Habitat use and diet selection of reintroduced white rhinoceros (*Ceratotherium simum*) in Pafuri, Kruger National Park

by

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Date: 14 January 2009
DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part, submitted it at any university for a degree.

Signature

Gayle Pedersen
Name in full

14 January 2009
Date

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I dedicate this thesis to my Dad, Svend Pedersen, for winning his fight against cancer.

Also to the memory of three of my heroes who were not so fortunate:

His ebullient mother, my Farmor, Dagny Pedersen 1917 – 2004

His inimitable partner, Joy van den Berg 1942 – 2004

And my good friend David Read 1972 – 2006.
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“In the bush, pride goeth before a fall, and if you’re lucky you will only be cast down and not dragged away and eaten.” Bruce Bryden, A Game Ranger Remembers.
ABSTRACT

In 2005, six white rhinoceroses (*Ceratotherium simum*) were reintroduced into Pafuri, in the far northern section of Kruger National Park (KNP), South Africa, as part of a large mammal reintroduction project. All six individuals were fitted with horn radio transmitters. Rhinos have been absent from Pafuri for over a century, and this project aimed to establish a breeding nucleus in the area. The aim of this study was to monitor post-release movement and habitat use of these animals within the 203 km$^2$ study area and assess the short term success of the re-introduction project as well as the suitability of the five landscape types in Pafuri as a habitat for white rhinoceros. Habitat suitability and selection was assessed at two ecological hierarchical scales: 1) landscape system, analysed further down to the spatial scale of range and territory establishment, and 2) feeding station for diet selection. Rhinos were tracked for 12 months and a database of 719 sighting records was compiled. These data were used to determine the utilisation of and preference between the Pafuri landscape types, using preference indices that compare utilisation versus availability. An $a$-LoCoH nonparametric kernel method was used to calculate home ranges and utilisation distributions of each rhino. Feeding surveys were attempted by backtracking along fresh rhino feeding paths and recording the grass species present and eaten in 0.7 m x 0.7 m quadrats. Faecal samples were collected and analysed using microhistological techniques and dietary composition was assessed for each rhino.

Landscape preference analyses showed that the rhinos favoured *Colophospermum mopane* Shrubveld on calcrete in the dry season, and the Punda Maria Sandveld in the wet season. The territory establishment of the dominant bull was substantially larger (44.8 km$^2$) than those of adult male rhinos in the rest of KNP. Ranging areas of the mature females (17 – 25.4 km$^2$), were consistent with sizes of previous studies. The two sub-adults ranged far more extensively, establishing an 84.1 km$^2$ annual range during the study period. The annual diet consisted of mostly perennial grass species, with moderate grazing value species dominating for most of the year. Dietary analyses showed that *Schmidtia pappophoroides, Eragrostis superba, Enneapogon cenchroides, Cenchrus ciliaris* and *Stipagrostis uniplumis* were the primary grass species consumed.
This study demonstrated that the Pafuri rhinos are behaving similarly to rhinos established in other areas, with movements around the landscapes being primarily influenced by rainfall and permanent water sources, and the high quality grazing that is more abundant in the wet season. Their range and territory sizes were inevitably large, for a low density area, but not uncommonly so. The most significant outcome of this study was the preference shown for the *Colophospermum mopane* Shrubveld on calcrite landscape that is classed as unique within South Africa, and was also ranked as ‘avoided’ by the earlier KNP studies into landscape preferences of rhinos. The grass cover in Pafuri, although sparse and very dry, contained a diversity of low to high grazing value grasses that the rhinos appeared to exploit to the best of their ability. The abundance of moderate grazing value species in their diets, and the low number of low grazing value species suggests that they are maximising the opportunities to graze on nutritious grasses when they are available. Our findings suggest that the Pafuri area is suitable for the establishment of a small breeding nucleus of white rhinos. The abundance of permanent water, in the form of springs, is a great advantage however, the potential for bush encroachment into grasslands in areas of such low rainfall needs to be considered if the population continues to grow at the current rate. The birth of two new calves in 2008 confirms that these rhinos have settled and adapted to their new habitat, and is a very promising sign for the future of this increasing subpopulation.
In 2005 is ses wit renosters (*Ceratotherium simum*) hervestig in Pafuri in die noordelike gedeelte van die Kruger Nasionale Park (KNP), Suid-Afrika, as deel van ‘n groot soogdier hervestigings projek. Al ses individue is gemerk met horing radiosiente toestelle. Renosters kom vir al meer as ‘n honderd jaar nie meer in Pafuri voor nie en hierdie projek was daarop gemik om ‘n teel-nukleus in hierdie gesied te vestig. Die doel van hierdie studie was om die verspreiding van die renosters na loslating en habitat-gebruik binne die 203 km² studie-omgewing te monitor, om die korttermyn sukses van die hervestigings program te evalueer en ook te kyk na die gepastheid van die vyf landskap-tipes in Pafuri as ‘n geskikte habitat vir die wit renosters. Habitatgepastheid en seleksie is geëvalueer volgens twee ekologiese hiërargiese skale: 1) landskapsisteem, wat in meer resolusie tot die ruimtelike skaal van reikwydte en omgewingsvestiging geanaliseer is, en 2) voedings-stasie vir dieet-seleksie. Renosters is vir 12 maande gevolg en ‘n databasis wat 719 waarneming-rekords bevat, is opgestel. Laasgenoemde data is gebruik om die gebruik en voorkeur vir die Pafuri landskap tipes te bepaal met behulp van voorkeur-indikators wat die gebruik met beskikbaarheid vergelyk het. ‘n a-LoCoH nie-parametriese kern metode is gebruik om die reikwydte en gebruikverspreidings van elke renoster te bereken. Voedingsopnames is gedoen deurdat vars renoster voedings-paadjes terugwaarts gevolg is en die grasspesies teenwoordig en waarop gevoed is, in 0.7 m x 0.7 m kwadrante te bepaal. Mismonsters is versamel en geanaliseer deur gebruik te maak van mikro-histologiese tegnieke en voedingswaarde-samestellings is vasgestel vir elke renoster.

Landskapsvoorkeur analises dui daarop dat die renosters in die droë seisoen *Colophospermum mopane* struikveld wat op kalkreet groei verkies en die Punda Maria Sandveld in die reën seisoen. Die terrein vestiging van die dominante bul was aansienlik groter (44.8 km²) in vergelyking met die volwasse bul renosters in die res van die KNP. Reikwydte van die volwasse koeie (17 – 25.4 km²) was ooreenstemmend met dié van vorige studies. Die reikwydte van die twee sub-volwassenes het baie meer gevarieer, deurdat ‘n 84.1 km² jaarlikse reikwydte gedek was binne die studie periode. Die jaarlikse dieet het meestal bestaan uit meerjarige
grasspesies, met spesies met matige weidingswaarde wat oorheers vir meeste van die jaar. Voedingswaarde analises dui daarop dat *Schmidtia pappophoroides, Eragrostis superba, Enneapogon cenchroides, Cenchrus ciliaris* en *Stipagrostis uniplumis* die primêre gras spesies was waarop gewei word.

Die studie het bewys dat die Pafuri renosters soortgelyke gedragspatrone vertoon het as renosters in ander gevestigde gebiede, deurdat bewegings binne die landskap hoofsaaklik beïnvloed word deur reënval en permanente waterbronnewe, asook die hoë gehalte weidingsbronnewe beskikbaar gedurende die reën seisoen. Hulle reikwydte- en terrein-groottes was uiteraardelik groot vir ‘n lae-digtheid areas, maar dit is nie buitengewoon nie. Die mees betekenisvolle gevolgtrekking van die studie was die voorkeur vir die *Colophospermum mopane* struikveld op kalkreet landskappe wat beskou word as uniek aan Suid-Afrika, en wat ook beskou was as ‘vermy’ deur vroër KNP studies tov. landskap voorkeure spesifiek vir renosters. Die grasbedekking in Pafuri, alhoewel yl en baie droog, het tog oor ‘n verskeidenheid grasse beskik wat van lae tot hoë weidings waarde het, en wat die renosters tot die beste van hulle vermoe benut het. Die oorvloedige teenwoordigheid van beide spesies met matige weidingswaarde in hulle dieët en die lae hoeveelheid van spesies met lae weidingswaarde, impliseer dat hulle die geleentheid om op voedingsryke grasse te voed ten volle benut wanneer dit beskikbaar is. Ons resultate dui daarop dat die Pafuri omgewing geskik is vir die vestiging van ‘n klein teel-nukleus van wit renosters. Die oorvloedige teenwoordigheid van permanente waterbronnewe in die vorm van fonteine is ‘n groot voordeel, maar die kans vir bosindringing in hierdie grasveld-gebiede met lae reënval moet oorweeg word sou die populasie aanhou toeneem teen die huidige tempo. Die geboorte van twee nuwe kalfies in 2008 staaf die moontlikheid dat die renosters gevestig en aangepas het in hulle nuwe habitat, wat ‘n baie belowende teken is vir die toekoms van die groeiende subpopulasie.
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CHAPTER ONE
GENERAL INTRODUCTION

CONSERVATION CRISIS
Hundreds of years ago the rhinoceros was a prolific inhabitant of this planet, with numbers and species diversity to marvel at, and a geographic distribution impossible to imagine today. Historically, the white rhino occurred in areas with annual rainfall exceeding 400 mm, such as the ideal areas of Limpopo, Mpumalanga, KwaZulu-Natal and the North West (Du Toit 2005).

However, after decades of being hunted and poached for their valuable horn and falling victim to drastic habitat encroachment across the globe, their numbers reached a critical stage a long time ago. Even the most abundant of the species (Balfour & Balfour 1991), the white rhino (Ceratotherium simum Burchell), whose numbers have increased admirably due to persistent conservation efforts over the last few decades, is still needing to be studied and monitored in fenced protected areas due to the continued demand for their horn (Emslie & Brooks 1999; African Rhino Specialist Group 2003). Despite the recent reversal in the white rhino population trends, captive breeding is still supported by the IUCN due to the risk of political instability in their range countries undoing the recent successes (Swaisgood et al. 2006). In 1947 the white rhino was reported to be confined to only two areas in the whole of Africa, “...the Zululand reserves, and a relatively small area to the west of the upper Nile”, and they were already locally extinct in the Kruger National Park (KNP) due to heavy poaching (Stevenson-Hamilton 1947). In 1958 Heppes wrote that the white rhinoceros was already being branded as a ‘vanishing species’, yet, despite the southern sub-species (C. s. simum) being hunted to near extinction within 50 years of being discovered, the Northern white rhino (C. s. cottoni) could still be seen in Uganda, Congo, Sudan and areas of French Equatorial Africa. Today sees this situation reversed with the northern sub-species being reported to have hit a critical low after an upsurge in poaching in the Garamba National Park (Democratic Republic of the Congo) saw the numbers drop to an estimated 22 (Hillman-Smith et al. 2003). This civil unrest is another primary contributor to the struggle for survival that these animals face (Foose & van Strien 1997; Emslie & Brooks 1999; Hutchins & Kreger...
2006; Hillman-Smith 2006). Recent reports have shown this figure to be a mere handful of surviving individuals seen within the last two years due to the aggressively destructive poaching by Northern Arab horsemen (Hillman-Smith, pers. comm.1).

