FEEDING PATCH SELECTION BY WHITE RHINOCEROS (*Ceratotherium simum simum*) IN THE SONGIMVELO NATURE RESERVE, SOUTH AFRICA

by

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DECLARATION

“I hereby declare that the dissertation submitted for the degree M Tech: Nature Conservation, at Tshwane University of Technology, is my own original work and has not previously been submitted to any other institution of higher education. I further declare that all sources cited or quoted are indicated and acknowledged by means of a comprehensive list of references”.

M.B. Wardjomto

DEDICATION

This study is dedicated to

Ange and Nathan

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ABSTRACT

The selection of food by large herbivores and the factors that affect this selection are important considerations in the management and conservation of species of high conservation value as well as their habitat. White rhinoceros (*Ceratotherium simum simum*) were introduced in the Songimvelo Nature Reserve (SNR), an area with limited habitat for this species due to its rugged and mountainous topography. This study sought to determine the factors driving the feeding of the white rhinoceros (WR) at a patch level in the reserve. White rhinoceros were observed during the late wet and the late dry seasons, and at every feeding patch identified, the grass species were identified, the attributes of the plants as well as the characteristics of the patch were recorded. White rhinoceros showed selection of available habitat types during the late wet season (they selected Open Low Woodlands and Shrublands and avoided Oldlands) whilst they used all habitats in proportion to availability during the late dry season. The most dominant grass species in the open low woodlands was *Heteropogon contortus* and was consequently the most selected during both seasons. At the patch level, species composition and mean tuft diameter were the most important factors influencing selection. Grass species composition, density and mean tuft diameter within seasons were the best drivers of species selection. Selection of food at patch level can result in a specific pattern of distribution by WR in SNR between seasons and have implications in the management of the area.

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GENERAL INTRODUCTION

1.1 BACKGROUND

In the wild, adequate quantities of usable resources are necessary to sustain animal populations (Manly *et al.*, 2002:1). However these resources are generally unevenly distributed in time and space and often found in patches (Zhang *et al.*, 2009:79), which large herbivores are confronted with. This uneven distribution of resources may, therefore, dictate a herbivore's movement, choice of specific foraging habitats, as well as diet (Albon & Langvatn, 1992:502; Wilmshurst, Fryxell & Hudson, 1995:209). It is therefore important to understand the underlying drivers of resource selection in order to guide and inform conservation decisions (Conneely, 2011:1) and understand the local ecology of species of high conservation value.

For large herbivores in the wild, food is the most important resource; herbivores have a choice on where to feed and what to feed on. This decision is controlled by a set of factors that are either interactive (e.g. forage biomass, nutritive quality, and plant morphology), non-interactive (e.g. topography, regional climate, geomorphology, physical barriers, and water location) or both. This decision is also governed by the patchy and uneven distribution of food in time and space (Senft *et al.*, 1987). This selection process has been observed to follow a hierarchical pattern where selection occurs at high, intermediate and low levels (Mårell & Edenius, 2006:413). The decisions made at a given level are trade-offs between forage quality and quantity (Stephens & Krebs, 1986:6) or predation and energy gain

(Mårell & Edenius, 2006:413). So when studying resource selection by animal, the importance of scale cannot be overemphasized (Manly *et al.*, 2002:2; Senft *et al.*, 1987:789).

1.1.1 Resource selection

Morrison and Hall (2002:50) defined a resource as any biotic and abiotic factor directly used by an organism (e.g. food, nutrients, water). Resource ecology is consequently defined as the ecology of trophic interactions between consumers and their resources including competition, plant-nutrient relationships, and predator-prey relationships such as herbivory, parasitism and carnivory (Van Langevelde & Prins, 2008:1). Resource ecology therefore entails the study of all aspects related to the selection of a resource by an animal at different spatial scales (feeding site selection, feeding patch selection, and habitat selection). Studying resource selection, therefore, involves looking at both habitat selection as well as the feeding pattern of the species of interest.

Several methods have been developed to assess habitat selection by comparing attributes of used *vs* unused locations. Habitat selection studies usually make use of a comparative evaluation between habitat use and habitat availability in order to show how animals select resources in the environment where they find themselves (Manly *et al.*, 2002:2). Available habitat however is complex to determine. Habitat availability is defined as the accessibility and procurability of physical and biological components of a habitat by animals (Krausman, 1999:86). In other words, if an animal cannot access the resources within a specified habitat, that resource is not available to the animal and consequently that habitat is not available. Estimating resource selection by animals can reveal what habitat features are selected or avoided in the landscape. The Resource Selection Function (RSF) is the most recent method used to study resource selection (Boyce *et al.*, 2002:281). Resource selection can be used to analyse the intensity of resource use and predict the distribution of a particular species by combining information of a point data and environmental variables

The discipline of landscape ecology on the other hand, the science that studies the development and dynamics of spatial heterogeneity (Senft *et al.*, 1987:789), addresses how landscape elements or patches are configured in relation to one another in an overall mosaic and how such landscape structure influences a variety of ecological patterns and processes (Wiens & Milne, 1989:87). This concept, in essence, is about habitat heterogeneity. The concept of patch dynamics comes in to provide a platform for understanding the concept of ecological heterogeneity in space and time, and the concept of interaction of species with all the components of the landscape (Stalmans *et al.*, 2001:390).

1.1.2 Ecological hierarchies

Ecological mechanisms in general are scale dependent (Wiens & Milne, 1989:88), and resource selection is dependent on this scale. The process of resource selection is one of the processes driving the distribution of species and populations in an area. And this process has been observed to occur at different spatio-temporal levels (Bailey *et al.*, 1996:388; Senft *et al.*, 1987:790; WallisDeVries, Laca &

Demment, 1999:356), due to the variation in the availability and quality of food in space and in time. Food resources of large herbivores have been studied at several scales level which can be broadly classified from large to specific (Senft *et al.*, 1987:790). Bailey and Provenza (2008:10) described seven spatio-temporal scales (Table 1.1) that were adapted from Bailey *et al.* (1996:388) and Owen-Smith (2002:39) namely: Bite, feeding station, food patch, feeding site, camp and home range. Selection at these different scales may be influenced by several factors. At feeding site level, selection may be influenced by topography, distance to water and predation, whereas feeding patch level selection may be influenced by forage quality, forage abundance, plant species and social interaction (Bailey & Provenza, 2008:25). It is also apparent that selection at the above-mentioned-scales may be influenced by the size of the animal as well as its feeding habit. A browser may for example identify a single tree as a patch while a grazer may identify a plot of variable size as a feeding patch.

Table 1.1: Temporal and spatial scales useful for describing and evaluating foraging behaviour of large herbivores.

Spatial level	**Spatial resolution of selected unit[1]**	**Temporal interval between decisions**	**Defining behaviours or characteristics**	**Response variable**	**Vegetation entity**
Bite	0.0001 – 0.01 m^2	1 – 2 sec	Jaw, tongue and neck movements	Bite size	Plant part
Feeding station	0.1 – 1 m^2	2 – 120 sec	Front-feet placement	Bite rate	Plant (grass tuft, shrub)

Food patch	1 – 10 000 m^2	1 – 30 min	Animal reorientation to a new location. A break in the foraging sequence	Feeding duration	Clump of plants
Feeding site	1 – 10 ha	1 – 4 h	Grazing bout	Foraging movements	Plant species association
Daily range	10 – 100 ha	12 – 24 h	Area where animals drink and rest between grazing bouts	Daily time allocation	Landscape unit
Seasonal range	100 – 1000 ha	3 – 12 m	Migration	Metabolic allocation	Landscape type
Lifetime range	> 1000 ha	Several years	Dispersal or migration	Life history schedule	Geographical region

Source: Bailey and Provenza (2008:10) as adapted from Bailey *et al.* (1996:388) and Owen-Smith (2002:39).

Several studies have looked at the patch selection of large herbivores and in the process provided a definition of a patch (Abeare, 2004:36; Bowers, 2006:15; Distel *et al.*, 1995:11; Ramp & Coulson, 2004:1053; Weckerly, 2005:630; Wilmshurst & Fryxell, 1995:297; Wilmshurst, Fryxell & Bergman, 2000:345). For large herbivores, a feeding patch can usefully be described as a nested hierarchy of aggregated resources (Senft, 1989:283), and the hierarchy theory provides a conceptual framework to direct the study of foraging by large herbivores across different spatial scales (Zhang *et al.*, 2009:80). Bailey *et al.* (1996:387) describe a patch as a cluster of feeding stations separated from others by a break in the foraging sequence when animals re-orient to a new location. They further describe a feeding site as a collection of patches in a contiguous spatial area that animals graze during a foraging bout; it may contain one or more plant communities. The most recent definition is from Prins and van Langevelde (2008:3) who define patches as regions that are more or less homogeneous with respect to a measured variable.

Perrin and Brereton-Stiles (1999:72) described the patch characteristics of white rhinoceros, depicting their selection of preferred feeding sites within the mosaic of the landscape and interaction with other grazers like the African buffalo (*Syncerus caffer*). Abeare (2004:30) investigated the dry season habitat and patch selection of African Buffalo using the Neu method and the k nearest-neighbour convex-hull (k-NNCH) model, and found that river density index and species preference index-3 where significant contributors to the model. The plant number scale (Westfall & Panagos, 1988) and canonical ordination was used by Bowers (2006:18) to floristically differentiate patches and compare forage patches against neighbouring control plots. Bowers found that feeding patches contained higher abundances of preferred forage species than did control patches. A similar approach was used by Zhang *et al.* (2009:80), where microhabitats were compared against control plots to determine the selection and abandonment of forage patches by wild giant pandas in winter. Giant pandas showed preference for gentle slopes and utilised old bamboo shoots in feeding sites, parallel with the predictions of the marginal value theorem. Le Corre *et al.* (2008:342), on the other hand, used the First-Passage Time Analysis method, which is based on the measure of foraging effort along a path, to study the multi-patch use by roe deer (*Capreolus capreolus*). They found that browse consumption was constant between the seasons but, browse on individual plant species varied. Ramp and Coulson (2004:1055) made use of the Ideal Free distribution (IFD) model to look at small-scale patch selection by eastern grey kangaroo (*Macropus giganteus*). They found that eastern grey kangaroos select for resources at the habitat scale but not at patch level. Wilmshurst *et al.* (1995:165) made use of an experimental approach where grass biomass was manipulated by mowing. They found that the rate of intake by wapiti is constrained by grass biomass and fibre content. These studies have all expressed the importance of examining the processes and factors driving the selection of feeding patches and habitat use.

1.1.3 Foraging theories

Laca (2008:85) suggests that the functional response is the cornerstone principle of all foraging models. This principle specifies the pattern of food intake with respect to food abundance and distribution. A number of foraging theories have been developed to predict what, when, and where a large herbivore would eat. Some of these theories can be grouped in the optimal foraging models (Stephens & Krebs, 1986:183), which include theories such as the marginal value theorem (Charnov, 1976:131). However, most optimal foraging theories were designed with predators in mind, and feeding of herbivores in general is different from that of predators in that for herbivores, search time and handling time are not mutually exclusive, but they are for carnivores (Spalinger & Hobbs, 1992:326). Fryxell, Fortin and Wilmshurst (2001:2) provide evidence that optimal foraging models can have reasonable success in predicting patch preferences by large herbivores. It has been hypothesized that generalist herbivores feed in sites with higher food quality or quantity, or both, following qualitative predictions of optimal foraging theory (Mårell, Ball & Hofgaard, 2002:854). Such predictions were also put forward by Stephens and Krebs (1986:25) who suggest that when resources are distributed in patches, a consumer should increase its intake rate in a high resource density patch. This will consequently slow down the consumer in such areas allowing for more time spent in patches of high food quality or quantity or both.

Optimal foraging models analyse the behavioural decision to optimise the net rate of intake. In other words, should a predator hunt for the prey encountered or skip and find another one? In the case of herbivores, should the forager stay in the current patch or look for another patch? The patch selection model / marginal value theorem is based on a net energy gain function that varies with time spent in a patch (Charnov, 1976:129; Searle, Thompson Hobbs & Shipley, 2005:420). The primary prediction of the patch model is that foragers should move to another patch when the instantaneous intake rates in any patch drops below the average rate of the entire habitat (Bailey & Provenza, 2008:16). This theory also predicts that the more widely-spaced patches are, the longer foragers would stay in each patch. In other words, an animal should stay longer in larger patches because they contain more food, and if the patches are more dispersed, animals may stay longer in the patch to compensate for long travelling. This is partly in line with the “clever ungulate model” (Owen-Smith & Novellie, 1982:160), which predicts that the greater the time invested to relocate, the less picky should a ‘clever’ animal be. In other studies, the Marginal Value Theorem failed to match its predictions mostly because there was no reliable way to determine the scale at which a herbivore perceives patches (Searle *et al.*, 2005:421). A browser may for example perceive a single tree or a whole stand as a patch.

The importance that the heterogeneity of resources play in the distribution and the survival of large herbivores in an area cannot be emphasized enough (Prins & van Langevelde, 2008:3). As a result of heterogeneity and interactions with other species and habitat characteristics, there are costs involved in herbivores moving between patches. They may include energy related cost, uncertainty to find a suitable patch with quality forage, topographical boundaries and the effect of predators (Skórka *et al.*, 2009:605).

