthermore, estimated nutritional gains were in excess of reproductive requirements throughout the year, in line with predictions relating reproductive success to individual nutritional status at Tswalu. Hence, the rhino population at Tswalu remained below the conceptual maximum productive habitat capacity during the data collection period. As predicted from other analysis on browsing herbivores (Bryant *et al*., 1980; Owen-Smith and Novellie, 1982; Owen-Smith and Cooper, 1989; Atkinson, 1995), projected energy gains were closer to requirements than protein throughout the year. Therefore, digestible organic matter was identified as being more likely to form the limiting nutrient and to form the more appropriate "currency" of the maximum productive habitat capacity model.

The clipping experiment described in Chapter 4 shows compensatory shoot growth by individual plants following shoot removal in comparison to control plants. Biomass removal from *A. haematoxylon* in all seasons caused an enhanced growth response during the following growing season. In fact, the compensatory growth response, particularly from epicormic resprouts on trees taller than 2 m following severe browsing impact, meant that available *A. haematoxylon* biomass could be increased in the short-term. The contribution of *A. haematoxylon* to rhino diet declines during the early growing period, as deciduous species increase in dietary importance during the time of new leaf production. Hence, browsing pressure is reduced during what appears to be the most vulnerable period for tree growth, which may aid a facilitatory relationship between black rhino and *A. haematoxylon* at Tswalu. This is the first experiment to test whether browsing by black rhino could have a facilitatory impact on a key woody plant species. However, the longer-term impacts of sustained browsing pressure under unpredictable rainfall conditions (Hall-Martin *et al*., 1982; Brett, 2001) could not be projected from this short-term experiment.

Analysis of rhino home range locations in chapter 5 shows that large areas of the reserve were not utilised. Rhino's home ranges were focussed around *M. incanum* and *H. burchelli* shrubveld, which contain greater biomass of *A. haematoxylon* than other habitat types. Perhaps more importantly, patterns of habitat selection during the dry season were selective for these two shrubveld habitat types. Conversely, habitat use was not selective under conditions of greater and more homogenous food resource availability during the wet season when deciduous species retained leaves. These findings further emphasise the importance of *A. haematoxylon* as the key resource influencing rhino's movements during the dry season. Results from this chapter also emphasise the importance of considering impacts of seasonal variation in resource availability when assessing habitat use and selection by black rhino. Again, the omission from this chapter for understanding habitat capacity for black rhino at Tswalu is the inability to predict how future patterns of habitat selection will change at increased rhino density.

Results from field research into black rhino diet, nutritional gains, plant growth response and habitat selection in different seasons all accentuate the importance of *A. haematoxylon* as a key resource during the dry season. Therefore, the aim of Chapter 6 was to combine data gathered in the above chapters, so as

5. To develop a habitat capacity model to project recommended densities for maximum productivity of a black rhino population, incorporating seasonal changes in resource availability and quality.

Model projections indicate that there is a wide range in suitability of different habitat types for black rhinos at Tswalu, in line with the results from Chapter 5. The two habitat types with greatest biomass of *A. haematoxylon* are projected to have the capacity to support relatively high densities of black rhinos in comparison to other arid reserves (Buk and Knight, 2010). Model outputs indicate that females in three further habitat types could meet energetic requirements for reproduction but only at much lower densities. Four habitat types covering approximately 50 % of the whole reserve area are projected as being unsuitable for providing the maximum energetic requirements for females for reproduction throughout the year. Comparison of recommended rhino densities from model projections with 95% MCP estimates of rhino density in different habitat types followed similar patterns, providing validation for the model outputs.

The modelling exercise also provides an opportunity to simulate future scenarios and make projections of recommended rhino densities based on simulated declines of the key dry season resource. Projections for scenarios with 50 % decline in availability of *A. haematoxylon* cause late dry season energy gains to fall below reproductive requirements at lower population densities and earlier in the late dry season. Total removal of *A. haematoxylon* prevents rhinos from meeting energetic requirements for reproduction during the dry as energy gains from other plant species are not able compensate. Therefore, reduced biomass of this key resource due to sustained browsing (Hall-Martin *et al*., 1982; Brett, 2001) or low rainfall would be expected to have a significant negative impact on population size and breeding rates of black rhino at Tswalu. The limitation of the modelling exercise is the knowledge gap relating to which plant species will form rhino diet once *A. haematoxylon* is consumed. Rhino nutritional gains and hence reproductive potential during the dry season at increased density will be dependent upon the availability, chemical content and intake rate of these resources.