The horn of the rhino has been used in traditional Chinese medicine (TCM) for centuries (Rabinowitz 1995) as a fever remedy, although it was originally thought to be used primarily as an aphrodisiac. It is a futile task to attempt to revise traditions, particularly one that has produced proven medicinal treatments for symptoms of HIV, Hepatitis C and possibly even cancer (Ellis 2005). Another tradition decimating the species is the popularity of the horn in North Yemen, where they are carved into ceremonial Jambiya dagger handles (Foose & van Strien 1997; Ellis 2005) that are given to government officials, ambassadors and others as welcome gifts. Although in North Yemen every member of the community must own a Jambiya, they do not all have to be fashioned from rhino horn (Martin, pers. comm.2).

The ever expanding human population (Shaffer 1987) has also placed higher demand on farmers in developing countries (which comprises 100% of the rhinos natural range) to increase crop production, hence impacting the destruction of rainforests for building roads and the reclamation of ideal rhino habitat for hunting, agriculture and human settlements (Olson et al. 2002). Added to these factors are the issues of human-wildlife conflict which can occur when wild animals encounter human settlements and destroy crops and plantations simply because they are in their path (Hutchins & Kreger 2006). This is an increasing problem now with parks dropping fences to allow animals larger ranging areas, as well as villagers refusing to move when their homes and farms fall directly on game paths around the borders of national parks (Hofstatter 2005).

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**Solutions**

The most important and effective conservation efforts for endangered species to date have involved intensive captive breeding (Ebenhard 1995; Ng 2001; Robinson et al. 2005; Swaisgood et al. 2006; Swaisgood 2007) at various international zoological facilities; well-trained and meticulously coordinated anti-poaching teams in parks and reserves (Rachlow 1997); and finally reintroductions and translocations of animals into their historical ranges or new areas with better protected facilities (Swart & Ferguson 1997; Emslie & Brooks 1999; Walpole et al. 2001). Although, once again, all of these efforts encounter numerous complications along the way. White rhinos are notorious for their issues with breeding in captivity (Kretzschmar et al. 2004; Hermes et al. 2005; Hermes et al. 2006; Swaisgood 2007), which continues to confound scientists and researchers to date. Some theories suggest that the cause could be an absence or adjustment of social or environmental stimuli as simple as day length, rainfall and temperature (Kretzschmar et al. 2004) that could promote hormone levels in the wild. There are also fatal accidents that have occurred, for example when a disease outbreak was responsible for eliminating an entire captive population of Sumatran rhinos (*Dicerorhinus sumatrensis*) in 2003 at the Rhino Conservation Centre in Sungai Dusun, Malaysia. Five of the seven rhinos died in the space of 3 weeks, and there is still no clarity on whether the cause was bacterial or viral (BBC NEWS 2003). Adding to this tragedy 3 years later, at the Sepilok breeding centre in Sabah (Malaysia), one of the two individuals belonging to a rare subspecies, the Bornean Sumatran rhino (*D. s. harrissoni*), was killed when a tree branch in his enclosure broke after bad weather conditions and fell on him (Li 2007). Human error has to be partly responsible for these accidents as these centres, staffed by qualified scientists and experts in this field, were entrusted with the task of preserving the last of these animals, and should have taken every precaution to ensure their health and safety. The shortcoming of anti-poaching is the high costs, and in the larger parks it is impossible to cover every metre on a regular enough basis to keep a check on every rhino.

Other, often overlooked, support includes research, which is essential to better our understanding of the species we are trying to conserve (Linklater 2003b). The only way captive populations will be able to thrive is if managers are able to accommodate the
animals’ needs and requirements from studies on wild populations, in order to recreate their captive surroundings to be as natural as possible (Linklater 2003b; Swaisgood 2007). Although, as Linklater (2003b) points out, in a conservation crisis research tends to fall in opportunistically alongside management interventions. This in itself limits the research potential as schedules and questions needing to be asked very rarely complement the management strategy and therefore tend to take second place.

Forboseh et al. (2007) state that the enforcement of wildlife legislations and a reduction in logging impacts are crucial for the conservation of large mammals in west and central Africa, but they also recognise the significance and impact that a community interest in wildlife management can have on the surrounding flora and fauna. This seems to be a key factor at present. David Craig of Lewa Conservancy in Kenya has been quoted stating that neither Lewa, nor its rhinos will prosper unless they create a periphery of wealth around the park. That is, some level of community-wildlife engagement policy is necessary to make the local people feel rhinos are useful to them (Merz, pers. comm.3). On a similar note, monitoring of rhinos by either wildlife service employees or researchers serves as a deterrent to poachers as they are unlikely to pursue animals that have a dedicated team of trackers, scouts or researchers on their trail on a daily basis, and it is also required to enable observation and recording of population recovery data (Walpole et al. 2001). This should involve a continuous and thorough check on all known reintroduced individuals in collaboration with updates and analyses on poaching activity (Conway & Goodman 1989). It can not be disputed that the recovery of Africa’s elephants and rhinos over the last two decades has relied greatly on extensive human surveillance of the animals in situ (Walpole et al. 2001; Walpole 2002). The monitoring and policing of the illegal trade in endangered species also plays an essential role in deterring the slaughter of these animals by making it publicly clear that these activities will not be tolerated (Wright 1989).

REINTRODUCTIONS

There is a lot of ambiguity in wildlife research with regards to the terms ‘reintroduction’ and ‘translocation’, as they both involve the movement of a species to another area, but the primary difference is that reintroductions focus on moving animals back into parts of their historical range. A translocation is simply the movement from one area to another, but was used originally when specifying the movement of flora or fauna from an area where they are at risk to a safer, protected environment (Primack 1998). According to the World Conservation Union (IUCN) definition, reintroductions involve: “An attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct” (IUCN 1998). Yet, according to Ostermann et al. (2001), the term reintroduction is reserved specifically for the movement of captive-reared animals to their historical range, which is not often the case. The focus of this study is on reintroductions specifically, but there may be an overlap of literature reviewed as many of the same management protocols apply to translocations.

It is recorded that the white rhino was extinct in the Transvaal (now Gauteng) by 1896, the Kruger National Park (KNP) being included in this area (Kirby 1896; Bigalke 1963; Pienaar 1970). Successful conservation efforts in South Africa (home to more than 80% of the world’s remaining white and black rhinos) have seen the numbers rising. The reason being that in October 1961, newly developed ‘translocation’ techniques (Harthoorn 1962a; Harthoorn 1962b; Player 1972), allowed the first, of what became many subsequent, successful relocations of rhinos from the Umfolozi Game Reserve (GR) in Natal (Pienaar 1970). This initiated the establishment of widespread new populations from this source (Emslie & Brooks 1999).

Risks

Reintroduction protocols have been put in place by teams of veterinary and game capture experts who have carried out many of these exercises over the years, to a wide variety of national parks and private reserves around southern Africa. It has to be a well planned and thoroughly thought out process in order to avoid any accidents and untimely oversights that may occur. However, even after decades of fine tuning these activities not every eventuality can be planned and prepared for (Raath & Hall-Martin
1989), as wildlife can be unpredictable. The events tend to involve a lot of trial and error, which is a gamble when dealing with endangered species. In the early days there were issues with anaesthetics used, when occasionally an animal would not wake up again. During the 1961 – 1964 reintroductions from Umfolozi GR to KNP two males and two females of the 98 animals moved, died as a result of anaesthetic or injuries during transit. By 1963 they had developed a safe drug known as M-99 (Etorphine hydrochloride) which at least eliminated the anaesthesia issue and meant there should be less risk of the animals injuring themselves in transit while immobilized with this drug. A new relocation crate was also designed to prevent the rhinos damaging their horns while in transit (Pienaar 1970), and these have advanced even further since then (Du Toit 2005). There can also be problems with the new arrivals being accepted into their new homes by the existing residents, as was witnessed on only their third transfer of rhinos into southern KNP in 1963. Two new bulls were attacked by the residing group of rhinos and one bull had to be destroyed due to the seriousness of his injuries (Pienaar 1970). Fighting is reputed to be one of the leading causes of injury and death of black rhinos in post-release situations (Linklater et al. 2006).

The other major risk of reintroducing animals with large ranging habits is their potential to stray into unsafe territories if they can not be regularly monitored or tracked. Some of the original Kruger rhinos drifted into Mozambique and were swiftly poached, and others wandered across the western boundary into settlements but these could at least be recaptured and returned to the safety of the park. This brings us back to the point made under 'Solutions' regarding the benefits of monitoring and regular tracking of these animals while they become acquainted with their new surroundings. However, this is not always logistically feasible as they cover vast distances and the expense of all these conditions has to be considered at every step.

The primary restriction when attempting to put a reintroduction plan into action is the cost. Even meticulously planned projects are expensive, intensive (Seddon et al. 2005) and logistically complex (Lindburg 1992; Earnhardt 1999). Today less than half the reintroduction projects attempted are a success (Morell 2008), but then perhaps these odds would improve if the targets set were more realistic. One study suggests that a
reintroduction project can be classed as a success with the establishment of a wild population up to or equalling 500 individuals (Beck et al. 1994). Such a general statement can not logistically and practically be applied to every case as, with the most endangered species that the majority of reintroductions are being carried out for, there may not have been 500 individuals existing on the planet at one time for years.