1.1.4 Feeding ecology of white rhinoceros

White rhinoceros (*Ceratotherium simum* (Burchell, 1817)) are essentially bulk grazers (Skinner & Chimimba, 2005:527), that feed on large amounts of low quality short grass species to maximize quantity although quality is important (Melton, 1987:647; Owen-Smith, 1988:51). They are area-selective and choose to feed on lower-lying areas, in particular grassland types (Owen-Smith, 1973:134), as well as on the more palatable broad-leaved grasses and grass height of 25 – 60 mm from the ground (Owen-Smith, 1999:118; Pienaar & Du Toit, 2002:186). Owen-Smith (1975:378) found that they concentrate on the most nutritious grassland available and suggested that diversity may be an additional factor of choice as well as the availability of the species (Perrin & Brereton-Stiles, 1999:78; Shrader, 2003:6). In Hluhluwe iMfolozi Park (HiP) for example, they fed on grass species such as: *Heteropogon contortus*, *Panicum maximum*, *P. coloratum*, *Themeda triandra*, *Urochloa mosambicensis* (Owen-Smith, 1973:120; Shrader, 2003:40). In the Pafuri section of the Kruger National Park (KNP), white rhinoceros were reported feeding primarily on species such as *Cenchrus ciliaris*, *Enneapogon cenchroides*, *Eragrostis* *superba*, *Schmidtia pappophoroides*, and *Stipagrostis uniplumis* (Pedersen, 2009:49). Forbs form less than 5% of the white rhinoceros diet though these might have been accidentally ingested because of its wide mouth (Owen-Smith, 1973:124; Shrader, 2003:50). White rhinoceros have also shown seasonal variations in species and habitat use (Owen-Smith, 1973:120; Pedersen, 2009:49; Shrader, 2003:50) where they would switch between areas with grasses in the wet season and wooded areas in the dry season. Perrin and Brereton-Stiles (1999:76) found that during the dry season, white rhinoceros grazed in areas with low community diversity and consumed grass species according to their availability while avoiding unpalatable grasses. They also highlighted the preference of bottomlands by white rhinoceros during that particular season. White, Swaisgood and Czekala (2007:349) found that female white rhinoceros in the iMfulozi section of HiP prefer grassland habitats, utilising them significantly more than expected based on availability. The white rhinoceros is also water dependent (Bothma, Van Rooyen & Du Toit, 2002:149), using water for drinking and wallowing, and can drink as often as possible especially when large quantities of roughage have been ingested. Although they can go for up to four days without water in dry conditions (Pienaar & Du Toit, 2002:186), they would not venture too far away from water points which could affect habitat use. Perrin and Brereton-Stiles (1999:72) depicted the occurrence of facilitation between the white rhinoceros and African buffalos (*Syncerus caffer*) and suggested that buffalos grazed ahead of white rhinoceros consequently reducing grass height to provide access to white rhino. However this theory has been extensively challenged by Arsenault and Owen-Smith (2002:317) who suggest that facilitation may arise mainly during the growing season whilst interspecific competition predominates during the dormant (winter or dry) season. They also suggest that ungulates the size of buffalos and smaller do not appear responsible for large scale habitat changes in African savanna ecosystems, but grazing by white rhinoceros can transform tall grasslands into grazing lawns. In other words, white rhinoceros can be a facilitator for other herbivores such as reedbuck (*Redunca arundinum*) and waterbuck (*Kobus ellipsiprymnus*). Waldram, Bond and Stock (2008) qualified white rhinoceros of ecological engineers by observing that their removal affected fire by increasing fuel loads and fuel continuity.

1.1.5 White rhinoceros in Songimvelo Nature Reserve

Twenty white rhinoceros were first introduced in the Songimvelo Nature Reserve (SNR) in 1991, followed by a second introduction of five individuals in 1996. Since these introductions, the rhinoceros population has been intensely managed and monitored, resulting in the steady increase in numbers. All of the rhinoceros in the reserve are micro-chipped, except for new born calves and up to two years. The rhinoceros in the SNR are monitored through daily identification patrols by the rangers, and all sightings recorded. A compilation of monthly reports of all rhinoceros sightings is subsequently done. All births and deaths are recorded as well including other information such as the condition of the animal, injuries, diseases, area where the animal was seen, their activity and social units. All the individuals in the reserve have specific files detailing their life history.

Previous studies undertaken on the white rhinoceros in the SNR included an intense data collection conducted between 1996 and 2003 (Steyn, 2004:1). The data collected during the period included group location with the exact Global Position

System (GPS) locations, individual distributions, social units, habitat preference (including landscape, aspect, land use), vegetation preference (including vegetation type, density, grass length), and fire history. A genetic study was also launched in 2003 to determine DNA structures and parentage of all MTPA rhinoceros (Steyn & Stalmans, 2004:787). None of the Mpumalanga Tourism and Parks Agency's (MTPA; the provincial governing body) rhinoceros populations is currently or potentially large enough to form a viable population (Steyn *pers. comm.*).

All the rhinoceros populations managed by MTPA in the Mpumalanga Province are managed as a metapopulation to avoid inbreeding and promote the conservation of genetic material: the translocation of individuals between the reserves are made by considering criteria such as family lineage, DNA structure, individuals' maturity and mating activity (Steyn & Stalmans, 2004:787). Nevertheless, the unavailability of suitable habitats for the growing number of rhinoceros, as well as intra-specific competition still remains a problem in the MTPA reserves. Stalmans (2001:1) reported that more than 50% of rhinoceros mortalities on the protected areas are due to territorial fights. This is possibly indicating that the areas are not large enough to accommodate the requirements of the growing number of rhinoceros. Other causes of death included drowning, falling off cliffs, capture and poaching (Steyn, 2004:1). In this study, due to the current rhinoceros poaching crisis, we were not allowed to publish detailed information on white rhinoceros in this dissertation. We therefore cannot show any information on white rhinoceros locations, actual numbers and densities.

1.2 RATIONALE OF THE STUDY

White rhinoceros were introduced into SNR with the prime objective of managing a viable population and contributing to their conservation. SNR is nevertheless not considered ideal habitat for white rhinoceros because of its rugged and mountainous topography (Steyn, 2003a:2). These features reduce the amount of habitat available to forage as white rhinoceros are plains animals and prefer flat low-lying areas both for feeding and other activities (Owen-Smith, 1975:164). Therefore, the reduced available habitat calls for the careful management of the stocking rate of rhinoceros in the SNR. It has also been suggested that gaps exist in our knowledge of white rhinoceros feeding behaviour (Linklater, 2003:970), especially in mountainous terrain. As such, understanding the behaviour of re-introduced populations in their habitat is essential for *in-situ* conservation (Emslie, Amin & Kock, 2009:22).

A secondary objective for SNR was to use the white rhinoceros for tourism purposes (Steyn, 2004:7). The presence of these animals in the SNR is thus proving a good source of revenue. The role of ecotourism in generating income for conservation and in providing a recreational opportunity to tourists cannot be overemphasized. The white rhinoceros is one of the “Big Five” and as such it attracts a number of local and international tourists.

With the growing number of white rhinoceros in SNR, MTPA management faces significant challenges which include the availability of suitable habitat and intra-specific competition between individuals (Steyn & Stalmans, 2004:787) for food, space and mates. Prior to this study, management of SNR were concerned about the availability of food in the conservation area for white rhinoceros, particularly during the dry season. The importance to understand the quality and the availability of food resources, especially during the dry season, is fundamental in explaining animals' movements, which in turn, is limited to habitat suitability (Macandza, Owen-Smith & Cross, 2004; Muya & Oguge, 2000; Owen-Smith, 2002). During the dry season, the grasses become dormant and depleted and quality drops thus affecting the distribution and the diet for different herbivore species (Arsenault & Owen-Smith, 2002; Owen-Smith, 1982). Mapping the distribution of food resources therefore becomes important (Skidmore & Ferwerda, 2008). In a previous study in SNR, Stalmans *et al.* (2001) recorded the presence of highly favoured areas by herbivores characterised by rich fertile soils and highly nutritious species. The question is, are those areas also selected by white rhinoceros?

There is a need for continuous research on the foraging behaviour of the white rhinoceros especially in areas where they have been re-introduced. The study on the feeding of rhinoceros in the reserve had not been dealt with yet. Stalmans *et al.* (2001) addressed the necessity of a landscape ecological approach towards research and monitoring for an area of the size and diversity of SNR. They emphasized on the existence of patches that are heavily utilized by herbivores. Shipley (2007) also suggests that small-scale foraging decisions (i.e. bites) can lead to large scale patterns (e.g. habitat use and movement), once again emphasizing on the importance of scale when studying resource selection by large herbivores.

1.3 OBJECTIVES AND KEY QUESTIONS

The broad aim of this project is to contribute towards the management of the white rhinoceros population in SNR by describing the factors that influence its feeding patch selection. The objectives and key questions for this project are as follows:

1. To determine feeding habitat selection by white rhinoceros
    - 1.1. Does white rhinoceros show preference for a specific habitat?
2. To describe the feeding patches selected by white rhinoceros
    - 2.1. Which areas do white rhinoceros prefer for feeding during the late wet and the late dry seasons?
    - 2.2. What are the characteristics (slope, aspect, elevation) of the selected areas?
3. To compare the floristic characteristics of feeding patches selected by white rhinoceros
    - 3.1. What is the grass species diversity of selected feeding patches?
    - 3.2. What is the grass species composition of selected patches?
    - 3.3. How does grass species composition relate to environmental variables (elevation, slope, aspect, rock cover, grass height) in the feeding patches?
4. To identify variables driving selection of grass species by white rhinoceros within the feeding patches
    - 4.1. What are the most selected grass species?
    - 4.2. What grass species characteristics are most important in explaining selection of grass species by white rhinoceros?

5. To provide MTPA with management recommendations for the conservation of white rhinoceros in SNR.

1.4 PREDICTIONS

White rhinoceros are area selective species which prefer feeding on lower-lying areas because of their morphology and in order to take advantage of the most nutritious grass species in those areas. Owen-Smith (1973:134) and Shrader (2003:6) have observed WR to prefer particular grassland types as well as the more palatable broad-leaved grasses. The optimal foraging theory suggest that when resources are distributed in patches, a consumer should increase its intake rate in a high resources density patch (Stephens & Krebs, 1986:25). The Jarman-Bell-principle suggests that larger herbivore species can feed on diets of lesser quality, i.e. higher fibre content (Clauss *et al.*, 2009:376). Large body size has been suggested to be a major digestive advantage because of the digesta retention time which improves digestibility therefore increasing nutrients absorption. In the case of WR, although it is able to tolerate large quantities of low quality grasses, it is also dependent on a dietary quality not that much lower than that needed by much smaller ruminant (Owen-Smith, 1988:99). In other words, quality is important to the WR. Owen-Smith (1988:99) stipulates that in sourveld regions, where grasses are mostly highly fibrous and lack nutrients in above-ground parts during the dry season, WR feed mostly in those areas of the landscape where soil nutrients accumulate. In the sweetveld to the contrary, WR occupy regions where soil nutrient-rainfall combination causes grasses to build up moderate levels of indigestible fibre in their leaves. Therefore, the following predictions were made:

- White rhinoceros will prefer lower-lying areas and select specific habitat types;
- White rhinoceros will show a difference in the types of habitats selected during late wet and late dry seasons
- White rhinoceros will select feeding patches with the highest density of nutritious grass species in order to meet their needs in term of quantity
- White rhinoceros will prefer grasses with moderate and high grazing value (Pedersen, 2009:1) during the late wet season and switch to less palatable species during the late dry season as grasses become more fibrous.

1.5 APPROACH

The approach employed in this study involved recording all feeding observations of white rhinoceros within the study area. A previous study conducted by Steyn (2004) identified the size of suitable habitat to white rhinoceros within the study area. Feeding patches were identified according to the temporal scale in Table 1.1, through direct observation of the rhinoceros feeding behaviour. Data on the identified feeding patches, were collected on grass species as well as on habitat and topographical variables (i.e. slope, aspect, elevation, rock cover, grass height, leaf table height, grass species composition, woody cover) during the late wet and the late dry season 2008. The data were analysed by first identifying the preferred habitat types and describing their characteristics. The grass species composition, diversity and richness of the feeding patches was determined and compared between seasons. The influence of environmental variables on species composition was determined through an ordination technique. A number of candidate models were generated and tested in order to determine the factors driving grass species selection by white rhinoceros within the feeding patches.

CHAPTER 2

STUDY AREA

2.1 LOCALITY

The 49 000 ha Songimvelo Nature Reserve (SNR) is situated south of Barberton, in the south-eastern part of the Mpumalanga Province. The reserve is found on the South African – Swaziland border at latitude 25°45' – 26°05' south and longitude 030°46' – 31°16' east. The reserve is comprised of the 31 000 ha game-fenced southern and central section, where white rhinoceros are kept and formed the study area of this project (Figure 2.1). The reserve also comprises of an unfenced section of approximately 3 900 ha between the game fence and the Swaziland border, which is leased to the local community; and an unfenced 12 500 ha “panhandle” area. The SNR stretches across a diagonal of 50 km from the Komati River Valley in the south-west, to the narrow mountainous north-eastern apex.

2.2 TOPOGRAPHY

The SNR is situated in the Barberton Mountainlands (Stalmans, Robinson & Balkwill, 1999:305). The study area is very rugged and mountainous with only the Komati Valley showing a more gentle terrain (Figure 2.1). Elevations range between 700 to 1 900 m above sea level. The area is drained by rivers (the Komati River and Mtsoli River being the most important) and numerous streams, which have formed deep gorges and valleys in the area. The Mtsoli Valley is located more or less in the centre of the study area but is not accessible to the white rhinoceros, who occur only around the Komati Valley, because of the mountainous features of the area.