It is important to note that analyses in this thesis are based upon the unusual situation at Tswalu, with a single semi-evergreen *Acacia* species forming the key resource. However, it is possible to extend the concept of maximising growth rates via individual female nutrition and reproductive success to management of rhinos in other fenced reserves. The focus for future research should be to test the applicability of this approach in other areas with different vegetation components and seasonal variation in resource availability. It is suggested that in some areas, vegetation composition and plant species phenology and chemistry may be such that female rhino can never attain energy requirements for reproduction during the late dry season. However, in these environments, managing population density around key dry season resources should minimise physiological losses at this time of year. Thus this approach ought to help maximise reproductive rates within the specific ecosystem, even if it is less suitable for achieving maximum black rhino breeding success.

In areas with greater availability of high quality resources such as forbs during the wet season, fat storage may provide an additional energy source through drier periods (Shrader *et al*., 2006; Meyer *et al*., 2010). This aspect was excluded from the model for simplicity given the low proportion of high quality resources in rhino diet at Tswalu and high availability of *A. haematoxylon* as a key dry season resource. The low inter-calving intervals recorded from Tswalu indicate that high quality resources during the wet season are not essential for high reproductive rates. This finding further strengthens the concept of key dry season resources as a basis for population management.

Overall, this study has contributed to ecological theory by demonstrating an alternative approach to assessing maximum productive habitat capacity for black rhino. Individual female energetic gains are related to requirements for reproduction throughout the seasonal cycle, based on spatial and temporal availability of key dry season resources.

Management recommendations

Tswalu Kalahari Reserve

Results from this research emphasize the need for wildlife managers to consider key resources and implications of their spatial and temporal variation when assessing habitat capacity. In particular, the major outcomes of this research for management at Tswalu are:

1. Availability of *A. haematoxylon* has been crucial to the high reproductive success of the black rhino population since re-introduction as a source of energy and protein all year, but particularly during the late dry season.
2. Projections from the modelling exercise indicate that habitat types covering a large proportion of the eastern and central regions of the Korannaberg section are less suitable for black rhinos. These areas contain low *A. haematoxylon* biomass and are not projected to provide energy gains necessary to support maximum reproductive performance for females during the dry season. These include dune valleys and plains, plains, bushy valleys and plains, and hills and mountains habitat types.
3. Rhino densities for maximum production of offspring could potentially be elevated by about one third above those prevailing during the study period within the *M. incanum* and *H. burchelli* shrubveld habitat types.
4. Suitability of the dunes habitat type at Tswalu for black rhino is questionable. Results indicate that energy gains during the dry season may not meet the additional energetic expense required to negotiate steep sandy dunes.

However, this habitat type has potential to form a spatial buffer which provides submaintenance energy requirements, thus enabling rhinos to starve more slowly during drought years (Owen-Smith, 2002).

Accordingly, if the aim is to manage black rhino at Tswalu for maximum productivity in terms of progeny, as per rhino conservation goals, the management recommendations are;

1. To maintain the local population below recommended densities for maximum productive habitat capacity by removing excess individuals as part of a *D. b. bicornis* meta-population management plan. The priority habitat types for management intervention have been identified as *M. incanum* and *H. burchelli* shrubveld.
2. To initiate an annual monitoring programme of availability of *A. haematoxylon* biomass at the end of the dry season. Limited availability of *A. haematoxylon* could act as an early indication of impending nutritional restrictions.

Additionally, the following individual-based monitoring of rhino is recommended;

3. To continue to monitor rhino body condition as a physiological indicator of seasonal nutritional status (Reuter and Adcock, 1998) with a focus on the late dry and early growing seasons when nutritional limitations are most likely.
4. To continue to record and review age at first calving and inter-calving intervals of individual females as indicators of density dependent impacts (Knight, 2001).
5. To relate inter-calving intervals with model projections of recommended rhino density to test efficacy of the model outputs (Chapter 6).
6. To introduce spatial analysis of individual sightings data to monitor habitat use during the dry season. Reduced availability of key resources in *M. incanum* and *H. burchelli* shrubveld may be indicated by use of other areas, particularly dunes habitat types, at this time (Chapter 5).