**Benefits**

One advantage is that we can assure the health of the animals selected for relocation before moving them, to prevent the spread of any disease, which is highly significant at present with the current prevalence of Bovine TB and Anthrax in some wild animal populations. It is vital that the health of animals for reintroduction is screened and monitored post-release (Mathews et al. 2006), particularly when dealing with highly endangered species from small populations with a severely reduced gene pool. The small population theory suggests that species with less than 500 individuals surviving may not be genetically viable due to the risks of inbreeding and disease (Primack 1998). As with translocations, reintroductions also provide a means for genetic rescue for species such as the rhino with so many fragmented metapopulations (Linklater 2003a). It is also vital to consider the age, sex, physiological and reproductive states of each individual when selecting them for reintroductions, as these factors all strongly influence post-release behaviour (Linklater et al. 2006). Lastly, when planning a reintroduction a thorough habitat assessment can, and should, be carried out in advance to ascertain the suitability of the available landscape types; ranging area; potential inter-species competition and other aspects relevant to individual projects and specific species. Despite the negative statistics on fatalities during and post-reintroduction of the original 1960’s KNP rhinos, out of 141 rhinos originally moved only 6 died (Pienaar 1970), so the benefits by far outweighed the costs.
CURRENT CONTEXT
The ultimate goal of most reintroduction projects is to establish a viable population (Caughley & Gunn 1996). This is a very long term goal so it is essential to have measurable goals for short term evaluations as the projects progress (Ostermann et al. 2001). Previous research has shown that in 1994, less than half the reintroduction projects being carried out produced reports on the assessment and consequences of their actions (Beck et al. 1994; Ostermann et al. 2001). This was thought to be due to oversights regarding the monitoring of the animals post-release, reluctance to report failures, and inadequate study durations (Beck et al. 1994). Linklater et al. (2006) state that the behaviour of reintroduced rhinos post-release needs to be monitored as there is still little known in this regard, with particular attention being paid to their movements around the landscape and establishment of ranges. It has also been suggested that there are gaps in the literature (Morell 2008) on the dynamics, particularly spatial, of reintroduced indigenous large mammals (Larter et al. 2000), as well as general in situ behavioural data on rhinos (Linklater 2003b). Olson et al. (2002) proposed that extra conservation research efforts need to be assigned to conserving species with “Minimum-area requirements” as they are frequently used as umbrellas to plan the ideal size limits of areas protecting various additional biodiversity features. They too, go on to emphasise the necessity of research into range size, population demographics and movement (Rachlow et al. 1999) to ensure effective design for future management and knowledge of area-sensitive species, such as rhinos. An understanding of their behaviour is an essential component of wildlife management when endeavouring to conserve extant populations in situ (Festa-Bianchet & Apollonio 2003; Hutchins & Kreger 2006).

In 2005, as part of the Makuleke Large Mammal Reintroduction Project, six white rhinos were moved to the Pafuri section (henceforth referred to as Pafuri) of the KNP by the Wilderness Safaris Wildlife Trust, with technical support from KNP. The long term goal being to establish a breeding nucleus in this area, and the short term goal being the study of their ecology within this new habitat whilst monitoring their behaviour and movements as they settled.
The development of landscape ecology is a major factor in the field of conservation biology. Landscapes are ecological systems containing patches of different community types (Lidicker Jr. 1995). The need for thinking on a landscape scale has been clearly demonstrated in previous conservation research (Fiedler & Jain 1992). The variety of habitat types within these landscapes, and the association of animals with these environments, are central to the study of animal ecology (Ben-Shahar & Skinner 1988). There has been a marked increase of studies into the relationship between large herbivore dynamics and the landscape patterns, as well as their movements through these landscapes (Weisberg et al. 2006).

Senft et al (1987) suggest there are four levels of ecological hierarchy encountered by foraging large herbivores: feeding station; plant community; landscape system; and regional system. Melton (1987) confirms this by quantifying habitat selection at three spatial scales: selection for habitat types; area selection for grasses; and diet selection from the chosen areas. In this study the region is excluded as it was not optional, and the landscape system (habitat types) and feeding station (diet selection) utilisation are considered in further detail in subsequent chapters. The major influences in the habitat selection of herbivores are maximising forage intake and minimizing the risk of predation (Riginos & Grace 2008), although to megaherbivores such as rhinos the only predator they face as adults are humans (Owen-Smith 2002). Habitat suitability is directly affected by food quality and availability (Muya & Oguge 2000), and food quality is directly affected by rainfall and soil nutrients (Georgiadis & McNaughton 1990; Augustine et al. 2003; Verweij et al. 2006; Anderson et al. 2007). In addition, herbivores need to balance their forage intake against their energy requirements (Weisberg et al. 2006), and the problem megaherbivores face is the quantity of forage required as balanced against units of body weight due to the low protein content of vegetation versus muscle (Halstead 1969). As well as body size, type of digestive system also influences efficiency and rate of foraging (Demment & Van Soest 1985; Shrader et al. 2006). In order to design an optimal conservation programme when considering reintroductions and translocations, it is important to have an awareness of ecological factors affecting herbivores’ diet selection (Muya & Oguge 2000).
Roughly one-third of the Earth’s vegetative cover is comprised of grass-dominated ecosystems (Jacobs et al. 1999). Savannas can be defined as seasonal tropical and subtropical ecosystems with a permanent herbaceous layer dominated by grasses and sedges (Frost et al. 1986; Jacobs et al. 1999), and are believed to owe their endurance to fire regimes and mega-herbivory rather than climate (Skarpe 1992). However, rainfall affects grazers more so than browsers as the herbaceous layer is much more sensitive to annual precipitation than the woody components of the savanna landscapes (Ogutu & Owen-Smith 2003). Hence, annual rainfall and subsequent vegetation production are closely correlated with herbivore biomass (Fritz & Duncan 1994; Arsenault & Owen-Smith 2002). In the dry season, grasses become dormant and available forage is severely depleted, creating a segregation of different herbivore species into distinct habitats (Arsenault & Owen-Smith 2002). During this time grasses become more fibrous and protein levels drop (Owen-Smith 1982), and the quality of perennial grasses declines before annuals (Prins 1988). The diet selection of grazing herbivores at this time of year is an effective indication of the habitat suitability, as their survival throughout the dry season almost guarantees that the habitat will be adequate in the wet season.

There are a number of well used techniques that have been used over the years to determine the feeding behaviour and dietary requirements of grazing animals. These can be simplified into five categories: Utilization Techniques; Direct Observations; Stomach analysis; Faecal analysis and Fistula Techniques (Holechek et al. 1982; Teague 1989; Carrière 2002; Mbatha & Ward 2006). Of these, the least invasive are the utilization, observation and faecal methods. The direct observation approach has been widely used under ideal field conditions (Page & Walker 1978; Laurie 1982; Hall-Martin et al. 1982; Abaturov et al. 1995; Perrin & Brereton-Stiles 1999; Macandza et al. 2004; Ganqa et al. 2005; Shrader et al. 2006), and was the initial plan for this project. This typically involves recording the grass species consumed by the study animals whilst under observation, and then taking further measurements of grass leaf table height of freshly grazed and previously grazed patches (Perrin & Brereton-Stiles 1999); grass greenness and steminess; number of bites taken (Macandza et al. 2004; Shrader et al. 2006); and other topographical features, depending on the questions needing answers.
Since the early 1940's (Baumgartner & Martin 1939) faecal analysis has progressed noticeably and advanced as a preferred tool for assessing herbivore feeding habits and diet quality (Sparks & Malechek 1968; Vavra & Holechek 1980; Holechek et al. 1982; Wrench et al. 1997; Maia et al. 2003) by identification of grass leaf blade cuticular fragments (Davies 1959; Carrière 2002) of the species within the faeces, using anatomical features (Metcalfe 1960; Stewart 1965; Stewart 1967; Ellis 1979; Ellis 1981; De Jong et al. 2004; Wegge et al. 2006). It is most advantageous under field conditions that make direct animal observations difficult, such as in thick vegetation; with study animals nervous of human presence; and in very dry habitats (Holechek et al. 1982). All of which were issues in the current study.
STUDY AREA

Pafuri (22°23’S, 031°08’E), otherwise known as The Makuleke Contractual Park, of the Kruger National Park, is an area of prime ecological significance due to the diversity of the 23 habitats and vegetation biomes that meet there, including Lebombo ironwood forests, high Mopane woodlands, big timber riverine woodland and Baobab forests (Tinley 1981). Falling between the natural barriers of the ancient Limpopo River, which was one of three major rivers dominating southern Africa’s drainage shortly after the split of Gondwana some 140 million years ago (McCarthy & Rubidge 2005), and the Luvuvhu River (Figure 1.1), Pafuri is bordered by Mozambique to the east, Zimbabwe to the north, and KNP continuing to the south. It has a limited road network compared to other areas of the park, with the KNP regulation forbidding off-road driving, strictly adhered to. Point-ignition fire management strategies are carried out by the SANParks section rangers across the park each year. The implementation of these protocols depends on factors such as soil fertility and rainfall patterns, which are taken into account during the planning stage (van Wilgen et al. 2008).

Figure 1.1 Map of the study area in the most NE corner of South Africa.
Climate
In 1981 Pafuri was reported to have the lowest rainfall in its region (362 mm per annum) and the highest local temperatures, making it a very arid area. This is primarily due to the frequent high pressure system that forms above the Limpopo Valley, causing drought conditions along the entire eastern border (Tinley 1981). The lowest annual rainfall ever recorded in the KNP was in Pafuri, 1982/83, when only 98 mm fell. During the 1991/92 drought Pafuri was recorded as being the second driest section of KNP, after Lower-Sabie (Zambatis & Biggs 1995). A report from 2003, however, places the long term annual average rainfall in Pafuri at 466 mm (Zambatis 2003). The daily minimum and maximum temperatures were recorded during the study period, with the lowest temperature dropping to 4°C, and the highest reaching 45°C. The annual average temperature was 34°C, and the annual rainfall was lower than previous years at 379 mm (pers. obs.).

Economic significance
As early as 1933 Pafuri was gaining recognition for being an area of high conservation value, achieving the area game reserve status under provincial legislation (De Villiers 1999). South African National Parks (SANParks) had been undertaking to proclaim the area as a national park in order to include it as part of the KNP, and talks commenced in 1947 with respect to this initiative. The Makuleke community at this time were living on this land and insisted that this had been the case for generations, but in 1957 the Secretary for Native Affairs announced that anyone residing in the area would henceforth be considered illegal occupants and treated accordingly. The Makuleke people were removed from their 20 000 hectares of land and relocated to a 6 000 hectare piece of land 60 km further south, outside the borders of the park (De Villiers 1999).