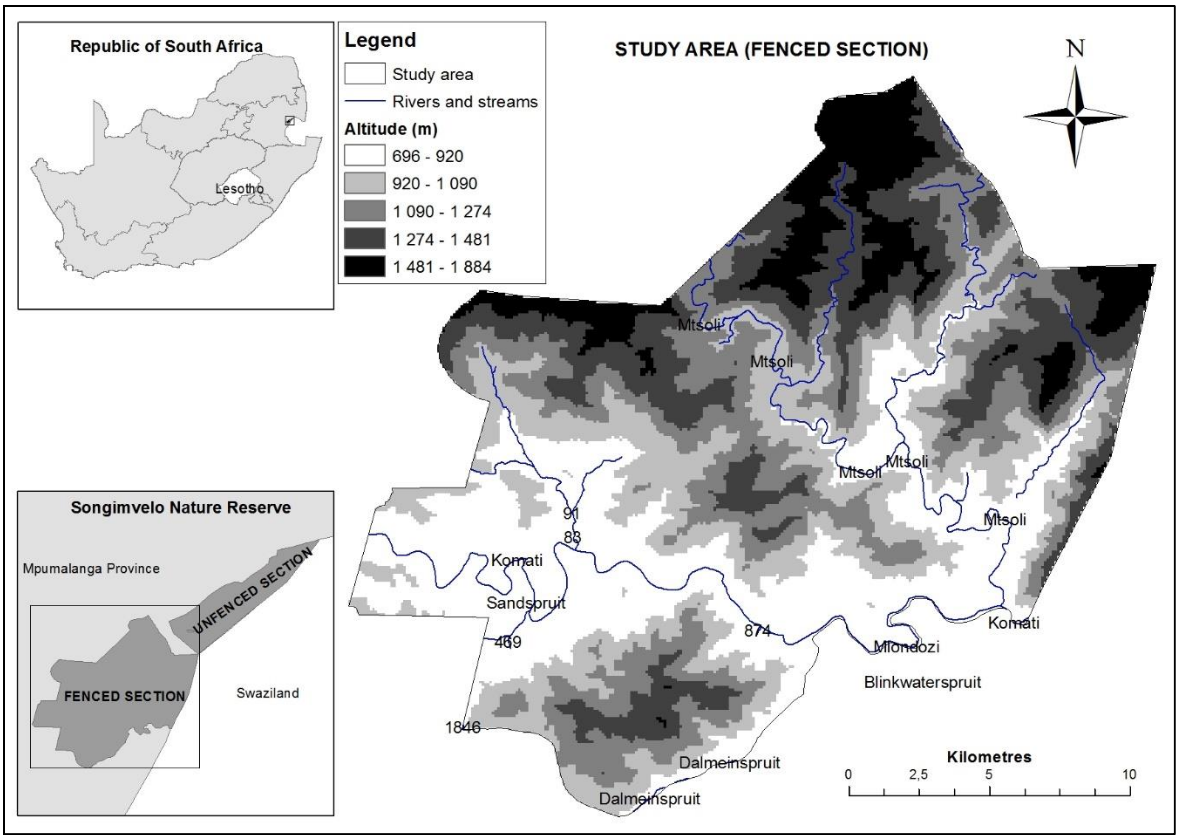

Figure 2.1: The location of the study area (fenced section of Songimvelo Nature Reserve) showing elevation ranges and water bodies.

2.3 PEDOLOGY AND SOILS

The study area can be broadly categorised into three landforms, i.e. midslopes, foot slopes and valley bottoms (Steyn, 2003b:13). The midslopes are characterized by slopes steeper than 12° (and often more than 30°). The Land Types in the study area correspond with this broad categorisation of landforms (Figure 2.2; Table 2.1). Two Land Types dominate in the Komati Valley (Ae54 and Fa169). Mispah soil forms and shallow, acid soils occur mostly on the midslopes. Mispah, Shortlands and Hutton soil forms dominate on foot slopes (with a slope of 6 to 12°). These soils are shallow to deep, neutral to acid loams and clays. Dominant soil forms in the valley bottoms along the Komati River are Oakleaf and Dundee soil forms consisting of deep neutral loamy and sandy soils.

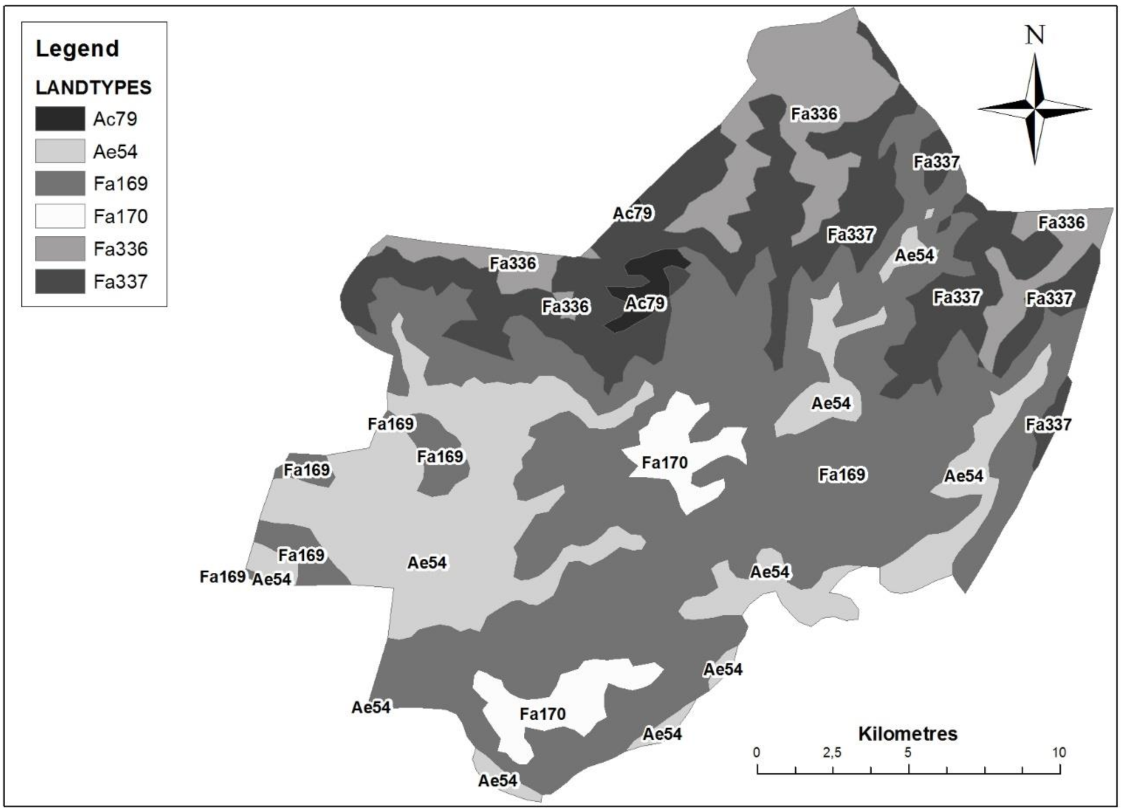

Figure 2.2: Land Types map of the study area in Songimvelo Nature Reserve. Description of landform codes in Table 2.1.

Table 2.1: Land Types characteristics of Songimvelo Nature Reserve.

Land types	Soil description	Geology
Ac79	Red-yellow apedal, freely drained soils; red and yellow, dystrophic and/or mesotrophic	Shale, sandstone, siltstone, chert, conglomerate, tuff, mafic and felsic lava of the Moodies, Fig Tree and Onverwacht Groups (Barberton Sequence).

Ae54	Red-yellow apedal, freely drained soils; red, high base status, > 300 mm deep (no dunes)	Diabasic lava, quartz porphyry, serpentinite, greenstone and chert of the Onverwacht Group, Barberton Sequence.
Fa169	Glenrosa and/or Mispah forms (other soils may occur), lime rare or absent in the entire landscape	Sandstone, grit, conglomerate, shale and quartzite of the Moodies Group; tuff, agglomerate, lava and graywacke of the fig tree Group and mafic to siliceous lava and schist of the Onverwacht Group, Barberton Sequence.
Fa170	Glenrosa and/or Mispah forms (other soils may occur), lime rare or absent in the entire landscape	Sandstone, grit, conglomerate, shale and quartzite of the Moodies Group: tuff, agglomerate, lava and graywacke of the Fig Tree Group and mafic to siliceous lava and schist of the Onverwacht Group, Barberton Sequence.
Fa336	Glenrosa and/or Mispah forms (other soils may occur), lime rare or absent in the entire landscape	Shale, sandstone, siltstone, chert, conglomerate, tuff, mafic and felsic lava of the Moodies, Fig Tree and Onverwacht Groups (Barberton Sequence).
Fa337	Glenrosa and/or Mispah forms (other soils may occur), lime rare or absent in the entire landscape	Tuff, shale, sandstone, siltstone, chert, conglomerate and mafic to felsic lava of the Fig Tree, Onverwacht and Moodies Groups (Barberton Sequence).

2.4 CLIMATE

Rainfall occurs mainly in the period from November to March, and varies from less than 800 mm per annum in the low-lying south-western area, to over 1 600 mm in the northern parts of the panhandle. During the study, rainfall data recorded between October 2007 and June 2008 (Figure 2.3) was below average (575.7 mm), in relation to the long term (1988 - 2008) average of 645.7 mm. There was no rain during the months of July, August and September 2008. Great variations in temperature are experienced between the highlands (5.4 – 22 °C) and lowlands (7.9 – 34 °C). During the study, the average monthly minimum and maximum temperatures varied respectively between 4 °C in July and 30.2 °C in September. The climatic data was obtained from Weather station 0481692 – Songimvelo (South African Weather Bureau, 2008).

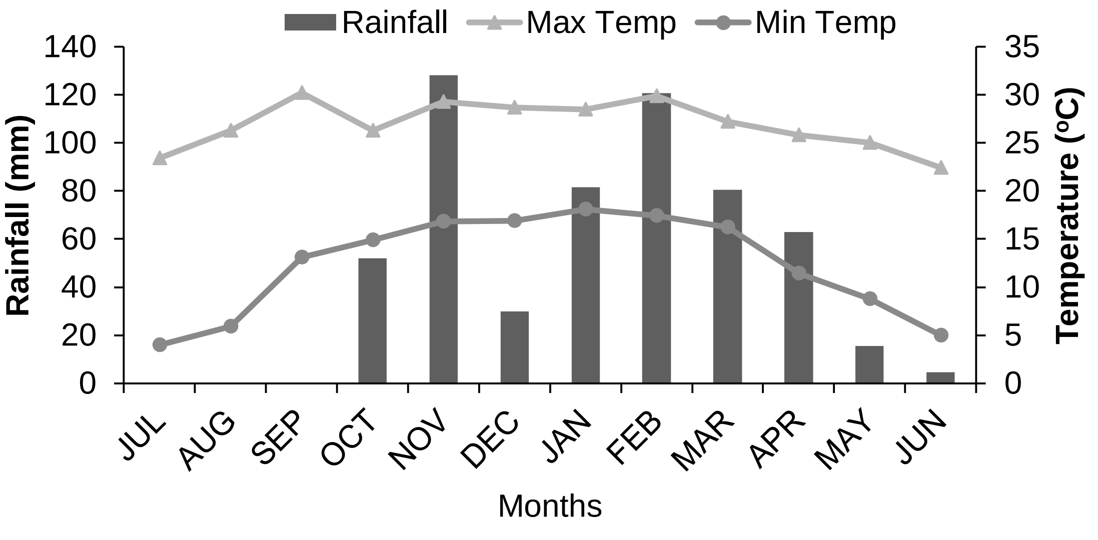

Figure 2.3: Mean monthly rainfall, average maximum (Max Temp) and minimum (Min Temp) monthly temperatures of Songimvelo Nature Reserve recorded between July 2007 and June 2008 (Weather station: [0481692 X] – Songimvelo).

2.5 VEGETATION

According to Mucina and Rutherford (2006), the vegetation of the higher-lying regions of the study area belongs to the Grassland Biome while the lower-lying Komati Valley falls within the Savanna Biome. The study area consists of five vegetation units namely: Barberton Montane Grassland, Barberton Scarp Forest, Barberton Serpentine Sourveld, Granite Lowveld, KaNgwane Montane Grassland, and Swaziland Sour Bushveld (Figure 2.4). The latter vegetation unit is situated in the Savanna Biome whilst the other four vegetation units are within the Grassland Biome.

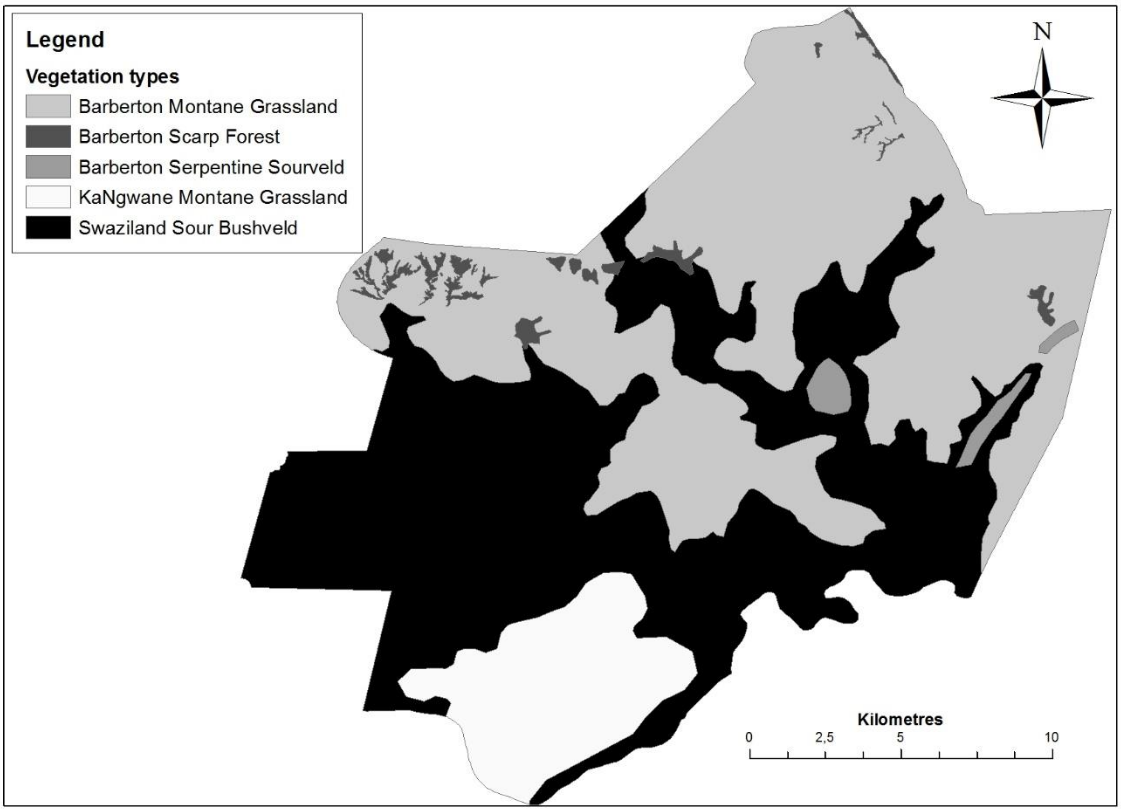

Figure 2.4: Vegetation units of the study area within Songimvelo Nature reserve according to Mucina and Rutherford (2006).