Black rhino conservation

The novel concept originating from this research is the idea of managing black rhino population densities to maximise individual female reproductive performance, considering spatial and temporal availability of key resources. It is intended to help maximise population growth rates by providing an estimate of rhino density at which reproductive rates are not affected by declines in female body condition (Rachlow and Berger, 1998).

Hence, findings from this research could be applied more broadly as follows;

1. Browse availability assessments for black rhino could be more focussed on spatial and temporal availability of plant species forming key resources at the most limiting time of year. This would allow habitat capacity for existing black rhino populations to be projected based upon individual female's energetic requirements for reproduction. Results from this project indicate that this may help minimise inter-calving intervals and hence maximise population growth rates.
2. Outcomes from this research indicate that key resources for black rhino are likely to consist of semi-evergreen or evergreen species, i.e. those retaining higher digestible organic matter content during the late dry season. Other studies suggest that plants from the *Euphorbiaceae* family and other succulent species (Hall-Martin *et al*., 1982; Loutit et al, 1987; Ganqa *et al*., 2005) could form key resources for black rhinos elsewhere.
3. The BRMP approach shows potential to provide a simple indicator of the suitability of new areas for black rhino re-introductions. Assessments of spatial and temporal availability of key resources may provide a quick technique to measure habitat quality for black rhinos. This could provide an indication of the extent of resources available to support black rhino reproduction under nutritional restrictions during the most resource limiting period.

4. Projections of rhino densities from the BRMP model show the extent to which individual females can meet seasonal energetic requirements for reproduction in different areas. Hence by using BRMP, habitat suitability for black rhino can be evaluated on projected population growth rates as well as future population size. Therefore, the BRMP approach could work as a decision making tool to help rate rhino habitat quality for re-introductions with high population growth rates. There is also potential to use this approach to guide funding and management of existing areas, in association with other vital considerations such as rhino security.

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Appendix I. Black rhino habitat capacity model programme in True Basic Bronze Edition.

Contact the author on korannaberg@gmail.com for details of the model programme.

Appendix II. Calculations of rhino eating rate made from video recordings

Data for the eating rate (I_P) of the five woody plant species making up 80% of the diet of black rhino at Tswalu throughout the year were calculated as follows;

1. Bite mass

Twenty twigs of *A. haematoxylon*, *A. mellifera*, *G. flava*, *R. trichotomum* and *M. incanum* in three diameter size classes (0-1mm, 1-3mm, 3-6mm) were collected in the wet season when mature leaf retention was greatest. Twigs and leaves were stored in paper bags and air-dried before the mass was obtained on an Ohaus Precision Plus TP4000D scale calibrated to an accuracy of three decimal places. The dry mass values and the associated twig diameter values for each species were regressed and the diameter (x) converted to twig and leaf dry weight (y) using equations of the type $y = ae^x$ (Basile and Hutchings, 1966).

For five days in each season in both years the diameter of all shoots within a bite on each plant species were measured and categorised into size classes (0-1mm, 1-3mm, 3-6mm). Mean bite mass for each plant species in each season could then be calculated from mean diameter size of twigs in bites from each plant species. The mass of each leaf and twig fraction was also used to calculate a maximum leaf:twig (=wet season leaf mass / wet season twig mass) ratio for each plant species, this was then modified dependent upon the mean proportion of mature leaves recorded as present for each species in different seasons.

$$M_P = \sum n_1 m_{1\ldots}\ n_3 m_3$$

Bite mass for a plant species (M_P) was the sum of the total mean number of twigs in a diameter class (n) and the value for mean twig mass (m).

2. Bite time

It was not possible to safely observe rhino browsing directly and record temporal data on browsing behaviour. Therefore, video recordings were made of black rhino browsing during the evenings over a period of two weeks in November 2005. Successful footage was taken for three of the focal rhino on two occasions each. The footage was then watched back and the time of each bite for each species (from the start of manipulation of a branch until the end of mastication or initiation of movement to the next feeding patch) was recorded in seconds.

$$B_P = 60 / t_P$$

Number of bites per minute (B_P) was calculated as 60 seconds / mean time per bite (t_P).

3. Eating rate

Therefore, the bite rate for a plant species (I_P) (g/min) was the product of bite mass (M_P) (g) and number of bites per minute (B_P) (1/min).

$$I_P = M_P B_P$$