In 1996 the Makuleke put in a land claim against this area, claiming they were removed against their will and consequently were deprived of their land rights. In addition to this they were paid no compensation to aid in the reestablishment of their entire village in a new area (De Villiers 1999). A settlement, described as a breakthrough for conservation in South Africa, was reached in December 1998 and submitted to parliament in 1999, where after the Minister of Environmental Affairs and Tourism proclaimed it a
contractual park that forms part of the KNP. The agreement is that the ‘Makuleke Contractual Park’ (as it is now known) be jointly managed by the Makuleke Communal Property Association (CPA); KNP and Wilderness Safaris, all parties forming the Joint Management Board (JMB) (De Villiers 1999). To date this has been a successful agreement, apart from one incident not long after regaining their land where the community made a deal to sell two buffaloes and one elephant for hunting, a move which was supported by NGO’s and the CEO of SANParks much to the anger and dismay of many opposed conservationists (Child et al. 2004). Another motivation for the great significance of this area is its geographic positioning as the heart of the Great Limpopo Transfrontier Park, formed in November 2000 (Duffy 2006) with the hope of combining conservation efforts between South Africa, Mozambique and Zimbabwe and extending the ranging areas for some of the large game herds that fences have thus far restricted (De Villiers 1999; Wolmer 2003).

**Ecological significance**

Until recently, four of the 35 KNP landscapes, defined by Gertenbach (1983), fell only or mostly in (Figure 1.2) this area and extended slightly to the south of the Luvuvhu River. These are:

- Punda Maria Sandveld on Cave Sandstone
- *Adansonia digitata*/*Colophospermum mopane* Rugged Veld
- *Colophospermum mopane* Shrubveld on Calcrete
- Limpopo/ Levubu Floodplains

The fifth landscape type, Mixed *Combretum* spp./*Colophospermum mopane* Woodland, is the smallest in Pafuri yet the more prevalent in the rest of the KNP (Gertenbach 1983). This data has since been updated by Mucina and Rutherford (2006) and Pafuri has been further classified into eight different landscape types within three highly diverse, major vegetation biomes: Savanna; Afrotemperate, Subtropical and Azonal Forests; and Inland Azonal Vegetation. This 203 km² area of immense biogeographic importance lies north of the Tropic of Capricorn and is renowned for the vast range of wildlife it houses, many species occurring nowhere else in South Africa (Tinley 1981; De Villiers 1999).
Figure 1.2 The study area split into the five landscapes defined by Gertenbach (1983).

Pafuri is best known for its birds, with tourists returning annually to catch glimpses of the rare Pel's Fishing Owl (*Scotopelia peli*); Racket-tailed Roller (*Coracias spatulata*); Saddlebilled Stork (*Ephippiorhynchus senegalensis*); Ground Hornbill (*Bucorvus leadbeateri*), as well as a huge diversity of raptors. The frequency of predator sightings has increased significantly since 2005, with Lion (*Panthera leo*); Leopard (*Panthera pardus*); Cheetah (*Acinonyx jubatus*); Spotted Hyaena (*Crocuta crocuta*); and even Wild Dog (*Lycaon pictus*) becoming regular visitors and well established occupants (pers. obs.). For the very fortunate few, a rare glimpse of Sable (*Hippotragus niger*); Pangolin (*Manis temminckii*); Four-toed Elephant Shrew (*Petromus tetradactylus*); White Rhinoceros (*Ceratotherium simum*) and the increasing large herds of Eland (*Taurotragus oryx*), may be experienced.
Pafuri is also known for its high numbers of Nyala (*Tragelaphus angasii*) which can be a rare sight in the southern parts of KNP (Tinley 1981).

However, after the rather troubled political history of this area, it has taken many years and some vigilant anti-poaching manoeuvres coupled with strategic and committed management, to return to this status of apparent, impressive ecological and biological diversity. Johnson (1980) described, in an article raising awareness about the potential threat to Pafuri from coal mining, the vast numbers of buffalo, sable and roan making their way to the waterholes as dusk approached. This is unlikely to ever be seen again in the case of roan (Harrington et al. 1999) and sable in much of KNP or any other South African national park, if the current population declines continue (Nicholls et al. 1996; Ogutu & Owen-Smith 2003). The white rhino has only returned to Pafuri due to management intervention, after a reported 110 year absence (Kirby 1896), with the exception of a few rhinos temporarily ranging that far north in the past (Pienaar 1970).
STUDY ANIMAL

The Rhinocerotidae

This family consists of five extant species, the African white or square-lipped rhino, and the black or hook-lipped rhino (*Diceros bicornis*). Then in Asia, the Indian (*Rhinoceros unicornis*), Javan (*Rhinoceros sondaicus*), and Sumatran rhinos (*Dicerorhinus sumatrensis*). They belong to the order Perissodactyla (Meester & Setzer 1971; Groves 1972; Balfour & Balfour 1991), odd-toed ungulates, which is split into two families, the Rhinocerotidae and Equidae (Meester & Setzer 1971; Skinner & Smithers 1990). The earliest records of rhino-like creatures date back 60 million years and for most of those years they were the dominant animals on the planet (Joubert 1996), but the rhinos that we are familiar with today evolved from these around 40 million years ago (Owen-Smith 1973; Downie & Mavrandonis 2006). The first horned perissodactyl, *Diceratherium*, emerged in the Miocene with paired nasal appendages (Berger 1994). The Javan rhino is thought to be the most primitive, having changed very little since the Pliocene, 5.3 million years ago (Owen-Smith 1973). One study suggests the divergence between the African and Asian lineages occurred 26 million years ago (Tougard et al. 2001), as the debate over the taxonomic relationships between them remains inconclusive. Historically species were grouped according to morphological differences and geographical distribution (Merriam 1918; Rausch 1963; Meester & Setzer 1971), but advances in Molecular Ecology have allowed us to investigate genetic diversity between species and subspecies when classifying their taxonomy and phylogeny (Swart & Ferguson 1997; Paetkau et al. 1998; Tougard et al. 2001).

One factor that unequivocally unites all five rhino species is that they have, and will continue to suffer near extinction at the hands of poachers and political rebels, as well as habitat encroachment from farmers, and they are all still on the IUCN Red Data List of Threatened Species (African Rhino Specialist Group 2003). In the very recent past a survey of the last refuge of the Western black rhino (*Diceros bicornis longipes*) in Northern Cameroon has resulted in this subspecies being declared ‘Probably extinct’ (Lagrot et al. 2007). The decades of poaching and the impact of habitat encroachment have left the five remaining species of rhino in very small, fragmented populations within Asia and
Africa. In early ecological reports it was stated that they have “No known predators except man” (Groves 1972).

The White Rhino

The white rhino is the third largest land mammal, after the African elephant (*Loxodonta africana*) and the Asian elephant (*Elephas maximus*), with estimated weights of 1600 kg in adult females and up to 2300 kg in males (Owen-Smith 1988; Balfour & Balfour 1991). Foster (1960) recorded maximum adult weights of 3200 – 3600 kg, but it is feasible to assume that their maximum body weights would gradually decrease over time due to the larger individuals fetching greater prices from trophy hunters and poachers alike. The white rhino was separated into two sub-species in 1900 when a skull was recovered in Sudan and confirmed to be distinct from the South African variety due to the depth of dorsal concavity of the skull. So the Northern white rhino, *Ceratotherium simum cottoni*, came to be, and the well known southern form became known as *C. s. simum*. Just over a century later and this *C. s. cottoni* looks soon to be classified as ‘Probably extinct’.

White rhinos are area-selective, bulk, short-grass grazers and have evolved high-crowned cement covered teeth to cope with their feeding demands, as well as a lengthened skull and wide lips (Owen-Smith 1973). They are adapted for rapid food intake and, as a result, can struggle to obtain maximum quality and nutrition from a highly fibrous diet (Perrin & Brereton-Stiles 1999). Their olfactory sense is the most powerful, followed by their hearing which is sensitive when not disrupted by other environmental noises such as animal herds and strong wind. Vision is not their greatest asset and it was found by Owen-Smith (1973) that they can only discriminate between stationary forms from 15 to 25 metres away.

According to the literature, the social structure of white rhinos sees bulls (adult males) as primarily solitary, but territoriality is only demonstrated by approximately two-thirds of the adult male population (Owen-Smith 1971). The dominant territory holder is always solitary and these territories do not overlap (Owen-Smith 1971; Owen-Smith 1972). These bulls are known to only leave their territories to gain access to water
(Owen-Smith 1988), if it is not already present within the range of the territory. They mark the boundaries of these territories with scent broadcasting, such as spray-urination, scrapings and dung scattering (Owen-Smith 1971; Owen-Smith 1972; Owen-Smith 1973; Rachlow 1997). Other features characterising an exclusive territory holder are ritualised encounters with other territorial males, and the confinement of cows in oestrous (Owen-Smith 1971). Cows will always be accompanied by their youngest calf, and occasionally the previous calf as well, but this calf usually departs at the age of 2 to 3.5 years to join other sub-adults or cows (Du Toit 2005). Sub-adults of both sexes are often seen in pairs with each other, and they are also known to form alliances with cow and calf pairs (Owen-Smith 1988). Female rhinos and sub-adults of both sexes form home ranges, which are generally larger than male territories (Pienaar et al. 1993b) as they are not exclusive or non-overlapping. These ranges are beneficial to the animals as they increase their knowledge of spatial and temporal resource availability within their environment (White et al. 2007).

For this project, six rhinos (Cows 1, 2, 3 and Bulls 4, 5, 6) were reintroduced from the Satara section of KNP, with estimated ages of 5 – 7 years. This is the minimum number of rhinos recommended for re-establishment, although the sex ratio is ideally two males to four females, with one male a dominant adult, and two females as mature cows (Du Toit 2005). In Pafuri, one bull walked straight out of the concession (bull 4) soon after reintroduction and was never seen again. His radio signal could be detected for a few months, south of the Luvuvhu River, but he eventually moved further south and out of range. This behaviour led me to believe that he was realistically a mature male in search of better territory options and mature females, which would put his age closer to 10 years old.

Another age discrepancy was confirmed when Cow 1 gave birth in January 2006. After a 16 month gestation period from the age of maturity (4.5 – 6 years) (Du Toit 2005), that would make her at least 7 years old. Bull 5 immediately began territory marking, suggesting that he is 10+ years old, as this is the approximate age that they become reproductive (Owen-Smith 1972) and territory establishment is a principle indication of sexual maturity. Cow 2 looked like a mature female (body size matching that of Cow 1)
but showed no signs of reproductive activity during the study period, however bull 5 was regularly seen with her so it is possible she was reaching maturity towards the end of the study period. Cow 3 and bull 6 were estimated at approximately 5 – 6 years of age.