Stalmans *et al.* (1999:305) described 19 distinct plant communities in the SNR. Four of these plant communities are found within the study area namely: *Vachellia nilotica - Heteropogon contortus* low woodland/low grassland, *Cynodon dactylon - Melinis repens* low grassland, *Vachellia nilotica - Euclea crispa* low woodland/low grassland and *Loudetia simplex - Themeda triandra* short Shrubland/low grassland.

For the purpose of this study, the area in and around the Komati Valley (Area available to white rhinoceros) was broadly classified into three habitat types that resulted from a description provided by Stalmans *et al.* (2001:397) and field observations namely: (1) Open Low Woodlands (OLW) on level or gentle slopes and dominated by *Vachellia nilotica*, *Euclea crispa* and *Heteropogon contortus;* (2) Oldlands (OL) founds on old settlement areas and cultivated lands, dominated by *Cynodon dactylon* and *Melinis repens;* (3) Shrublands (SL) characterised by shrubs and dominated by grass species such as *Loudetia simplex* and *Themeda triandra*. All these habitats fall under the Swaziland Sour Bushveld vegetation unit (Mucina & Rutherford, 2006). These habitat types were available to the white rhinoceros and were situated less than 2 km from a permanent water source, mainly the perennial Komati River. Other key grass species found in the area include i.e. *Hyparrhenia hirta*, *Hyperthelia dissoluta, Bothriochloa spp.* and *Aristida spp.*

CHAPTER 3

METHODOLOGY

3.1 STUDY DESIGN

3.1.1 Identification of feeding patches

A feeding patch is functionally characterised by the duration of feeding (1 – 30 min) and size (1 – 10 000 m^2) both depending on body size and foraging strategy of the herbivore involved (Bailey & Provenza, 2008). In this study, a feeding patch was identified as an area where white rhinoceros spent 1 – 30 min feeding. The animals were observed at a distance (i.e. 200 m at least) that would not influence their natural feeding behaviour. Natural markers (rocks or trees) were used to visually mark the area where rhinoceros were observed feeding for further sampling. It was sometimes necessary to follow the rhinoceros for a distance in order to clearly identify the feeding patch.

3.1.2 Size and position of vegetation sampling plots

Once a feeding patch was identified and the rhinoceros had vacated the feeding area, the sampling of the patch was undertaken. A 10 m x 10 m plot was placed in the centre of the grazed area, and five 1 m x 1 m subplots were placed in each corner of the plot and one in the centre of the grazed area (Figure 3.1). The size of the plot was decided after repeated observations of rhinoceros group sizes and feeding behaviour on the reserve undertaken during a preliminary study. Grass species present within each 1 m^2 sub-plots as well as all woody species rooted within the 100 m^2 quadrat were recorded. According to Bonham (1989), plots of sizes 1 m^2, 16 m^2, and 100 m^2 are appropriate to determine densities for herbs, shrubs and trees, respectively. The sampling areas of 100 m^2 for the woody species and 1 m^2 for the grass species within the patch were therefore considered sufficient and adequate for the purpose of this study. The woody species were sampled in order to help determine the cover types in the selected feeding areas as well as assist in the classification of habitat types.

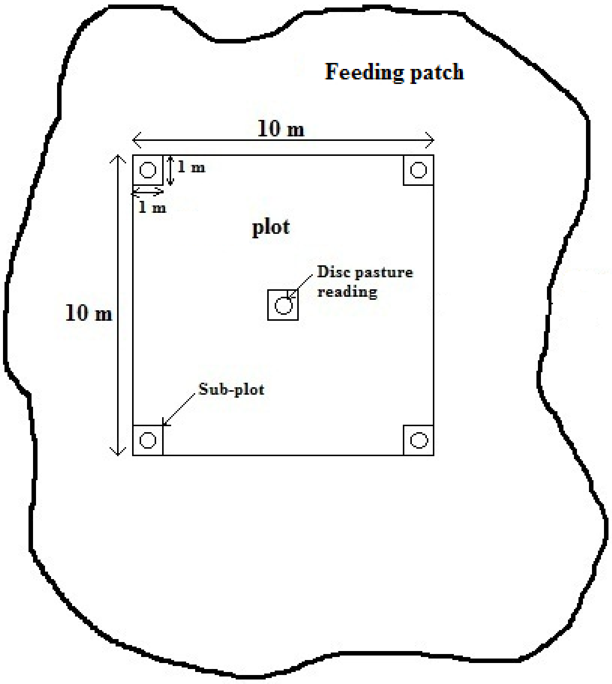

Figure 3.1: Illustration of the position of a feeding plot and subplots within the feeding patch.

3.2 DATA COLLECTION

The field data collection was undertaken during the late wet season (February to April) and the late dry season (June to August) of the year 2008. These periods were chosen because they are respectively associated with periods where food is abundant and periods where food is limited (Arsenault & Owen-Smith, 2008:1711; Macandza *et al.*, 2004:113; Owen-Smith, Fryxell & Merrill, 2010:2267). In order to observe the seasonal movements of white rhinoceros in the area, it was important to compare feeding patch selection during periods of high food abundance (late wet season) against periods of low food abundance (Late dry season).

3.2.1 Feeding patch data collection

In order to identify the feeding patches, white rhinoceros were located and observed at least three days weekly. The rhinoceros in the SNR were not fitted with radio nor GPS collars during the study; tracking and observations of the rhinoceros were therefore chance events. Two main routes (north and east) from the main office were travelled on weekly by vehicle. Each of those routes covered specific sections of the area where rhinoceros were suspected to occur. Rhinoceros in SNR are identified using the ear-notch technique. The identification of rhinoceros individuals helped in distinguishing groups and reduce sampling errors (i.e. avoid sampling the same group on consecutive occasions). Rhinoceros groups remained generally stable throughout the study with a few instances of group changes observed. Shrader and Owen-Smith (2002:255) attributed a number of reasons for these groups changing (sexual maturity, mother at time of birth, territoriality, for security, to gain experience, for dispersal).

White rhinoceros were located at least three days per week by systematically driving the two main routes by vehicle, or patrolling on foot or on horseback in areas that were inaccessible by vehicle. It was sometimes necessary to combine these methods in order to cover larger areas. Previous studies found that season and day temperatures dictate when rhinoceros are most active (Owen-Smith, 1975:339). Feeding mainly occurs during mornings and late afternoons (Owen-Smith, 1998:185; Shrader & Owen-Smith, 2002:85; Shrader & Perrin, 2006:378) as rhinoceros restrict their feeding during the hotter times of the day to avoid overheating (Owen-Smith, 2008). As such, in this study tracking commenced at daybreak until 11h00, and when possible the afternoon between 15h00 and 18h00. To maintain independence among observations, the same group of rhinoceros was not observed on consecutive days.

At all sightings, binoculars (Nikon Monarch 10 x 42 DCF) were used to accurately identify rhinoceros ear-notch number and observe their feeding behaviour. A Garmin *e*trex 12 channel GPS (Garmin LTD, 2007) was used to record the coordinates of each feeding sight. These GPS coordinates were later plotted on a digital elevation model (DEM) with 90 m resolution in Arcmap 9.3 (ESRI, 2008) to extract topographical variables such as slope (in degrees), aspect (0 - 360°) and elevation (in meters). The habitat types (Open Low Woodlands, Oldlands and Shrublands) in which white rhinoceros were observed feeding was also recorded.

Other information such as surface rock cover were visually estimated as a percentage of a 1 m x 1 m quadrat and grouped into 4 categories: 0) non-rocky (< 2 %), 1) slightly rocky (2–20 %), 2) moderately rocky (20–50 %) and 3) very rocky (> 50 %). These categories were adopted from a previous studies undertaken by Steyn (2004) on elephants in the area. Because of the presence of the perennial

Komati River flowing through the area, the distance to water was not measured as the availability of water was likely not limiting in the area (Stalmans, Witkowski & Balkwill, 2002:129).

3.2.2 Vegetation data collection on feeding patches

Vegetation data were recorded on grass species and woody species. Forbs were also identified but the data were not used in this study as they were not consistently recorded throughout the study. Forbs also form less than 5% of the diet of white rhinoceros and in many instances are ingested accidentally (Owen-Smith, 1973:9; Shrader, 2003:50).

All rooted grass species within the 1 m x 1 m subplots were identified with the help of field guide by Van Oudtshoorn (1999), and counted. Grass species which could not be positively identified in the field were collected, pressed and submitted to the South African National Biodiversity Institute (SANBI) office for identification. Densities per grass species were determined as well as the average basal diameter of each grass species recorded. Basal diameter is an indication of basal area or basal cover and has previously been observed to affect selection of plants by large herbivores (Ganskopp & Rose, 1992:538).

Grass species heights were measured and categorised into height classes of 1) 0–10 cm, 2) 11–30 cm, 3) >30 cm. These categories were adopted from the study by Shrader (2003:52). The tuft diameter of grass species was recorded within each 1 m x 1 m subplot. Three grass tufts of each species were randomly selected per subplot and measured using a calliper. Leaf table height was measured by means of a disc pasture meter (DPM; Bransby & Tainton, 1977): one DPM reading was recorded within each 1 m x 1 m subplot and the reading recorded in centimetre.

Woody species were identified and their growth form categorized as 1) trees (rooted, woody, self-supporting plants greater than 2 m high with a single stem (≥2 m) or multi-stemmed (≥5 m), normally branching above the ground); 2) shrubs (rooted, woody, self-supporting and multi-stemmed plants <5 m high or single-stemmed <2 m high); and 3) dwarf shrubs (rooted perennial woody plants < 1 m high). Woody cover was visually estimated and categorized into: 0) no woody plants, 1) open, 2) sparse and 3) closed.

Grass species that were selected by white rhinoceros were recorded by walking in random patterns within the 10 m x 10 m plot and identifying all grass species that showed signs of fresh grazing. Grasses were recorded as either being selected (1) or not selected (0). Grass species such as *Eragrostis curvula* and *Eragrostis chloromelas* were grouped as *Eragrostis spp*. This was done because some of the grass species could not be clearly identified due to the degree of grazing. Other grass species that were combined included *Bothriochloa insculpta* and *Bothriochloa bladhii* (as *Bothriochloa spp.*), and *Aristida* species grouped as *Aristida spp*.

3.3 DATA ANALYSES

3.3.1 Habitat selection and use by white rhinoceros

In order to determine the habitat types preferred by white rhinoceros for feeding, the chi-square goodness of fit test (Equation 1) was used. The available area was determined by using rhinoceros sightings of a previous study (1996 - 2001) as well as those recorded during this study. The outer points of the sightings were connected to define an area and the size was measured. The expected number of rhinoceros in each habitat was determined by multiplying the available proportion of each habitat type by the total number of rhinoceros observations in each season. When significant differences in the habitat use by rhinoceros was found, the Bonferroni Z-statistic (Equation 2) was used following the methodology described by Byers and Steinhorst (1984:1052) in order to construct Bonferonni confidence intervals.

$$\chi^2 = \sum \frac{(observed - expected)^2}{expected} \qquad \text{(Equation 1)}$$

$$P_{oi} - Z_{\alpha/2k}\sqrt{P_{oi}(1 - P_{oi})/n} \leq P_i \leq P_{oi} + Z_{\alpha/2k}\sqrt{P_{oi}(1 - P_{oi})/n} \qquad \text{(Equation 2)}$$

in which P_i is the calculated confidence interval for habitat type i, P_{oi} is the proportion of rhinoceros observation in habitat type i, n is the number of total observations, $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$, and k is the number of habitat types tested. During the late dry season, expected observations for the Oldlands were less than five. It was therefore necessary to combine Oldlands and Shrublands in order to perform the chi-square test during the late dry season.

The frequency of white rhinoceros observed feeding at different habitat types was determined in order to explain any differences observed. The utilisation of terrain factors within the feeding patches (i.e. slope in degrees, elevations in meters above sea level and aspects in degrees) between the late wet and the late dry season was also measured. The values obtained from the measurements of terrain factors were tested through independent t-tests to compare the different terrain variables (slope, elevations and aspects) between the late wet and the late dry season. The t-tests were performed when the data was normally distributed and Mann-Whitney U-tests were performed when distributional assumptions were not met. To further explain any significant differences, the proportion of feeding patches within predetermined categories of these variables was determined by adding the total number of patches utilised in each of the categories in each season. The categories included:

- Slope: 0-6, 6.1-12 and >12 as categorised by Steyn (2003a);
- Elevation: <750, 751-800, 801-850, 851-900 and >900;
- Aspect: north (N) – 315-45˚, east (E) – 46-135˚, south (S) – 136-225˚ and west (W) – 226-314˚ as suggested by Palmer (2013)

3.3.2 Grass species diversity and ordination of feeding patches

A diversity index is commonly used to measure the biodiversity of an ecosystem and takes into account the number of species present as well as abundance of each species and evenness (Rad, Manthey & Mataji, 2009:389). The grass species diversity index in this study was calculated following the method of Shannon and Weaver (1949). The Shannon index of diversity is the most commonly used measure of species diversity (Hirunkitrangsee, 2008; Kent & Coker, 1992). It combines both species richness and evenness into a single value (Dörgeloh, 1999:519). A measure of richness and evenness together would give a comprehensive measure of diversity. Shannon-Wiener diversity index was calculated as:

$$H' = -\sum_{i-1}^{S} P_i \ln P_i \qquad \text{(Equation 3)}$$

Where S = the number of species also called species richness; P_i the relative abundance of each species, and ln is the natural logarithm.