It is important to note at this point, that the rhinos were referred to initially as cows and bulls, due to the lack of clarity on ages and social dynamics when they were first reintroduced. The correct usage of the terms ‘cow’ and ‘bull’ refers specifically to adults of this species, and not to sub-adults. But for consistency purposes we continued to use these terms, despite the eventual confirmation that two of the study animals were sub-adults. For the purpose of this study, the terms ‘cow’ and ‘bull’ are solely an indication of sex of the rhinos (for identification), and not of age.
OBJECTIVES AND THESIS OUTLINE
The IUCN reintroduction guidelines emphasise the necessity for suitable available habitat assessments during the planning stages of reintroductions (IUCN 1998). In order to make effective conservation and management decisions regarding the maintenance of threatened species, an awareness of their habitat needs at a local and landscape scale are vital (Finlayson et al. 2008). Food resources have been studied at feeding patch, community and landscape level (Perrin & Brereton-Stiles 1999) and this can be measured by studying habitat choice (Pienaar et al. 1992; Pienaar et al. 1993a; Shrader & Perrin 2006), grasses eaten, plant parts eaten and leaf table height preference (Page & Walker 1978; Laurie 1982; Perrin & Brereton-Stiles 1999; Macandza et al. 2004; Shrader & Perrin 2006; Shrader et al. 2006). This study aims to provide a thorough habitat suitability assessment in the form of three primary areas of focus:
- Landscape preferences
- Range and territory establishment
- Dietary composition.

Pafuri can be described as a semi-arid savanna, due to its high temperatures and low seasonal rainfall. Savannas are defined as “tropical and subtropical grass-dominated landscapes with varying densities of trees and shrubs” and today they are found in areas with seasonal precipitation (Jacobs et al. 1999). The only information published to date on Pafuri has been in the form of landscape surveys (Van Rooyen et al. 1981; Gertenbach 1983; Mucina & Rutherford 2006), even KNP annual aerial surveys only occasionally ventured as far north as Punda Maria and Pafuri (Ogutu & Owen-Smith 2005). It is the landscape surveys however, that Chapter II focuses on. The study site was split into the landscape types as defined by Gertenbach (1983) for comparative purposes with studies carried out in the 1990’s (Pienaar et al. 1992; Pienaar et al. 1993a). I analysed the locations of the rhinos throughout the study period to determine whether they showed any preference or avoidance for any of the available landscapes, considering resources such as available forage and surface water.
By far the most important factor to consider with rhino reintroductions is range availability for the establishment of territories by dominant bulls, as this is solely responsible for ordering reproductive competition amongst adult males (Owen-Smith 1971; Owen-Smith 1972; Rachlow et al. 1998; Rachlow et al. 1999). No study is yet to dispute that the bull with the female in his territory is the bull that gains the opportunity to mate. As mentioned previously, if the primary aim of most reintroductions is to establish viable populations, then it is in the managers best interest to maximise the space available for numerous concurrent territories. In Chapter III I studied the movements of the reintroduced rhinos and the developing group dynamics, recorded any signs of territory establishment and compared this behaviour to previous studies carried out on the topic. The home ranges of the females was calculated and considered in relation to the male territory as well as previous literature.

The final and most fundamental element of any habitat assessment is the availability and utilisation of adequate forage, and this formed the core of Chapter IV. Due to the amount of research carried out to date on rhino dietary requirements, their feeding preferences under optimal conditions are well publicised. The interest in this case lies in the feeding preferences of rhinos in a habitat they have not been studied in before, and also under harsher conditions due to the low annual rainfall in Pafuri. Due to the negligible months with green grasses, coupled with dense shrub and tree cover, observational diet analysis was substituted with faecal analysis. Pienaar (1970) reported that, after an unsuccessful reintroduction of white rhinos into the mopane woodlands of the northern sector of KNP, some were seen to venture as far as Pafuri and even cross into Zimbabwe (then Rhodesia), before returning to the south. This excursion taking them approximately 130 km, one-way, from their original reintroduction site at Mopani. This study sees the first in depth analysis of white rhino behaviour in the Mopane dominated landscapes of Pafuri, since the 1970 and 1993 studies indicating their avoidance of this area (Pienaar 1970; Pienaar et al. 1992; Pienaar et al. 1993a). Chapter V outlines the concluding management recommendations for the Pafuri rhinos, following management plan outlines utilised by various rhinoceros conservation organisations.
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CHAPTER TWO

LANDSCAPE PREFERENCES OF WHITE RHINOCEROS IN PAFURI, THE FAR NORTHERN KRUGER NATIONAL PARK

INTRODUCTION

The white rhino, *Ceratotherium simum* Burchell, was extinct in the Kruger National Park (KNP) before the 20th Century commenced (Kirby 1896). After the initiation of intensive reintroductions in the 1960's, however, the numbers had risen to a healthy 1565 by 1991 (Pienaar et al. 1992). Most of these reintroduced rhinos were translocated to the southern and central parts of the park and, when they attempted to reintroduce rhinos further north, some were seen to venture as far as the Pafuri section (the northern most section of KNP, commonly and henceforth referred to as Pafuri) and either crossed through it into Zimbabwe (then Rhodesia), or turned around and returned to the south (Pienaar 1970). In 1992 and 1993, Pienaar et al. published a number of papers on landscape preferences and range size of white rhinos in the southern, central and northern KNP. However, they excluded certain landscape types on the basis that no rhino had been seen in these particular areas for 13 years (Pienaar et al. 1993a). Three of these five disregarded landscapes fall within the boundaries of Pafuri (Gertenbach 1983). In 2005, as part of a Large Mammal Reintroduction Project, six white rhinos were translocated from the Satara section of the KNP to Pafuri, after a 110-year absence (Kirby 1896). It is critical that the behaviour of reintroduced rhinos post-release is monitored, as there is still little known in this regard, particularly their movements around the landscape (Linklater et al. 2006).

Grasslands and savannas, making up approximately a third of the Earth’s vegetative cover, need to be studied to improve the ecological management and conservation thereof (Jacobs et al. 1999), and a crucial aspect of ecosystem management is the understanding of spatial and temporal dynamics of grazers and their landscape use (Bailey et al. 1996). Distribution patterns of large herbivores in African savannas may be directly influenced by the combination of biotic (plant morphology, forage quality) and abiotic (slope, distance to water) factors (Bailey et al. 1996; Redfern et al. 2003). This habitat selectivity
can affect an animal’s potential to reproduce and survive, which for ungulates depends on readily available food, water, and shelter from harsh weather and predators (Melton 1987). The food of herbivores is more likely to be widely distributed across landscapes, unlike that of carnivores (Senft et al. 1987), which is why studies of herbivore movements and habitat utilisation, versus availability, are essential to improve our understanding of the animals’ requirements. Of the four ecological hierarchy levels encountered by foraging megaherbivores (Senft et al. 1987), the landscape system is the primary area of focus in this study.

Within the landscapes, the primary habitat requirements of rhinos are food, water, wallows, rubbing posts, shelter and often mineral licks when the nutrient quality of the grasses available is particularly low (Owen-Smith 1973; 1988). All of these factors will define landscape preferences if more than one is abundant in a particular landscape type. Large African savanna herbivores utilise a disproportionately large quantity of resources, allowing them to survive in a wider range of habitats not suitable for smaller species (Du Toit & Owen-Smith 1989), so it is important to consider this when assessing the surrounding habitat suitability. Also critical, when making informed conservation and management decisions regarding threatened animals, is that as much detail about habitat preferences and patterns of use is understood (Finlayson et al. 2008).

This study investigated the post-reintroduction dispersal and subsequent landscape preference or avoidance, of a small population of rhinos in an area never before studied, within the five landscape types available to them, as outlined by Gertenbach (1983) (for comparative purposes with previous studies), and recently updated by Mucina and Rutherford (2006). By analysing any potential preference or avoidance of landscape types, the physical characteristics thereof can be considered when making reintroduction and management plans in the future. The hypotheses were that rhinos would not utilise the landscapes merely in proportion with their availability, and they would express preferences for any landscape type showing an abundance of quality graze and permanent water.
METHODS

Study Area

Pafuri is located in the far northern corner of the KNP, South Africa (22°23’S, 031°08’E). The study area covers 203 km² of KNP, bordered by Mozambique to the east, Zimbabwe to the north, with the Luvuvhu River forming the natural boundary between Pafuri and the rest of the park to the south (Figure 2.1). The area has a reputation for low rainfall and high temperatures (Tinley 1981), with long term average annual rainfall (1984 - 2002) at 466 mm (Zambatis 2003). The study period experienced lower rainfall (383 mm), and average monthly temperatures ranged from a minimum of 9 °C in June to a maximum of 40 °C in December. The area is split into five landscape types based on differing geomorphology, climate, soils, vegetation and fauna (Gertenbach 1983), as detailed in Table 2.1.

![Figure 2.1](image)

Figure 2.1 The five landscape types and their locations within the study area, including permanent, seasonal and ephemeral water points and the original boma site.
<table>
<thead>
<tr>
<th>LANDSCAPE NUMBER</th>
<th>LANDSCAPE NAME</th>
<th>BRIEF DESCRIPTION</th>
<th>SIZE (km²)</th>
<th>SIZE %</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
<td>Limpopo/Levubu Floodplains <em>(Floodplains)</em></td>
<td>One of the lowest rainfall areas of KNP, flat to concave, low-lying area between 200 and 250 m a.s.l. Comprises tree savanna on basalt footslopes, river forest and tall tree veld that opens up into grassveld. Soils: alluvial, originating from granite, sandstone, basalt and dolerite. Grasses: <em>U. mosambicensis, C. gayana, S. consimilis, L. afrum,</em> <em>C. ciliaris, S. sphacelata, Panicum spp.</em></td>
<td>75.9</td>
<td>38</td>
</tr>
<tr>
<td>16</td>
<td>Punda Maria Sandveld on Cave Sandstone <em>(Sandveld)</em></td>
<td>Recognised for high number of koppies, sandy plateaus and bottomlands, from 300 to 317 m a.s.l. Soils: lithosols or solid rock supporting tall shrub savanna on deep, sandy soils. Grasses: <em>D. eriantha, B. serrata, P. squarrosa, P. patens,</em> <em>S. pappophoroides, Aristida spp.</em></td>
<td>15.2</td>
<td>7</td>
</tr>
<tr>
<td>27</td>
<td>Mixed <em>Combretum spp./Colophospermum mopane</em> Woodland <em>(Mixed Woodland)</em></td>
<td>Flat basalt and gravel area between 230 and 475 m a.s.l., with open tree veld dominated by medium shrubs. Soils: deep, white sand, but well drained. Grasses: <em>D. eriantha, S. pappophoroides, P. maximum, Aristida spp.</em></td>
<td>7.2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td><strong>202.9</strong></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>
Field data collection

The rhinos were fitted with radio transmitters in the anterior horn before reintroduction (following the methods of Pienaar & Hall-Martin, 1991). They were tracked on foot daily, for at least two weeks of every month from April 2006 to February 2007 (preliminary data were collected during March 2006 on a less regular basis while familiarity with the study area was gained), and tracks were checked from a vehicle for the remainder of the month. Tracking commenced at sunrise and continued until between 11h00 and 17h00, depending on the heat and weather conditions. Radio telemetry (using a Communications Specialist R-1000 handheld receiver and AWT ‘H’ Two-element Yagi antenna) aided in location of the animals, along with spoor identification, which became the only aid once the lifespan of the radio transmitters was depleted (3 – 9 months after study commenced). Radio fixes were not trusted as exact locations until the animal was tracked on foot and visually identified (Pienaar et al. 1993b).