Species richness (N0) was measured as the total number of species within a square meter. Evenness was also determined using Pielou's evenness index (J). Evenness expresses how evenly the individuals are distributed among the different species. A One-way Anova was performed to compare the different diversity indices between the feeding patches utilised by white rhinoceros in the late wet and late dry seasons.

In order to observe species composition of feeding patches, a Detrended Correspondence Analysis (DCA) was performed on feeding patches of both late wet and late dry seasons. When performing an ordination, the rule of Lepš and Šmilauer (2003) suggest that to decide whether to apply linear or unimodal ordination method, calculate the DCA first and check the length of the first DCA axis. If the value is larger than 4.0, the data is heterogeneous and the unimodal methods (DCA, CA, or CCA) are used. If the longest gradient is shorter than 3.0, the linear method is probably a better choice. If the gradient length ranges between 3 and 4, both linear and unimodal ordination methods can work reasonably well. The relative abundance data of the grass species were used for the purpose of this analysis (see Annexure A for the list of species and abbreviations). Environmental variables (Table 3.1), were also used to investigate their relationship with species data through a canonical correspondence analysis (CCA). Palmer (2013) advises to transform variables such as aspects before CCA analysis into trigometric function or to use dummy variables such as north, south, east and west. The Monte Carlo permutation tests were used to test the significance of environmental variables.

The species and samples distribution was analysed using the idea of continuous change of composition along the gradients and the idea that proximity implies similarity. In other words, samples that lie near to each other will be much more similar in terms of the list of species occurring and relative importance of species compared to samples far apart (Lepš & Šmilauer, 2003:30). Similarly, the proximity of species to the sample sites shows the significance of the species to the floristic composition of the sample site. All analyses were conducted in R version 3.0.0 (R Core Team, 2013) using the R package “Vegan” (Oksanen *et al.*, 2013).

Table 3.1: Environmental variables used during ordination of white rhinoceros feeding patches.

Variable	Code / Abbreviation	Unit
Elevation	ELEV	Meters
Slope	SLO	Degree
Aspect	ASP	Degree
Rock cover	RCOV	categorical
Leaf table height	LTH	cm
Mean grass height	MGH	cm
Mean tuft diameter	MTD	cm
Woody cover	WCOV	categorical
Woody density	WDEN	count

3.3.3 Grass species selection by white rhinoceros

All grass species selected by white rhinoceros compared in terms of their density within the patch, their contribution (percentage) in the diet of white rhinoceros and their grazing value. The frequency at which a specific grass species was selected during particular seasons was determined. The grazing value of the selected grass species was assigned followed Van Oudtshoorn (1999).

In order to determine what variables drive grass species selection, candidate models were generated from a number of hypotheses at the species level. Using multi-model inference (Anderson, 2008), a number of models were developed from the following hypotheses:

- The presence of certain grass species determines in the selection of the patch
- The presence of grass species within the feeding patches during the late wet and late dry seasons determines selection
- The presence of grass species and a combination of other variables (grass density, mean tuft diameter and leaf table height) during specific seasons, drive the selection of the patch

These models were fitted using the logistic regression. For each model, a binary response variable (used or not used) was used and explanatory variables such as grass species (Species), grass density (density), season, leaf table height (LTH), and mean tuft diameter (MTD). For the variable species, *Bothriochloa* species (N=2) were grouped as *Bothriochloa spp*., *Eragrostis* species (N=5) as *Eragrostis spp*. and *Sporobolus* species (N=3) as *Sporobolus spp*. Other species used included *Heteropogon contortus*, *Cynodon dactylon*, *Setaria sphacelata* and *Themeda triandra*. The other species were grouped as other. Prior to fitting the models, an exploratory data analysis (EDA) was undertaken in order to test for collinearity.

Model selection was performed using Akaike's Information Criterion (AIC) and corrected using AIC_c because of the small sample size in relation to the number of parameters (Burnham & Anderson, 2002). The model with the lowest AIC_c value was considered the best model (Anderson, 2008), and all models with a $\Delta AIC_c<4$ were considered to be the best models in predicting grass species selection. The likelihood of each model was further calculated, as well as the evidence ratio (ER) between the best models. An ER value of 2.7 or more supports the ranking of the model whilst a value of less than 2.7 is indicative of a degree of uncertainty regarding the best model. Akaike weights (ω_i) were calculated for all models. Akaike weights give the probability estimate for each model (Burnham & Anderson, 2002). Model-averaged estimates were also determined for each variable. Odd ratios as well as confidence intervals for all explanatory variables of the best models was also calculated. All statistical analyses were done in R version 3.0.0 (R Core Team, 2013) using the package “AICcmodavg”.

CHAPTER 4

RESULTS

4.1 HABITAT SELECTION BY WHITE RHINOCEROS

An area of 6488 ha was determined to be available to white rhinoceros in this study. The selection of the different habitat types between the seasons differed. During the late wet season (Table 4.1), there was a significant difference between the overall available habitats and their usage (χ^2=*18.09, df=2, P<0.001*). White rhinoceros showed selection of the available habitat types in the late wet season. The Bonferroni interval (Table 4.2) revealed that the Open Low Woodlands and Oldlands were used by white rhinoceros in proportion to their availability. The expected proportion of usage of Shrublands did not lie within the bonferroni interval indicating a significant difference between expected and actual utilization of the habitat type. Shrublands were less frequently utilised by white rhinoceros during the late wet season.

Table 4.1: White rhinoceros late wet season feeding habitat selection in the Songimvelo Nature Reserve (χ^2=*18.09, df=2, P<0.001*).

Habitat types	Total area (ha)	Relative area	Observed Usage	Expected Usage
Open Low Woodlands	4542	0.70	64	56.71
Oldlands	452	0.07	12	5.64
Shrublands	1494	0.23	5	18.65
Total	6488	1	81	45.00

Table 4.2: Bonferroni intervals of white rhinoceros' feeding habitat selection during the late wet season.

Habitat type	Expected proportion of usage	Actual proportion of usage	Bonferroni intervals for P
Open Low Woodlands	0.70	0.79	$0.68 \leq P \leq 0.88$
Oldlands	0.07	0.15	$0.05 \leq P \leq 0.24$
Shrublands	0.23	0.06	$-0.00 \leq P \leq 0.12$*

* Indicates a difference at the 0.05 level of significance.

During the late dry season (58 feeding observations), the Oldlands recorded an expected observation of less than five. The Oldlands and Shrublands were therefore merged in order to perform the chi-square test. There was no significant difference detected between overall habitats available and used ($\chi^2=1.06$, $df=1$, $P>0.05$). Consequently, a Bonferroni Z-statistic was not necessary. White rhinoceros did not show selection of overall habitats during the late dry season. This could suggest that all habitats were used proportionally to their availability or could be due to the small sample size. During both seasons, white rhinoceros were feeding mostly in the Open Low Woodlands (79 % and 63 % for the late wet and late dry seasons respectively), which made up more than half of the observations. The utilisation of the Oldlands remained consistent between the seasons because white rhinoceros used that habitat at almost the same frequency during the late wet and the late dry season. But the utilisation of the Open Low Woodlands declined during the dry season to the favour of Shrublands, which increased from 6 % in the late wet season to 22 % in the late dry season. This is indicating that rhinoceros increased their use of that habitat which was less frequented during the late wet season.

Of all the nine variables measured within the feeding patches during both late wet and late dry seasons (Table 4.3), only three showed significant differences (aspects, rock cover and leaf table height). The aspects were significantly higher (t=-3.98; P=0.00) in the late dry season (253.51±73.94) than in the late wet season (151.32±109.80). Rock cover as well was significantly higher (U=245.5; P=0.04) in the late dry season (28.19±17.93) and in the late wet season (17.75±16.87). Leaf table height however, was significantly higher (t=2.41; P=0.02) in the late wet season (4.36±1.20) than in the late dry season (3.57±1.23).

Table 4.3: Comparison of habitat variables in feeding patches between the late wet and the late dry season.

	Mean ± SD			
	Late wet	Late dry	t or U	P
Elevation	853.96±27.88	861.15±24.05	-1.01	0.32
Slope	3.80±2.25	4.90±3.25	-1.46	0.15
Aspect	151.32±109.80	253.51±73.94	**-3.98**	**0.00**
Rock cover	17.75±16.87	28.19±17.93	**245.5**	**0.04**
Mean grass height	40.18±22.13	30.58±21.32	265.5	0.08
Woody cover	1.00±0.66	1.00±0.50	356.00	0.89
Woody density	17.43±17.60	6.27±5.60	260.00	0.07
Mean tuft diameter	13.75±5.70	15.42±13.10	332.50	0.59

Leaf table height	4.36±1.20	3.57±1.23	**2.41**	**0.02**

Values in bold are significant

4.2 GRASS SPECIES DIVERSITY AND ORDINATION OF FEEDING PATCHES

4.2.1 Grass species diversity

A total of 52 grass species were identified in the feeding patches during both seasons. *Heteropogon contortus* was the most frequent and most represented species in the area as it was found in all feeding patches. Other species that were dominant include *Aristida spp*., *Bothriochloa spp*., *Eragrostis spp*., *Loudetia simplex*, *Sporobolus spp*. and *Hyparrhenia spp*.

A one-way Anova revealed no significant differences in grass species richness, diversity indices and evenness between the late wet and the late dry season (Table 4.4). This indicates that white rhinoceros fed on patches with similar grass species richness, diversity and evenness during both seasons.

Table 4.4: Summary of diversity indices results between the late wet and the late dry seasons.

	Mean±S.E.	
	Late wet	Late dry
Species richness (N0)	10.86±0.51	10.23±0.65
Shannon diversity index (H')	1.50±0.06	1.39±0.06
Pielou's evenness (J)	0.64±0.02	0.62±0.02

4.2.2 Grass species composition of feeding patches

The DCA ordination of grass species on feeding patches has resulted in the total inertia of 4.20 (Table 4.5). The first axis recorded the longest length of gradients (4.50 S.D.), suggesting a unimodal response (CCA) with the environmental variables. The first two axes recorded the highest eigenvalues, indicating that they were the most important. An eigenvalue of 0.60 was also recorded on the first axis which is indicative of a good dispersion of grass species along the first axis. The first axis produced 14.3 % grass species variation.

Table 4.5: Summary of Detrended Correspondence Analysis (DCA) of white rhinoceros feeding patches.

	DCA1	**DCA2**	**DCA3**	**DCA4**	**Total inertia**
Eigenvalues	0.60	0.27	0.22	0.20	4.20
Axis lengths	4.50	2.36	2.09	1.71	
Variance of species data	14.30	6.43	5.24	4.76	

From the ordination diagram (Figure 4.1), there were no distinct underlying factors that could be inferred. However, the sites showed a grouping of feeding patches into two clusters possibly according to their floristic similarities: One large cluster contained the majority of feeding patches around the centre of the plot and a second cluster right of the first cluster, contained few feeding patches. It was therefore necessary to conduct a CCA ordination to look at the corresponding environmental variables. The position of the feeding patches around the first axis is an indication of the importance of this axis in the ordination. The large cluster included the majority of feeding patches of both the late wet and late dry seasons indicating similarities among these patches. These similarities could indicate that either white rhinoceros did not change their habitat use pattern or the selected habitats contain similar habitat characteristics i.e. slope, aspect, elevation, rock cover, grass height, and woody cover.

The grass species on the other hand formed three recognisable clusters (Dash lines in Figure 4.1) with the majority of the species being associated with the largest cluster of feeding patches. *Heteropogon contortus* was in the centre of the large cluster whilst *Aristida congesta* was situated the closest to the small cluster indicating the association of these species with the corresponding clusters. Other species found in the proximity of the large cluster include *Setaria sphacelata* and *Aristida spp*. The feeding patches in the second cluster were observed during the late dry season. Species like *Cynodon dactylon* were associated with old lands and old settlement areas. This could explain its position as an outlier in the ordination graph. The smaller cluster of feeding patches could as well be associated with the old lands and settlement areas because of their proximity with the *Cynodon dactylon* plot. Other outliers included, *Tristachya leucothrix*, *Hyparrhenia hirta*, *Bothriochloa insculpta*, *Setaria sphacelata*, *Eragrostis rigidior* and *Sporobolus pyramidalis*. These species were less associated with feeding patches during both late wet and late dry seasons.

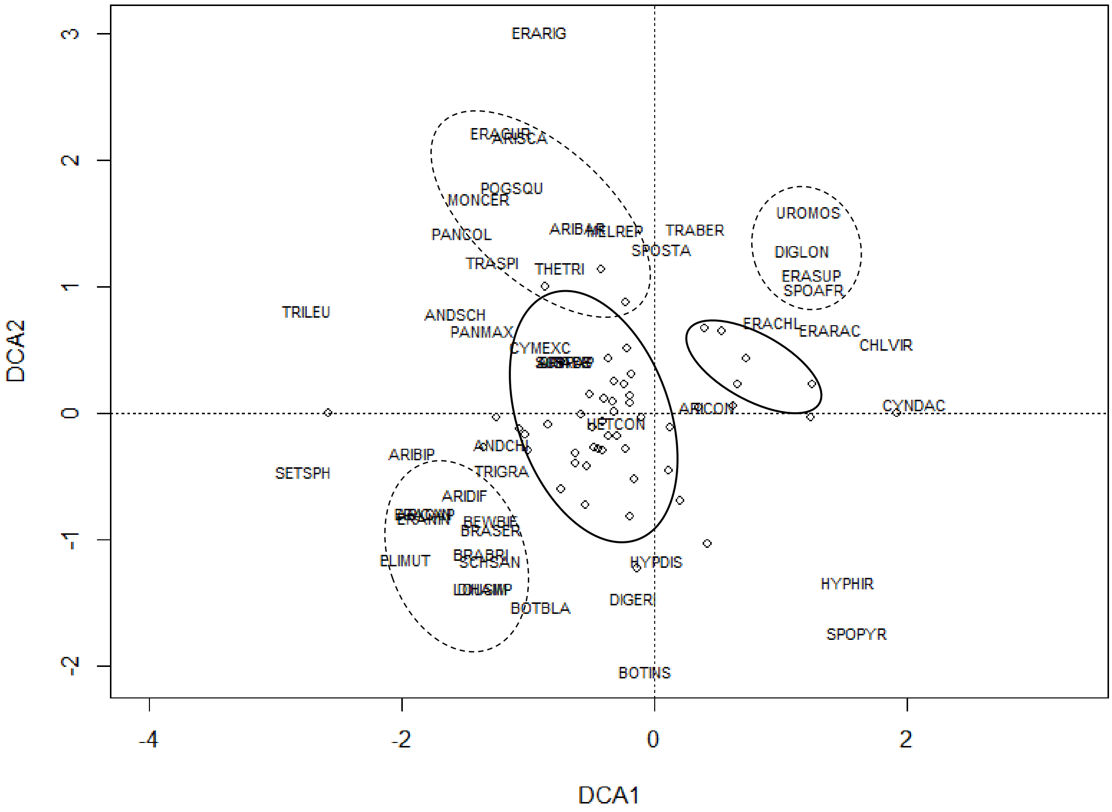

Figure 4.1: DCA ordination plot of grass species and feeding patches. Grass species are listed by the first three letters of the genus and the specific epithet (see Annexure A for full names). Dashed lined circles represent the grass species clusters; plain circles represent feeding patch clusters.