During each tracking session, either on foot or from the vehicle, every sign of fresh rhino activity (since sunset the previous day when they become most active and the last tracking session was concluded) was logged and recorded using a GPS Garmin iQueM5. Information on the type of activity, such as feeding, resting, drinking, wallowing, defecating, male territory marking, and the estimated time each activity took place, were recorded as evidence of habitat utilisation. Due to the low density of rhinos and the distances they would travel daily through dense vegetation, the specific individuals encountered while tracking was random and not guaranteed on a daily basis. When encountered they were approached from downwind to minimise disturbance and allow time for individual identification.

Data Analysis

The GPS data were checked to ensure independence of data points by confirming that only one sign of activity was recorded per rhino individual or group per day. The cow and calf pair were analysed as one animal due to the dependence of the calf on his mother, and any periods of activity that saw social groupings of the animals were
recorded per group, as opposed to individual. These GPS locations of all rhino sightings (see Appendix 2.1) and signs of recent activity were entered onto the map of the study area with the five landscape types using ArcGIS 9 (ESRI 2006), and then exported to a database in order to ascertain which landscape type each data point fell within. These data were pooled and frequency of occurrence in each landscape type was calculated for the year, and further broken down by season. Season was split into four categories directly reflecting the dry and wet seasons during the study period (see Appendix 2.2 for temperature and rainfall table): Early dry (ED) = April–June; Late dry (LD) = July–Sep; Early wet (EW) = Oct–Dec; and Late wet (LW) = Jan–Feb.

To evaluate landscape preferences of the rhinos, the proportion of rhino occurrence in each landscape type throughout the study period was used, in comparison to the proportion of the landscape sizes within the study area, to calculate preference indices (P.I.) as outlined by Viljoen (1989) and followed by Pienaar et al. (1992; 1993a). There have been many papers published on the different analyses available for evaluating resource and habitat use versus availability (Neu et al. 1974; Johnson 1980; Byers et al. 1984; Alldredge & Ratti 1986; Scogings et al. 1990; Alldredge & Ratti 1992; Aebischer et al. 1993; Mysterud & Ims 1998; Conner et al. 2003), but the preference index (Viljoen 1989) was considered suitable for the current purpose of comparing results with previous research utilising the same method. Following this method, results obtained range from -1 to +1, with -1 indicating avoidance, a zero indicates random association (suggesting utilisation is in proportion to availability), and +1 indicates a preference. The four variables used to calculate these values were:

\[ n_x = \text{the number of rhinos in landscape} \ 'x'. \]

\[ N_t = \text{the total number of rhinos observed.} \]

\[ a_x = \text{the surface area of landscape} \ 'x' \ (\text{km}^2). \]

\[ A_t = \text{the total area available to the rhinos} \ (\text{km}^2). \]

\[ n_x / N_t = \text{the proportion of rhinos recorded in landscape} \ 'x' \ \text{relative to the total number of rhino sightings.} \]

\[ a_x / A_t = \text{the proportion of the study area covered by landscape} \ 'x'. \]
IF \( n_x/ N_t > a_x/ A_t \), then P.I. \((x) = 1/ (1- a_x/ A_t) \times (n_x/ N_t - a_x/ A_t) \),

but,

IF \( n_x/ N_t < a_x/ A_t \), then P.I. \((x) = 1/ (a_x/ A_t) \times (n_x/ N_t - a_x/ A_t) \).

As a preference index is merely an indication of landscape use versus landscape availability, it does not provide an indication of statistical significance. A chi-square test was carried out to test for goodness-of-fit of landscape utilisation to landscape availability, following Byers et al. (1984) and Pienaar (1992). The null hypotheses to be tested by the chi-square test were as follows (following Alldredge and Ratti (1986)):

\[ H_{01} \] Landscape usage occurs in proportion to availability, considering all landscapes simultaneously.

\[ H_{02} \] Landscape usage occurs in proportion to availability, considering each landscape separately.

When a significant difference was detected by the chi-square test, a Bonferroni z-statistic was carried out to construct confidence intervals around the proportion of utilisation within each landscape type, in order to ascertain which landscape types are utilised significantly more or less than expected. This calculation, following Alldredge and Ratti (1986), was as follows:

\[ \hat{p}_i - Z_{\alpha/2k} [\hat{p}_i (1 - \hat{p}_i)/ n]^{1/2} \leq \hat{p}_i \leq \hat{p}_i + Z_{\alpha/2k} [\hat{p}_i (1 - \hat{p}_i)/ n]^{1/2} \]

where \( \hat{p}_i \) is the actual proportion of utilisation per landscape type, and \( n \) is the total number of occurrences across all landscapes. \( Z_{\alpha/2k} \) is the upper standard normal table value corresponding to a probability tail area of \( \alpha / 2k \), where \( \alpha = 0.05 \) (for 95% confidence) and \( k \) = number of categories being tested (five landscapes in this case).
The expected proportions of utilisation per landscape were then checked against the confidence intervals, and if they fell within the interval the landscape was considered to be utilised in proportion to availability. If they did not fall within these intervals, we concluded that expected and observed landscape utilisation were significantly different. The expected and observed values were then compared to assess whether the difference was a preference or avoidance.
RESULTS

A total of 719 data points were collected and used for subsequent analysis. From the landscape utilisation results the Baobab/ Mopane landscape was the most utilised landscape overall (41%), as well as in three of the four seasons, apart from the early dry season (Table 2.2). However, when the P.I ratings were calculated, taking the landscape size into account, this landscape was only preferred in the late dry season (P.I = 0.19) and avoided in the others. When considered over the entire study season, it was used in proportion to availability (P.I = 0.04).

Table 2.2  The proportion of occurrence of all rhinos per landscape, per season, as well as their preference index ratings.

<table>
<thead>
<tr>
<th>LANDSCAPE</th>
<th>SIZE</th>
<th>EARLY DRY</th>
<th>LATE DRY</th>
<th>EARLY WET</th>
<th>LATE WET</th>
<th>ALL SEASONS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(%)</td>
<td>N = 111</td>
<td>N = 277</td>
<td>N = 184</td>
<td>N = 147</td>
<td>N = 719</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
</tr>
<tr>
<td></td>
<td>P.I</td>
<td>P.I</td>
<td>P.I</td>
<td>P.I</td>
<td>P.I</td>
<td></td>
</tr>
<tr>
<td>Baobab/Mopane</td>
<td>39</td>
<td>32</td>
<td>-0.19</td>
<td>50</td>
<td>0.19</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>36</td>
<td>-0.06</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>36</td>
<td>-0.07</td>
<td>41</td>
</tr>
<tr>
<td>Floodplains</td>
<td>38</td>
<td>11</td>
<td>-0.71</td>
<td>8</td>
<td>-0.80</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>-0.73</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>-0.47</td>
<td>11</td>
</tr>
<tr>
<td>Mopane Shrub</td>
<td>13</td>
<td>50</td>
<td>0.42</td>
<td>32</td>
<td>0.22</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>17</td>
<td>0.05</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11</td>
<td>-0.03</td>
<td>27</td>
</tr>
<tr>
<td>Sandveld</td>
<td>7</td>
<td>6</td>
<td>-0.16</td>
<td>9</td>
<td>0.01</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>35</td>
<td>0.30</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>33</td>
<td>0.27</td>
<td>20</td>
</tr>
<tr>
<td>Mixed Woodland</td>
<td>3</td>
<td>2</td>
<td>-0.49</td>
<td>1</td>
<td>-0.59</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>-0.85</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>-0.81</td>
<td>1</td>
</tr>
</tbody>
</table>

The overall preferred landscape type for the year was the Mopane Shrubveld (P.I = 0.16) (Figure 2.3), as well as in the early dry (P.I = 0.42) and late dry (P.I = 0.22) seasons, followed very closely by the Sandveld (P.I = 0.14). The Sandveld was also the preferred landscape in the early wet (P.I = 0.30), and late wet (P.I = 0.27) seasons. The Mixed Woodland was rarely utilised during any season, and was avoided overall (P.I = ~0.69). The Floodplains similarly were not utilised often (11%), and due to the larger area covered (75.9 km²) were considered to be avoided slightly more than the Mixed Woodland (P.I = -0.70).
Figure 2.3 The preference index ratings for each landscape type in the study area, reflecting preference and avoidance per season and for all seasons combined. (Landscapes displayed in descending size order.)
Figure 2.3 illustrates the results of the preference indices, in order of landscape size for all seasons, and the subsequent seasonal breakdown. The avoidance of the Mixed Woodland and Floodplains can be seen very clearly here, as the closer to -1 the P.I rating is, the more the landscape was avoided. The remaining three landscapes, Baobab/ Mopane veld, Mopane Shrubveld, and Sandveld, appeared to fluctuate throughout the year between slightly avoided and slightly preferred. No landscape type appeared to be markedly preferred in the way that the Mixed Woodland and Floodplains were consistently and clearly avoided.

The chi-square test showed a significant difference between expected and observed landscape utilisation ($X^2 = 398.898; p < 0.0001; df = 4$), when considering all landscapes simultaneously, therefore the $H_{01}$ was rejected. To determine which landscapes were significantly preferred or avoided, the proportion of expected utilisation was compared to the confidence intervals, and those values that did not fit within the intervals were classified as significantly different (Table 2.3). When the expected utilisation was then compared to the observed utilisation, the Sandveld and Mopane Shrubveld landscapes were classified as significantly preferred ($p = 0.05$), and thus the $H_{02}$ was rejected. It was also rejected for the Mixed Woodland and Floodplains, as they were significantly avoided, but the Baobab/ Mopane veld appeared to be utilised in proportion to its availability.

Table 2.3  Landscape preference and avoidance for all seasons, within Pafuri, Kruger National Park. ($\alpha = 0.05; k = 4; Z_{\alpha/2k} = 2.57$)

<table>
<thead>
<tr>
<th>Landscape</th>
<th>$X^2$</th>
<th>Confidence interval</th>
<th>Expected utilisation</th>
<th>Observed utilisation</th>
<th>Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandveld</td>
<td>150.839</td>
<td>0.162 $\leq p \leq$ 0.239</td>
<td>0.075 *</td>
<td>0.200</td>
<td>Preferred</td>
</tr>
<tr>
<td>Mopane Shrubveld</td>
<td>103.602</td>
<td>0.225 $\leq p \leq$ 0.309</td>
<td>0.130 *</td>
<td>0.267</td>
<td>Preferred</td>
</tr>
<tr>
<td>Baobab/Mopane</td>
<td>1.029</td>
<td>0.362 $\leq p \leq$ 0.456</td>
<td>0.385</td>
<td>0.409</td>
<td>Neutral</td>
</tr>
<tr>
<td>Mixed Woodland</td>
<td>12.023</td>
<td>0.001 $\leq p \leq$ 0.021</td>
<td>0.035 *</td>
<td>0.011</td>
<td>Avoided</td>
</tr>
<tr>
<td>Floodplains</td>
<td>131.355</td>
<td>0.082 $\leq p \leq$ 0.143</td>
<td>0.374 *</td>
<td>0.113</td>
<td>Avoided</td>
</tr>
</tbody>
</table>

* indicates a difference at the 0.05 level of significance.
The chi-square results for the seasonal breakdown showed the Mopane Shrubveld to be significantly preferred ($X^2 = 113.893; p < 0.001; df = 4$), and the Floodplains were significantly avoided ($X^2 = 20.990; p < 0.001; df = 4$) in the early dry season. The Floodplains were in fact avoided in every season. The Mixed Woodland was avoided in every season apart from the early dry season, when it was used in proportion to its availability. The Baobab/ Mopane veld ($X^2 = 9.737; p < 0.001; df = 4$) and Mopane Shrubveld ($X^2 = 77.816; p < 0.001; df = 4$) were preferred in the late dry season, and the early wet and late wet seasons saw a shift to the Sandveld as the only significantly preferred landscape type ($X^2 = 190.296$ and $124.233; p < 0.001; df = 4$). These results substantiate the preference index ratings as seen in Table 2.2 and Figure 2.3.
DISCUSSION

The primary aim of this study was to establish whether a newly reintroduced population of white rhinos exhibited any preference or avoidance for the landscape types available to them, in order to improve our understanding of their spatial and temporal resource utilisation. The secondary aim was to compare the landscape preferences of the Pafuri rhinos, to those expressed by the rhinos in the central and northern Kruger National Park (Pienaar et al. 1993a).

Pienaar et al. (1992; 1993a) gathered rhino location data over 12 years (1979 – 1991) from annual aerial surveys carried out within the park, whereas our locations were collected over one year, on a daily basis with confirmed sightings on foot of individually known rhinos recorded. Aerial surveying is not the most accurate method for determining landscape preferences due to the inherent bias’ in certain landscapes having thicker vegetation, therefore making it more difficult to locate the animals. This discrepancy was confirmed in 2006, during the study period, when an aerial survey reported zero rhinos in Pafuri (pers. obs.), despite six being regularly located, at that time, for the purpose of this study. The difference in sample size between the current study and the previous studies was substantial, as this study followed only six individuals and recorded a total of 719 sightings and evidence of activity over the course of a year. Pienaar et al. (1992) recorded 10 273 aerial sightings in southern KNP, of an unknown number of individual animals, over the course of 12 years. In 1993 the same authors (Pienaar et al. 1993a) recorded 2320 sightings of rhinos in central and northern KNP, over the same 12 year period. Despite the methodological and data collection differences between the studies, the data analysis used was consistent so as to allow comparisons and therefore add to the previous findings.

Results showed that the Mopane Shrubveld was the overall preferred landscape, due to greater utilisation by rhinos in the dry season. The most notable feature of this landscape was the occurrence of sandy drainage lines that the rhinos were regularly tracked along. Many of these were run-offs from two semi-permanent springs that occurred in the northern sector of the study area, Mashikiri and Ndaekezane Springs,
but very few drainage lines contained any water during the study season. These two springs were most frequently in the early dry season and start of the late dry season, by which stage they did not appear to be providing sufficient water for the large mammals relying upon them. The rhinos utilised drainage lines a great deal when moving between water sources, as they were also a very good source of shade for resting, as well as grazing on shade loving grass species, such as *Panicum maximum*. Rhinos have been reported to show preferences for the higher nutrient lowlands and drainage lines in Hluhluwe-Umfholozi Park, Kwa-Zulu Natal (Perrin & Brereton-Stiles 1999). Another consideration to explain the higher utilisation of this landscape despite its average forage availability, is the length of tar road that intersects it. The rhinos frequently used this as a highway at night when exiting the Floodplains or the Baobab/ Mopane Veld and heading into the northern block, and this transit route could account for the increased utilisation. Familiarity with the abundant mud wallows in the Mopane Shrubveld, as the previous wet season progressed into the early dry season, could also have influenced their subsequent preference for this landscape. It is worth noting that the revised vegetation units (Mucina & Rutherford 2006) for this area have since combined the Mopane Shrubveld and the Baobab/ Mopane Veld landscapes to form the Limpopo Ridge Bushveld. This classification reports a field layer including palatable grass species such as *Schmidtia pappophoroides*, *Enneapogon cenchroides* and *Panicum maximum*, which were primary species consumed by the rhinos in the dry season (Chapter IV, this study).

Gertenbach (1983) originally suggested that the Mopane Shrubveld deserved special conservation status as it was unique within South Africa, making our findings significant that one of the most rare and unique landscapes in the country, is the one most preferred by white rhinos, in proportion to its size. Contrastingly, Pienaar et al. (1993a) stated that the Mopane Shrubveld was “obviously avoided” by rhinos on the basis that no rhinos had been observed in these areas for over 13 years, and they subsequently omitted this landscape from their analyses, along with the Baobab/ Mopane veld and the Floodplains. This information was gathered primarily from aerial surveys (that failed to detect these six rhinos in 2006). To suggest that a landscape is avoided by an animal, implies a conscious decision to neglect the landscape, after experiencing it, which was unlikely to
be the case here. It is feasible that white rhinos, having been originally reintroduced primarily in southern and central KNP (Pienaar 1970), never had cause to venture as far north as Punda Maria and Pafuri, if the landscapes available to them further south met all of their habitat requirements.

The Punda Maria Sandveld was preferred overall, and was also the most preferred landscape in the wet season. This landscape became a favourite for the rhinos after the first rains, potentially due to the immediate, post-burn growth of *Brachiaria serrata*. Herbivores tend to be attracted to the green flush of vegetation that occurs after fires (Mills & Fey 2005). Unfortunately burn data was not collected as part of this study and was only considered as an influence on landscape preference once the field season had concluded. The location of another permanent water source, namely Palm Spring, within this landscape meant it was regularly frequented throughout the year for drinking. The shift of all the rhinos to the southern sector of the study area towards the end of the late dry season was indicative of the declining water availability in the northern sector. Smit et al. (2007) found that white rhinos were more often associated with areas close to waterholes, than those far away, as was the case in this study. Palm Spring also became more utilised in the late dry season when the water at Mashisiti Spring started turning slightly stagnant. This was evident in the increased activity within the Punda Maria Sandveld landscape from the late dry to the early wet season, when the grasses became the major attraction for the rhinos.

African savanna herbivores must meet their daily dietary requirements within the limitations set by surface water availability (Redfern et al. 2003), and the Limpopo/ Luvuvhu Floodplains (as they are now known) included one of the most frequently utilised permanent water sources, namely Mashisiti Spring, that the rhinos were seen to visit on a regular basis throughout the year. This particular area of the Floodplains falls directly between the Baobab/ Mopane veld and Mopane Shrubveld, and could explain why the rhinos were more regularly located in these other two landscapes on their way to and from water, and not as often within the Floodplains themselves. The Floodplains also provided abundant shade and numerous mud wallows in the late wet season after
periods of heavy rain. Despite rhinos only needing to drink every 2 – 3 days, they will drink daily if water is readily available (Owen-Smith 1973; 1988). These results suggest that in the driest parts of their historical range the landscape preferences by white rhinos are influenced by available surface water, as a substitute for moisture gained from fresh, green grazing (Owen-Smith 1988) as is possible in areas of higher rainfall, such as central and southern KNP and Hluhluwe-Umfolozi. Permanent water was available in a number of locations around the study area, so the low rainfall did not negatively impact the availability of this vital resource. The dense perennial tree cover and numerous drainage lines provided ample shelter and resting opportunities, and the abundance of average grazing, with nutritious grasses such as Schmidtia pappophoroides, Enneapogon cenchroides, Panicum maximum, Stipagrostis uniplumis and Urochloa mosambicensis dominating certain landscapes, suggests that this area is not lacking any of the vital habitat resources required by rhinos.

Pienaar (1970) originally suggested that a possible reason for the choice of landscapes exhibited by the first rhinos reintroduced into KNP, was the similarity between the new landscapes and the topography of the area they originated from in the Umfolozi Game Reserve. When considering this possibility with the Pafuri rhinos, the only landscape common to both Satara (the central KNP area from which they were translocated) and Pafuri was the Punda Maria Sandveld (Gertenbach 1983). This was the most preferred landscape in Pafuri in the early wet and late wet seasons, when it most represented the conditions in the slightly wetter central parts of KNP. The dominance of Combretum, Mopane and Acacia sp. in the central KNP could have influenced their preference for the mopane dominated Pafuri landscapes in the dry season. Pienaar et al. (1993a) concluded that the primary characteristics of the preferred landscapes in central and northern KNP were:

- moderate to dense grass cover of good quality species
- open to moderate low-shrub cover and moderate tree stratum
- undulating topography with uplands, bottomlands and watercourses
- sandy soils with few rocks on the surface
- permanent water
- small pans for mud wallowing.

When considering these characteristics within the boundaries of Pafuri, the only aspect lacking is the dense, high quality grass cover. The field layer throughout much of Pafuri is sparse, but the grazing quality of dominant grass species is sufficient. The shrub and tree strata are also more dense than the preferred open to moderate, particularly in the two landscapes favoured by these rhinos. Characteristics of the avoided landscapes in central and northern KNP (Pienaar et al. 1993a) were listed as:

- sparse, poor quality grass cover
- dense, low-shrub stratum
- plains with sparse tree and high-shrub strata
- very mountainous or broken terrain
- soils with abundant rocks on surface
- shortage of permanent water.