4.2.3 Influence of environmental factors

The CCA was executed because of the unimodal response shown by the pattern of grass species distribution in the DCA results. The CCA ordination summary recorded a total inertia of 4.20 and a constrained inertia of 1.29. The CCA ordination of grass species showed very high species-environment correlation for all axes

(Table 4.6). The first two axes were the most important with the highest eigenvalues of 0.54 and 0.24 for axes 1 and 2 respectively. The first axis recorded the highest species-environment correlation (*r=0.88*) and 13.50 % species variation. A 31 % total variability was captured by the CCA ordination indicating that the CCA was successful at capturing variability in grass species composition.

Table 4.6: Summary of Canonical Correspondence Analysis (CCA) of white rhinoceros feeding patches.

	CCA1	**CCA2**	**CCA3**	**CCA4**
Eigenvalues	0.54	0.24	0.13	0.13
Species environment correlation	0.88	0.82	0.72	0.62
Cumulative percentage variance				
of species data	13.50	18.55	21.61	24.60
of species-environment relation	42.15	60.37	70.32	80.04

The Monte Carlo permutation test revealed significant difference (χ^2=1.29, F=2.16, P=0.005). The permutation test by axes revealed significant differences for the first four axes (Table 4.7), with axes 1 and 2 computing the highest significance (p=0.005 for both axes) and axes 3 and 4 the lowest (P=0.017 for axis 3 and P=0.015 for axis 4). This is indicating that in the CCA ordination, axes 1 and 2 were the most important. The permutation test by terms (Table 4.8) showed that mean tuft diameter was significant (χ^2=0.38, P=0.01). All the remaining variables showed no significant difference.

The interset correlation of these variables (Table 4.9) showed that the highest correlations were observed with mean tuft diameter (0.84 in axis 1), leaf table height (0.43 in axis 2) and rock cover (-0.59 in axis 2). Other variables such as aspect and woody cover recorded correlation of -0.46 and -0.51 respectively for the second axis. The Variance Inflation Factors (VIF) indicated all environmental variables were modest.

Table 4.7: Canonical Correspondence Analysis (CCA) permutation test results by axes.

	χ^2	F	P>F
CCA1	0.54	8.22	0.005**
CCA2	0.24	3.56	0.005**
CCA3	0.13	1.94	0.016*
CCA4	0.13	1.90	0.015*

*=P<0.05; **=P<0.01

Table 4.8: Canonical Correspondence Analysis (CCA) permutation test results by terms under reduced model (terms added sequentially from first to last).

	χ^2	F	P>F
ELEV	0.14	2.10	0.17
SLOP	0.14	2.06	0.12
ASP	0.15	2.21	0.11
RCOV	0.11	1.70	0.24
MGH	0.12	1.84	0.09

WCOV	0.13	1.93	0.10
WDEN	0.07	1.10	0.55
MTD	**0.39**	**5.83**	**0.01****
LTH	0.05	0.80	0.85

ELEV=elevation, SLO=slope, ASP=aspect, RCOV=rock cover, MGH=mean grass height, WCOV=woody cover, WDEN=woody density, MTD=mean tuft diameter and LTH=leaf table height. Value in bold were the most significant and strongly associated with the second axis.

Table 4.9: Interset correlations for environmental variables.

	CCA1	**CCA2**	**CCA3**	**CCA4**
ELEV	0.30	0.21	0.37	0.03
SLO	-0.09	-0.40	0.16	0.28
ASP	0.23	**-0.46**	0.41	-0.06
RCOV	-0.17	**-0.59**	0.30	0.04
MGH	-0.25	0.18	0.13	0.15
WCOV	-0.07	**-0.52**	-0.50	0.10
WDEN	-0.19	-0.21	-0.35	0.31
MTD	**0.85**	-0.10	-0.05	0.04
LTH	-0.27	**0.43**	0.28	0.19

The values corresponding to the each variable are the coefficient indicating the contribution of that variable to each axis. The values in bold show variables with greater influence in the respective axes. ELEV=elevation, SLO=slope, ASP=aspect, RCOV=rock cover, MGH=mean grass height, WCOV=woody cover, WDEN=woody density, MTD=mean tuft diameter and LTH=leaf table height.

The importance of the fitted environmental variables on the first two axes (Table 4.10) showed significant differences for aspect, rock cover, woody cover, mean tuft diameter, and leaf table height. Mean tuft diameter and leaf table height were positively correlated with the first and second axis respectively whilst aspect, rock cover and woody cover were negatively correlated with the second axis. These variables had the most influence on community composition of the patches along the two axes and consequently are the determinants of feeding patch selection by white rhinoceros.

Table 4.10: Significance values of fitted environmental variables on the first axis and the second axis.

	CCA1	**CCA2**	**r^2**	**P>r**
ELEV	0.82	0.56	0.12	0.23
SLO	-0.23	-0.97	0.15	0.10
ASP	0.48	**-0.88**	0.26	0.02*
RCOV	-0.29	**-0.96**	0.37	0.00***
MGH	-0.81	0.59	0.09	0.32
WCOV	-0.09	**-0.99**	0.27	0.05*
WDEN	-0.65	-0.76	0.07	0.36
MTD	**0.99**	-0.13	0.73	0.00**
LTH	-0.59	**0.81**	0.27	0.03*

ELEV=elevation, SLO=slope, ASP=aspect, RCOV=rock cover, MGH=mean grass height, WCOV=woody cover, WDEN=woody density, MTD=mean tuft diameter and LTH=leaf table height. Values in bold show the direction of the relationship for variables that showed significant differences.

The ordination plot (Figure 4.2) shows an overlap between patches of both late wet and late dry season, indicating their similarity in terms of species composition and evenness. However, there were two outliers observed; one associated with the first axis dominated by *Cynodon dactylon* associated with oldlands and the second one associated with the second axis. The first axis associated with decreasing aspect, woody cover and rock cover, and increasing leaf table height and mean grass height. Feeding patches were found on relatively low slopes. Given their position on the ordination graph, we can conclude that slopes, rock cover and woody cover were similar and associated together, whilst leaf table height and mean grass height were also associated together. Mean tuft diameter was however unique and negatively related to leaf table height and mean grass height. In other words, mean tuft diameter increased with reducing grass height and leaf table height, suggesting that short grasses had larger tuft diameter.

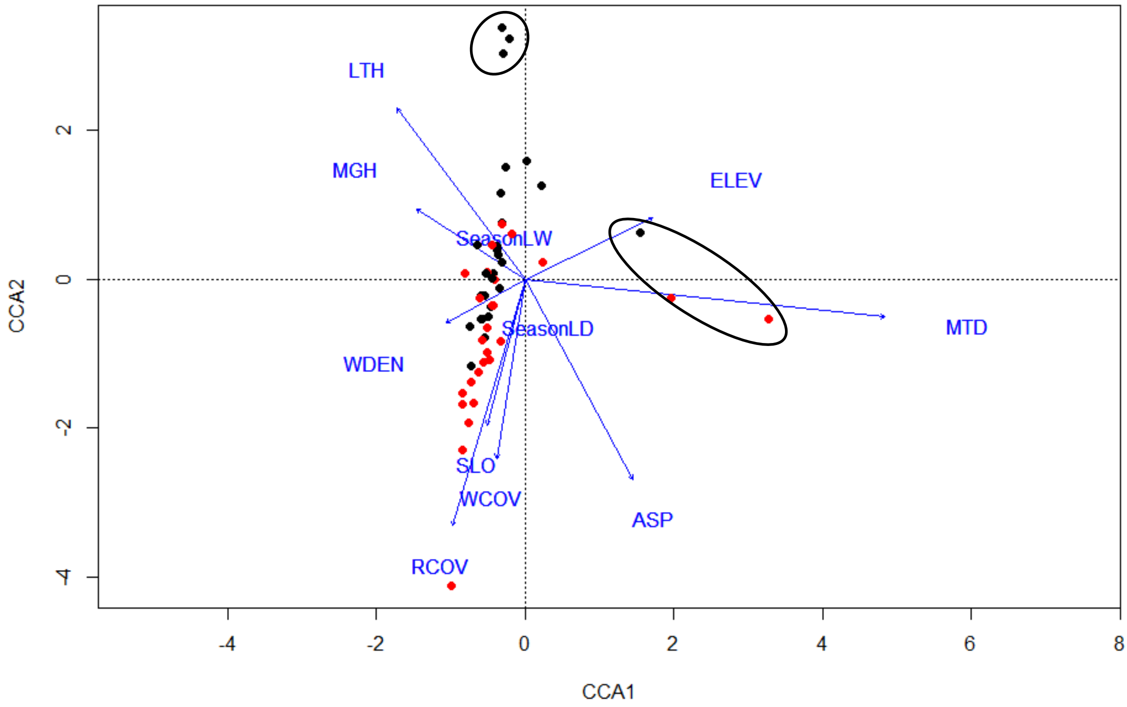

Figure 4.2: Canonical Correspondence Analysis (CCA) ordination graph showing feeding patches (black dots=late wet season; red dots=late dry season) and environmental variables (arrows). The ellipses are highlighting outliers. LTH=leaf table height; MGH=mean grass height; ELEV=elevation; MTD=mean tuft diameter; WDEN=woody density; SLO=slope; WCOV=woody cover; ASP=aspect; RCOV=rock cover.

4.3 GRASS SPECIES SELECTION

4.3.1 Grass species selected

Cynodon dactylon, Heteropogon contortus and *Eragrostis spp.* recorded the highest densities in the feeding patches (Table 4.11). These species have a grazing value ranging between average and high. During direct observations, 21 and 18 grass species were utilised respectively during the late wet and late dry seasons by white rhinoceros for the duration of the study (Table 4.11). There was a significant difference in the contribution of the different grasses in the diet of the rhinoceros during the late wet season (χ^2=69.03, df=47, P=0.02) but not during the late dry season (χ^2=47.12. df=47, P=0.42). The most selected grass species during the late wet season included *Heteropogon contortus* (22.81 %) with an average grazing value, *Eragrostis spp.* (a combined 14.02 %) with average to high grazing value, *Themeda triandra* (10.53 %) with high grazing value, and *Bothriochloa insculpta.* (10.53 %) with an average grazing value. Species such as *Cynodon dactylon* and *Setaria sphacelata* were species of high grazing value that were not selected during the late wet season. *Heteropogon contortus* also contributed the highest during the late dry season (25 %), followed once again by *Eragrostis spp.* (a combined 14.49 %) and *Themeda triandra* (10.42 %). *Cynodon dactylon* and *Setaria sphacelata* were, as opposed to the late wet season, selected during the late dry season. *Bothriochloa insculpta* on the other hand was not used during the late dry season. The proportion of total diet of these key species comprise seven species in the late wet season (58 %) and six species in the late dry season (50 %).

Table 4.11: Density of selected grass species in feeding patches, their grazing value and their contribution in the diet of white rhinoceros between the late wet and the late dry season of 2008 in the Songimvelo Nature reserve.

Grass species	**Grazing value**	**Density (Mean±SD)**		**Utilisation (%)**	
		Late wet	Late dry	Late wet	Late dry
ARISPP	L	9.63±12.86	5.83±0.58	1.75	4.17
BEWBIF	L	5.88±7.83	3.51±5.63	3.51	2.08
BOTBLA	L	3.50±6.67	0.00±0.00	1.75	-
BOTINS	A	14.38±36.28	14.80±1.97	10.53	-
BRABRI	A	4.80±8.02	2.25±14.05	1.75	2.08
BRASER	A	2.71±4.24	2.46±1.53	1.75	2.08
CYNDAC	H	39.38±15.21	119.85±131.09	-	4.17
DIGSPP	H	8.83±6.04	4.67±8.45	1.75	-
ERACHL	A	4.83±10.15	15.26±10.16	1.75	4.17
ERACUR	H	8.25±10.92	9.60±15.38	1.75	4.17
ERARAC	A	11.19±4.87	5.56±1.50	1.75	2.08
ERASUP	A	10.73±2.14	4.81±1.75	7.02	4.17
HETCON	A	34.20±4.41	26.58±7.27	22.81	25.00
HYPDIS	A	5.72±6.24	6.75±9.36	3.51	2.08
HYPHIR	A	7.66±4.90	10.52±3.78	3.51	6.25
LOUSIM	A	5.62±2.49	7.32±18.50	5.26	-
PANMAX	H	2.00±1.15	6.67±8.07	1.75	-
SETSPH	H	0.00±0.00	17.91±0.58	-	8.33
SPOAFR	L	2.38±12.13	0.00±0.00	3.51	-
SPOPYR	L	0.00±0.00	2.67±12.15	-	2.08
SPOSTA	L	19.17±0.00	13.83±0.00	1.75	2.08
THETRI	H	8.67±2.14	4.33±0.58	10.53	10.42
TRABER	L	8.77±4.29	0.00±0.00	3.51	-
TRASPI	L	1.00±0.55	6.27±1.26	-	4.17
TRILEU	A	0.00±0.00	9.88±2.12	-	2.08
UROMOS	H	9.35±12.80	0.00±0.00	1.75	-

The full names of grass species can be found in Appendix A; Grazing values: H=High, A=average and L=low.

4.3.2 Factors influencing grass species selection

The fitted models indicated that the first two models (rank 1 and 2) were the best at describing grass species selection within forage patches ($\Delta AIC_c<4$; cumulative probability=0.71; Table 4.12). The first model (rank 1) was the best of all models (ΔAIC_c=0.00; ω_i=0.51) and included grass species, density of grass species and mean tuft diameter as variables in the model. This model indicated that the presence of grass species as well as their density and basal cover were the best drivers of species selection by white rhinoceros in feeding patches. The model also shows that in a feeding patch, WR are more likely to select *Themeda triandra*, *Heteropogon contortus*, *Setaria sphacelata* and *Bothriochloa spp*. and avoid other species (Table 4.13). The second best model (rank 2) included season, grass species, mean tuft density and grass density as important variables (AIC_c=275.59; ΔAIC_c=1.93; ω_i=0.20) indicating that season may also play a role in the selection of grass species by white rhinoceros. The evidence ratio between the first and the second model is 2.63 confirming that the first model was the best (evidence ratio ≈ 2.7). The models ranked 1 to 7 totalled a model probability sum of 0.96.

Table 4.12: Candidate models to test the importance of grass species and other variables in the feeding patches selected by white rhinoceros in the Songimvelo Nature Reserve. All selected models with $\Delta AIC_c<7$.

Rank	Explanatory variables	AIC_c	ΔAIC_c	k	ω_i	LL
1	Species + MTD + Density	273.66	0.00	11	0.51	-125.27
2	Season + Species + MTD + Density	275.59	1.93	12	0.20	-125.13
3	Season + Species + MTD + Season x Density	277.67	4.00	13	0.07	-125.06
4	Season + Species + Density + Season x MTD	277.75	4.09	13	0.07	-125.10
5	Species + MTD	277.80	4.14	10	0.06	-128.44
6	Season + Species + MTD	279.73	6.06	11	0.02	-128.30
7	Species + Density	279.81	6.15	10	0.02	-129.44
8	Season + Species + Season x MTD + Season x Density	279.85	6.19	14	0.02	-125.02

MTD=mean tuft diameter; AIC_c: Akaike's information criterion corrected for small sample size; ΔAIC_c: differences in Akaike's information criterion; k: number of parameters; ω_i: AIC_c weights; LL: log likelihood

Table 4.13: Odds ratios, log (odds ratios) and confidence intervals of selected grass species in the best model.

			Confidence intervals	
	Odds ratio	Log (odds ratios)	2.5 %	97.5 %
Cynodon dactylon	0.13	-0.89	0.00	1.94
Eragrostis spp.	0.55	-0.26	0.10	2.63
Heteropogon contortus	3.81	0.58	0.48	36.51
Other	0.28	-0.55	0.05	1.25
Setaria sphacelata	1.99	0.30	0.16	51.34
Sporobolus spp	1.09	0.04	0.13	9.24
Themeda triandra	5.96	0.78	0.57	141.51

CHAPTER 5

DISCUSSION AND MANAGEMENT IMPLICATIONS

5.1 FEEDING HABITAT SELECTION BY WHITE RHINOCEROS

The anatomy and morphology of an animal may affect its choice of food (Shipley, 1999) and to a certain extent its choice of habitat. This may be evident with the white rhinoceros where, because of its large body size, short neck and low slung large head, prefers flat low-lying areas (Owen-Smith, 1973:130; Pienaar, Bothma & Theron, 1993:79; Shrader, 2003:53) and may not be able to select steep slopes. Habitat selection on the other hand, was reported to coincide with seasonal changes and correspond to food availability (Babaasa, 2000:116). Measuring habitat availability for white rhinoceros in an area like Songimvelo Nature Reserve can prove to be quiet difficult because of its mountainous and steep topography. White rhinoceros are generally known to prefer low-lying area and avoid highly rocky and steep areas (Myers, 1998). In the SNR, only the Komati Valley and the Mtsoli Valley seem to meet the requirements to qualify as potential habitat for white rhinoceros. But the Mtsoli Valley, because of its position in the centre of the reserve, the mountainous features separating it from the Komati Valley and the presence of the Komati River, is not accessible to the white rhinoceroses. This leaves only the Komati Valley as available habitat. The size of the area identified as available habitat was 6488 ha and was more or less similar to the 6500 ha area previously determined as suitable habitat for the white rhinoceros by Steyn (2004). Only about 21% of the southern section of the reserve is available to white rhinoceros.

The area is largely covered by the Open Low Woodlands which is dominated by *Heteropogon contortus*, and provides white rhinoceros with food during both late wet and late dry season. The observed selection of the overall habitats by white rhinoceros in the late wet season was possibly to maximise intake of the most nutritious grasses (quality) during that season. Numerous studies have shown that during the wet season, white rhinoceros fed on short grasslands taking advantage of the most nutritious grasses available (Owen-Smith, 1973:120; Pedersen, 2009:91; Shrader, 2003:41; Shrader & Perrin, 2006:313). During the late dry season, white rhinoceros were reported to be less selective and fed on less nutritious species when the grassland were depleted (Owen-Smith, 1988:204; Shrader, 2003:15; Shrader & Perrin, 2006:382). This could explain the lack of selectivity of the overall habitats during the late dry season observed in this study. These results may also be related to the small sample size during the late dry season, and thus may not truly reflect what happened.

The selection of Open Low Woodlands (OLW) and Oldlands (OL) in proportion to their availability could mean that those two habitat types contained sufficient food for the white rhinoceros during the late wet season. *Heteropogon contortus* for example, which is dominant in OLW, is a grass species of average grazing value and is palatable during the early summer (Van Oudtshoorn, 1999:66); however, it may remain palatable to white rhinoceros throughout the year if it is kept short in a lawn form through grazing (Shrader, 2003:48). Shrader (2003:48) also reported a high acceptance of *H. contortus* by white rhinoceros during the late dry season. The Shrublands were less frequented during the late wet season possibly because of their species composition (Shrubs and grass species such as *Loudetia simplex* and

Themeda triandra). During the late dry season, white rhinoceros showed no preference for a specific habitat probably, because at that stage they were more concerned about quantity than quality. Shrader (2003:102) suggests for example that white rhinoceros relies on fat reserves to maintain them during periods of low food quality and availability.

Within the selected habitats, white rhinoceros did not use all topographical variables evenly between the seasons. There was a significant difference in aspects, rock cover and leaf height table of the selected feeding patches between the late wet and late dry season (Table 4.3). A close examination of the proportion of observations in the different aspects revealed that rhinoceros predominantly used south-facing slopes during the late wet season and shifted to predominantly using west-facing slopes during the late dry season. Auslander, Nevo and Inbar (2003:405) pointed out that in the northern hemisphere, south-facing slopes may receive as much as six times more solar radiation than north-facing slopes. The opposite may be true in the southern hemisphere where north-facing slopes may receive more solar radiation than south-facing slopes. Depending on the season, animals grazing on different slopes may experience dissimilar temperatures and wind speeds (Houseal & Olson, 1995:501) that can affect thermoregulation (Harris *et al.*, 2002). White rhinoceros do not graze during the hottest part of the day (Owen-Smith, 1973:112), as such their use of certain slope aspects may be explained by a thermoregulation benefit. However, animals can always adjust or move around when they eat to get around the thermoregulation issues. Auslander *et al.* (2003:405) further discuss that in the northern hemisphere, south-facing slopes are more xeric environments, warmer, drier and have a more variable microclimate than north-facing slopes. Consequently, in the southern hemisphere, south facing slopes should be wetter and thus influence the rate senescence of plants on these aspects and influence the difference in food quality and availability. Since WR are known to prefer the greener more palatable grasses (Shrader, Owen-Smith & Ogutu, 2006:376), the microclimate differences could also be a determinant in the selection of slope aspects. Between thermoregulation and microclimate differences, we speculate that the former could play a major role than the later because of the observed shift from south aspects in the late wet season to west aspects in the late dry season.

Furthermore, feeding patches contained more rocks and less vegetation because of the lower leaf table height during the late dry season. However, although not significant (Table 4.3), elevations were lower in the late wet season (853.96±27.88 m) than in the late dry season (861.15±24.05 m), and slopes were also lower in the late wet (3.80±2.25 degrees) than the late dry season (4.90±3.25 degrees). This change in elevation and slope could be the cause of the significant difference in rock cover between the late wet and the late dry season (feeding patches in the late wet season were less rocky than patches in the late dry season). This result was also confirmed by the CCA ordination graph (Figure 4.2) which showed that slope and rock cover were positively correlated. Available phytomass could also be limited on higher-lying slopes because the rocky features limit grass growth. In the SNR, the higher the elevation, the rockier the area, and the rockier the area is, the less vegetation would be found, explaining the low leaf height table. The low leaf height table could also be a result of grazing by other herbivores as well as depletion of vegetation during the late dry season. Following the broad classification of slopes in the reserve, we observed that white rhinoceros used valley bottom (0-6°) more than footslopes (6-12°) and did not use midslopes (>12°). This pattern of using valley bottoms and footslopes is consistent with previous studies (Owen-Smith, 1973:53; Pedersen, 2009:51; Perrin & Brereton-Stiles, 1999:76; Waldram, 2005:14) which reported that white rhinoceros preferred grazing on low-lying areas.

The change observed in the position of feeding patches during the late dry season could be due to the resources being depleted in the areas selected during the late wet season, thus driving the rhinoceros to use other areas during the late dry season. This has resulted in an even use of available habitats during the late dry season indicated by the non-significant results reported by the chi-square analysis. A study by Bailey and VanWagoner (2004) reports on cattle utilising steeper slopes, higher elevations and areas further from water sources as the nutrient rich valley bottoms became depleted. White rhinoceros on the other hand might not be able to go up very high elevations because of their morphology, but will be able to change habitats and take advantage of resources that are within their reach. No rhinoceros were observed utilising Grassland Biome on the top of the mountains during the study although Owen-Smith (1973:128); 1988:120) found that white rhinoceros in iMfolozi move onto and utilise hillslope *Themeda* grasslands in the very late dry season. White rhinoceros introduced in Kenya as well have previously been reported to use high-lying areas. The elevations in iMfolozi range between 45 m and 579 m whilst in the current study elevations ranged between 700 and 1 900 m. In this study area, about 80 % of the area is mountainous and the grasslands are situated on the top of mountains, at very high elevations. We speculate in this study that there was probably enough food available to meet the nutritional needs for the rhinoceros in the lower-lying areas. Consequently there was no need for the rhinoceros to go to higher-lying areas.

Catenal position has been reported to influence soil moisture availability with the lower levels, such as bottomlands, containing more clay than uplands (Scholes, 1990:417; Scoones, 1995:232). These higher clay concentrations, in turn, retain soil moisture which sustain green grass and produce a higher grass biomass (Bell, 1970:111; McNaughton, 1985:259; Scoones, 1995:221). Macandza *et al.* (2004:113) as well as Bowers (2006:111) also found that grasses remained greener in bottomlands and in nutrient-rich soils during the latter part of the late dry season. Although greenness of feeding patches and grass species was not measured in this study, this could also have played a role in the selection of the feeding patches and grass species. *Setaria sphacelata* for example, as well as short *Heteropogon contortus,* tended to remain green throughout the late dry season. These species might have been maintained in this state because of grazing by rhinoceros or other species, and by available moisture in the soil.

5.2 GRASS SPECIES DIVERSITY AND COMMUNITY STRUCTURE OF FEEDING PATCHES SELECTED BY WHITE RHINOCEROS

Species diversity as expressed by Shannon's diversity index combines both species richness and evenness into a single value and can be seen as both a strength and a weakness. It is a strength because it provides a simple summary, a weakness because it makes it difficult to compare communities that differ greatly in richness. In this study, the areas sampled were small and did not show any significant differences in species diversity between the late wet and the late dry seasons, indicating a more equitable distribution of grass species in feeding patches of both seasons. Generally, Shannon diversity index increases as both the richness and the evenness of the community increase. The non-significant results obtained in this study indicate that grass species diversity cannot explain the selection of feeding patches of white rhinoceros as the latter can be affected by environmental factors (Dörgeloh, 1999:519; Reddy, Balkwill & McLellan, 2009:365).

The community ordination of feeding patches was important in determining the compositional gradients in the data within the patches of both late wet and late dry seasons. The DCA ordination showed an overlap between patches of the late wet and late dry season and little variability in grass species composition and distribution (30.73% explained by the four axes). This analysis revealed once again that grass species composition alone cannot account for all the variation as well as selection. The dispersion of the grass species around the patches however, according to the "centroid principle" and the "distance rule", showed that *Heteropogon contortus,* was at the centre of the large feeding patch cluster (Figure 4.1) indicating that it was the most important species largely associated with feeding patches. Other species that were in close proximity included *Aristida spp*. and *Eragrostis spp*.

The results of the DCA ordination also revealed a close correlation between the position of the plots and the environmental variables. The ordination graphs revealed that environmental variables, in combination with grass species, could explain the feeding patch selection pattern of white rhinoceros. These results confirm the argument of Senft (1989:283) who state that abiotic constraints must be combined with resulting biotic factors to predict grazing distribution pattern.

In general, feeding patches occurred in open areas, contained short grasses, were less rocky, and occurred on cooler aspects. This preference has been described by previous studies (Pedersen, 2009:46; Shrader, 2003:128) and is highlighted in this study by observing the proportion of patches in each of the measured habitat variables. The disturbed areas in this study included old lands as well as old settlements which were avoided by white rhinoceros during the late wet season. These disturbed areas were characterised by highly unpalatable grasses. In conclusion, grass density explained selection of feeding patches, strongly related and influenced by environmental factors i.e. landscape position and slope gradient.

5.3 GRASS SPECIES SELECTION BY WHITE RHINOCEROS

Factors that affected selection on the patch level may also play a role in the selection of species (Van Der Merwe & Marshal, 2012:410). In this study, species like *Heteropogon contortus* were important on both the patch scale as well as in the selection of species by white rhinoceros. Other species of importance included *Eragrostis spp*. as well as *Themeda triandra*. White rhinoceros were observed feeding on a total of 22 grass species during both late wet and late dry seasons and the majority of their diet consisted of species such as *Heteropogon contortus* to *Eragrostis spp*., *Cynodon dactylon*, *Themeda triandra* and *Setaria sphacelata*. The nutritional value of these grass species could have played an important role in increasing feeding patch selection by white rhinoceros. This study also found that white rhinoceros selected feeding patches with a high proportion of nutritious species (Table 4.11). *Heteropogon contortus* for example, is nutritious during early stages of growth and may remain green and palatable throughout the year through the action of grazing by other herbivores and it forming short lawn-like patches. Species such as *Tristachya leucothrix*, *Hyparrhenia hirta*, *Bothriochloa insculpta*, *Eragrostis rigidior* and *Sporobolus pyramidalis*, that showed less association with feeding patches, were either less utilised or not utilised at all.

Perrin and Brereton-Stiles (1999:72) observed a facilitation in grazing between buffalo and rhinoceros where the former species grazed ahead of the latter. Waldram *et al.* (2008:108) on the other hand found that white rhinoceros were able to maintain short grass patches in mesic areas (rainfall of 750 mm per annum) whilst other species also played a role in semi-arid area (600 mm rainfall) by observing facilitation and competition. Long term average rainfall in the area is 645 mm but during the study only 575.7 mm was received. Consequently, other game species could also play a role in maintaining the short grass patches in this area and may compete with the WR. *Heteropogon contortus* was the dominant grass species in the area and is commonly associated with open grassland (Van Oudtshoorn, 1999:66). This may explain the use of open low canopy areas during both seasons, and confirm the findings of previous studies. Another variable of interest is the mean tuft diameter of the grass species, which was important both on the patch level and on the species level. Basal cover has been known to influence selection of plants by large herbivores (Ganskopp & Rose, 1992:538). Grass species with large diameters would tend to have more foliage and thus attracting large herbivores especially during the late dry season. *Cynodon dactylon* had a higher likelihood of being avoided possibly because it had smaller tuft diameters and occurred in previously disturbed areas. Kraaij and Novellie (2010:21) found most herbivores to favour *Cynodon dactylon* lawns even when they occurred in previously disturbed areas in the Bontebok National Park. In the case of SNR, WR probably had enough food available in the most selected areas.

5.4 MANAGEMENT IMPLICATIONS

Formulation of sound management strategies of a specific species requires an understanding of the ecology of this species in its environment and the relationship and adaptation the species develop in the environment. This management strategy holds true for the application of the metapopulation theory to all MTPA rhinoceros populations in Mpumalanga Province, South Africa.

The feeding of white rhinoceros is well documented (Owen-Smith, 1973:12; 1975:337; Perrin & Brereton-Stiles, 1999:72; Pienaar, 1994; Shrader, 2003:1; Shrader *et al.*, 2006:376) but universal conclusions are inappropriate on the level of feeding patches and species, because the results are specific to a given area. Songimvelo Nature Reserve is a mountainous area with a restricted amount of low lying areas and the majority of the vegetation being in the Sourveld. The area also has a combination of Grassland and Savanna Biomes which are evenly distributed across elevation ranges (savanna on the lower-lying areas and grasslands at high elevations). Management should therefore take these factors into consideration when managing the white rhinoceros population as well as the habitat. Management should take cognisance of the physiological, ecological and environmental requirements of the WR when formulating management actions in the reserve. Management should focus on maintaining a viable carrying capacity by keeping an effective population biomass and reducing overgrazing, proper sex ratios by taking into consideration the restricted available area and the male WR's territorial behaviour and, enough nutritive grass species available through adequate veld management and monitoring programs.

A selective grazer is an animal that is able to aim for and get a particular species or part of a species. White rhinoceros are not selective grazers in the true sense of the term but may be selective of grassland types. They may be able to select certain areas with a high density of high to moderately nutritious grasses, but might not able to select specific species or species parts as a result of their broad muzzle. This study has shown that white rhinoceros are selective of the areas they feed in. They selected patches of similar grass species diversity during both late wet and late dry seasons and utilised specific aspects, slopes and elevation. The management in the reserve should aim at preserving and maintaining grazing that play a great role in the movement of WR. The management of the habitat should also take into consideration the facilitation role that other herbivores could play in maintaining grazing lawns whilst maintaining an appropriate stocking rate to avoid excessive competition between species. During this study, WR was observed feeding with other herbivores in their proximity implying that either mechanism (facilitation or competition) may be present to a certain extent.

It is also essential that the management of white rhinoceros habitat focuses on protecting the preferred species. Intensive grazing over long periods has a negative effect on preferred grass species and may promote the growth of unpalatable species through the lack of competition. Furthermore, the use of excessive fire can create a fire climax where species that respond well to regular burning start to dominate. Grazing by herbivores does not affect basal cover but rather moisture content does. In an attempt to protect the preferred species and create suitable grazing habitat for white rhinoceros, management has to take cognisance of all variables at play.

The mountainous feature of the reserve has reduced the amount of habitat available for the white rhinoceros in this area. However, these features may not be the only limiting factor for habitat availability in Songimvelo Nature Reserve.

CHAPTER 6

GENERAL CONCLUSION

6.1 SUMMARY

The main aim of this study was to describe the factors driving feeding patch selection by WR in the SNR during the late wet and the late dry season. This would contribute towards the management of this species in the reserve by providing an insight in their distribution and movement pattern between periods of high and low food availability and as well as factors driving this distribution. The first objective of the study was to determine feeding habitat selection by observing preference of habitats available to WR in the reserve. The second objective sought to describe characteristics (slope, aspect, elevation, rock cover) of the selected feeding patches during the late wet and late seasons in the reserve. These involved observing the rhinoceros feeding, identifying their feeding patch and recording the GPS coordinates of the patches. The third objective sought to compare the floristic characteristics of feeding patches selected by looking at grass species diversity and grass species composition in the selected feeding patches, and observe the influence of environmental variables on grass species composition. The fourth objective was to identify factors driving the selection of grass species within the feeding patches through modelling. And finally this study tried to provide management recommendations for the conservation of the WR in the SNR.

This study mainly showed that the selection of feeding areas by white rhinoceros is driven by both biotic (grass species composition) and abiotic factors (slope, elevation and aspect). Because of the rugged and mountainous characteristic of the

SNR, the white rhinoceros movements were restricted to the lower-lying Komati Valley, which was the only area available to them. White rhinoceros were observed to be selective of specific habitats during the late wet season whilst using all available habitats in proportion during the late dry season. During the late dry season, rhinoceros used habitat types that were avoided during the late wet season. This study suggests that white rhinoceros adapt to changing availability of resources as seasons change.

Furthermore, the ordination analyses showed an overlap between feeding patches of the late wet and the late dry season indicating a similarity in species composition. The most important environmental variables in the ordination of feeding patches were aspects, rock cover, woody cover, mean tuft diameter and leaf table height. This animal used open and less rocky areas. They used southern and western aspects during the late wet and late dry seasons respectively. Mean tuft diameter appeared to be the most important variable of all. At species level, the combination of species, the grass density and mean tuft diameter proved to be the best model in explaining selection of grass species within feeding patches. *Heteropogon contortus* was the most favoured grass species and the model showed that it had a higher likelihood of being selected if it occurred in a feeding patch. This study indicates that white rhinoceros select feeding patches on the basis of species composition and abundance of the high quality grasses available in the lower-lying areas of the reserve. The model of species selection showed that given the presence of certain species, *Cynodon dactylon* had the highest likelihood of being avoided possibly because it occurred on previously disturbed areas and has low leaf material production. However, previously disturbed areas with *Cynodon* *dactylon* are favoured by grazers such as bontebok, impala and wildebeest because of its high nutritional value (Kraaij & Novellie, 2010:21). Therefore, the feeding of white rhinoceros does not constitute optimal foraging.

6.2 FUTURE RESEARCH

Studies on the impact of white rhinoceros on new habitat as well as potential competition and facilitation with other grazers should be carried out (Okita-Ouma, Amin & Kock, 2007). Waldram *et al.* (2008:101) found that white rhinoceros compete in low rainfall areas and facilitate for other grazers during the wet season in high rainfall areas. In Hluhluwe iMfolozi Park for example, white rhinoceros open up grazing patches for other species, such as impala (*Aepyceros melampus*), zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*). One could investigate the extent to which white rhinoceros are creating and maintaining grazing patches in Songimvelo Nature Reserve. Nutritional studies could also be undertaken, looking at forage quality and changes in diet between seasons. Another study could look at factors that may limit habitat availability to white rhinoceros in the reserve.

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ANNEXURES

Annexure A: List of grasses, trees and forbs recorded in feeding patches and control plots of white rhinoceros in Songimvelo Nature Reserve.

SCIENTIFIC NAMES	COMMON NAMES	ABBREV.
GRASSES		
Andropogon chinensis	Hairy blue grass	ANDCHI
Andropogon schirensis	Stab grass	ANDSCH
Aristida bipartita	Rolling grass	ARIBIP
Aristida congesta subsp. barbicollis	Spreading three-awn	ARIBAR
Aristida congesta subsp. congesta	Tassel three-awn	ARICON
Aristida diffusa	Iron grass	ARIDUF
Aristida scabrivalvis	Purple three-awn	ARISCA
Bewsia biflora	False love grass	BEWBIF
Bothriochloa bladhii	Purple plume grass	BOTBLA
Bothriochloa insculpta	Pinhole grass	BOTINS
Brachiaria serrata	Velvet Signal grass	BRASER
Brachiaria brizantha	Common signal grass	BRABRI
Cymbopogon excavatus	Broad-leaved turpentine	CYMEXC
Cynodon dactylon	Couch grass	CYNDAC
Digitaria eriantha	Common finger grass	DIGERI
Digitaria longiflora	False couch grass	DIGLON
Digitaria ternata	Black-seed finger grass	DIGTER
Diheteropogon amplectens	Broad-leaved bluestem	DIHAMP
Elionurus muticus	Wire grass	ELIMUT
Eragrostis chloromelas	Narrow curly leaf	ERACHL
Eragrostis curvula	Weeping love grass	ERACUR
Eragrostis nindensis	Wether love grass	ERANIN
Eragrostis racemosa	Narrow heart love grass	ERARAC
Eragrostis superba	Saw-tooth love grass	ERASUP
Eragrostis rigidior	Broad curly leaf	ERARIG
Heteropogon contortus	Spear grass	HETCON
Hyparrhenia hirta	Common thatching grass	HYPHIR
Hyperthelia dissoluta	Yellow thatching grass	HYPDIS
Loudetia simplex	Common russet grass	LOUSIM
Melinis repens	Natal red top	MELREP
Monocymbium ceresiiforme	Boat grass	MONCER
Panicum maximum	Guinea grass	PANMAX
Paspalum scrobiculatum	Veld paspalum	PASSCR
Pogonarthria squarrosa	Herringbone grass	POGSQU
Schizachyrium sanguineum	Red autumn grass	SCHSAN
Setaria sphacelata	Golden bristle grass	SETSPH
Sporobolus africanus	Ratstail dropseed	SPOAFR
Sporobolus centrifugus	Olive dropseed	SPOCEN

Sporobolus stapfianus	Fibrous dropseed	SPOSTA
Themeda triandra	Red grass	THETRI
Trachypogon spicatus	Giant spear grass	TRASPI
Tragus berteronianus	Carrot-seed grass	TRABER
Trichoneura grandiglumis	Small rolling grass	TRIGRA
Tristachya leucothrix	Hairy trident grass	TRILEU
Urochloa mosambicensis	Bushveld signal grass	UROMOS
TREES		
Aloe marlothii subsp. *Marlothii*	Mountain aloe	ALO MAR
Berchemia zeyheri	Red ivory	BER ZEY
Celtis africana	White stinkwood	CEL AFR
Combretum erythrophyllum	River bushwillow	COM ERY
Combretum hereroense	Russet bushwillow	COM HER
Combretum zeyheri	Large-fruit bushwillow	COM ZEY
Dichrostachys cinerea	Sickle bush	DIC CIN
Dombeya rotundifolia	Common wild pear	DOM ROT
Erythrina lysistemon	Common coral tree	ERY LYS
Euclea crispa	Blue guarri	EUC CRI
Faurea rochetiana	Broad-leaved beech	FAU ROC
Faurea saligna	Transvaal beech	FAU SAL
Olea europaea	Wild olive	OLE EUR
Ozoroa sphaerocarpa	Currant resin tree	OZO SPH
Peltophorum africanum	Weeping wattle	PEL AFR
Rhoicissus tridentata	Bushman's grape	RHO TRI
Searsia dentata	Nana-berry	SEA DEN
Searsia pentheri	Common crowberry	SEA PEN
Searsia rehmanniana	Blunt-leaved currant	SEA REH
Senegalia ataxacantha	Flame thorn	SEN ATA
Senegalia caffra	Common hook-thorn	SEN CAF
Vachellia davyi	Corky thorn	VAC DAV
Vachellia karroo	Sweet thorn	VAC KAR
Vachellia nilotica	Scented thorn	ACA NIL
Ziziphus mucronata	Buffalo-thorn	ZIZ MUC

ABBREV. = Abbreviation