These factors are characteristic of the Mixed Woodland landscape, which was significantly avoided in Pafuri, as well as certain parts of the Baobab/ Mopane Veld that was used in proportion to its availability. Despite these avoided characteristics being dominant in the rest of KNP, the rhinos in Pafuri regularly utilised mountainous/broken terrain with rocky surfaces when in transit. In addition they often utilised the open Floodplains with sparse tree cover as resting areas. The conclusion that can be drawn from this is the fact that these preferred and avoided landscape characteristics are ideals that can be applied when animals have a wider range of landscapes to select from. This study emphasises the need for an understanding of the seasonal changes in landscape preference expressed by white rhinos, when attempting successful reintroductions and establishment of new populations. The dry season behaviour is of particular interest due to the influence the depleting food and water can have on the animals' movements. Pienaar et al. (1992) stated that the lack of migration by rhinos implied that dry season data only, would be sufficient as an indicator of landscape use throughout the year. The lack of migration does not eliminate seasonal changes in movements around landscapes, however, and this is supported by our findings. Despite a lack of migration, a distinct shift in landscape preferences between the wet and dry seasons was apparent, and will influence management protocols for these animals and their habitats.
CONCLUSION

Statistical avoidance of a landscape type does not infer unsuitability thereof (Steinheim et al. 2005). The fact that the rhinos’ wet and dry season landscape preferences appeared to converge around permanent water sources, emphasises the demand for this resource in an semi-arid area of low rainfall, such as Pafuri. It also implies that the availability of water is a primary factor that will determine the success of these animals in this area of below average forage availability. The only landscape type that the rhinos avoided almost entirely, was the Mixed Combretum spp./ C. mopane Woodland, and the reason for this is unclear. Sparse grass cover is one possibility, and the seasonality of the one spring located in this landscape suggests that they were better situated in the southern section of Pafuri, where tree cover was less dense and hence grasses more abundant, as well as there being two preferred permanent sources of water.

The suggestion that reintroduced rhinos will prefer landscape types most resembling those of the area they originated from (Pienaar 1970) is something that should be considered in more detail with future reintroductions, as this study certainly supported that. The Pafuri rhinos are behaving in very similar manners to those studied in other areas, with regards to movements around the landscape, favouring areas that benefit most from the first rains (Punda Maria Sandveld), and utilising drainage lines a great deal for transit, resting and feeding (Perrin & Brereton-Stiles 1999). The significant preference by white rhinos of the Punda Maria Sandveld in this area is something that can be utilised by KNP management in other parts of this landscapes range, as it was previously classified as ‘neutral’ (Pienaar et al. 1993a). The impact of burns on the increased utilisation of this landscape would need to be considered further however. The most significant finding of this study, was the preference shown by the Pafuri rhinos for a landscape claimed to be unique in South Africa, C. mopane Shrubveld on Calcrete (Gertenbach 1983), and classed as ‘obviously avoided’ by white rhinos (Pienaar et al. 1993a) in the existing literature. It is advisable that, in order to carry out accurate assessments of rhinoceros landscape utilisation and preference, these studies need to be undertaken on foot (as opposed to aerial surveying), allowing positive identification of individual rhinos over a range of seasons.
REFERENCES


APPENDICES

Appendix 2.1

Map of all the rhino locations in relation to their landscape positions.
Appendix 2.2

The average minimum and maximum temperatures in Pafuri during the study period, as well as total rainfall.

<table>
<thead>
<tr>
<th>MONTH</th>
<th>MIN TEMP (˚C)</th>
<th>MAX TEMP (˚C)</th>
<th>RAINFALL (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 2006</td>
<td>20.9</td>
<td>32.5</td>
<td>4.5</td>
</tr>
<tr>
<td>April 2006</td>
<td>18.5</td>
<td>32.3</td>
<td>-</td>
</tr>
<tr>
<td>May 2006</td>
<td>9.5</td>
<td>28.5</td>
<td>-</td>
</tr>
<tr>
<td>June 2006</td>
<td>11.2</td>
<td>28.4</td>
<td>-</td>
</tr>
<tr>
<td>July 2006</td>
<td>9.1</td>
<td>32.4</td>
<td>-</td>
</tr>
<tr>
<td>August 2006</td>
<td>10</td>
<td>33.1</td>
<td>-</td>
</tr>
<tr>
<td>September 2006</td>
<td>12</td>
<td>35</td>
<td>-</td>
</tr>
<tr>
<td>October 2006</td>
<td>22</td>
<td>38</td>
<td>38</td>
</tr>
<tr>
<td>November 2006</td>
<td>21</td>
<td>37</td>
<td>89</td>
</tr>
<tr>
<td>December 2006</td>
<td>24.3</td>
<td>39.5</td>
<td>73</td>
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<tr>
<td>January 2007</td>
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<td>36.5</td>
<td>60</td>
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<tr>
<td>February 2007</td>
<td>24.7</td>
<td>35.2</td>
<td>119</td>
</tr>
<tr>
<td>Total</td>
<td>17.2</td>
<td>34</td>
<td>383.5</td>
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CHAPTER THREE
RANGING PATTERNS OF REINTRODUCED WHITE RHINOS IN
PAFURI, KRUGER NATIONAL PARK

INTRODUCTION
The behaviour of reintroduced rhinos needs to be monitored post-release as there is still little known in this regard, particularly with regards to their movements around the landscape and establishment of ranges (Linklater et al. 2006). The restrictions that fences and conservation area boundaries impose upon large mammals suggest that their use of space could be affected by the lack of permitted dispersal (Rachlow et al. 1999). It was suggested many years ago that no wild animal roams the land randomly (Seton 1909). The home range of an animal is defined as the non-random (White et al. 2007) area within which it travels in the process of normal activities such as feeding, mating (White & Garrott 1990) or resting, for example. The primary advantage of the home range is the increased knowledge of spatial and temporal resources within the ranging area, allowing for greater exploitation of these resources (White et al. 2007), such as water sources and productive feeding sites.

The white rhinoceros (*Ceratotherium simum*) is behaviourally distinguishable from the other rhino species by the degree of sociality it exhibits (Owen-Smith 1988; Shrader & Owen-Smith 2002). Sub-adults (from ±3 to 9 years) are known to form permanent associations with single adult females (7+ years of age), and those with calves, but are chased away by the adult when she is expecting her next calf (Owen-Smith 1973). Adult females develop overlapping (Owen-Smith 1973; Shrader & Owen-Smith 2002), undefended (Rachlow et al. 1999), and often large ranges (White et al. 2007). The adult males (10-12 years) hold mutually exclusive territories (Owen-Smith 1972) that are generally smaller than female home ranges (Pienaar et al. 1993; White et al. 2007), but this ability is determined by density of animals within enclosed areas, and the subsequent competition it provokes. In areas of high rhino density, not all adult males are dominant territory holders (Rachlow 1997). The dominant males maintain the exclusion of their territories by regular scent-marking techniques such as spray-
urination, scraping and dung kicking (Owen-Smith 1972; Rachlow et al. 1999), but they do allow subordinate males to reside within the area providing they do not pose any threat to their status. It is well established that the territorial bull is the only reproductively active male within his territory (Owen-Smith 1971; Owen-Smith 1972; Rachlow 1997; Owen-Smith 2002), allowing him the sole entitlement to mate with oestrus females when they enter the area. Hence, the occupation of a territory gives the dominant male a reproductive advantage, and a link has been found between the utilisation by females of particular territories, and the amount of grassland habitats within it (White et al. 2007). This suggests that females select the territories of the males with the better available grazing.

To improve our understanding of the spatial patterns of a small group of reintroduced white rhinos, in an area never before studied, range and territory establishment were examined while considering the influence of spatial and temporal availability of resources on this behaviour. The purpose of this study was to gain some insight into the size of ranges and territories established post-reintroduction. This information is crucial when attempting to establish a breeding nucleus of a species from an initially small population. It was expected that the Pafuri rhinos would establish larger ranging areas than rhinos in higher density areas, particularly in the first year after reintroduction when animals are unfamiliar with their new surroundings. Dry season ranging was expected to be larger than in the wet season due to the decline in available food and water resources.
METHODS

Study Area

The study was conducted in Pafuri, in the far northern section of the Kruger National Park (KNP), South Africa (22°23'S, 031°08'E). The study area covers 203 km$^2$ of KNP, bordered by Mozambique to the east, Zimbabwe to the north, with the Luvuvhu River forming the natural boundary between Pafuri and the rest of the park to the south. The area has a reputation for low rainfall and high temperatures (Tinley 1981), with long term average annual rainfall at 466 mm (Zambatis 2003). The dry season of the study period saw much lower rainfall than the long term average, yet the wet season showed a marginal increase (Figure 3.1).

![Figure 3.1](image-url) Mean monthly rainfall totals for Pafuri Camp from 1984 to 2002, and monthly rainfall totals from the March 2006 to February 2007 study season.

The area is split into five landscape types based on differing geomorphology, climate, soils, vegetation and fauna (Gertenbach 1983). These are:

- Punda Maria Sandveld on Cave Sandstone
- *Adansonia digitata/ Colophospermum mopane* Rugged Veld
- *Colophospermum mopane* Shrubveld on Calcrete
- Limpopo/ Levubu Floodplains
The fifth landscape type, Mixed *Combretum* spp./ *Colophospermum mopane* Woodland, is the smallest in Pafuri yet the more prevalent landscape type in the rest of the KNP (Gertenbach 1983).

**Field data collection**
The rhinos were fitted with radio transmitters in the anterior horn before reintroduction (see methods described in Pienaar & Hall-Martin, 1991) and tracked on foot daily for at least two weeks of every month from April 2006 to February 2007 (preliminary data were collected during March 2006 on a less regular basis while familiarity with the study area was gained), and tracks were checked from a vehicle for the remainder of the month. Tracking commenced at sunrise and continued until between 11h00 and 17h00, depending on the heat and inclement weather conditions. Radio telemetry (using a Communications Specialist R-1000 handheld receiver and AWT ‘H’ Two-element Yagi antenna) aided in location of the animals, along with spoor identification, which became the only aid once the lifespan of the radio transmitters was depleted (3 – 9 months after study commenced). Radio fixes were not trusted as exact locations until the animal was tracked on foot and visually identified (Pienaar et al. 1993).

During each tracking session, either on foot or from the vehicle, every sign of fresh rhino activity (since sunset the previous day when they become most active and the last tracking session was concluded) was logged and recorded using a GPS Garmin iQueM5. Information on the type of activity, such as feeding, resting, drinking, wallowing, defecating, male territory marking, and the estimated time each activity took place, were recorded as evidence of habitat utilisation. Due to the low density of rhinos and the distances they would travel daily through dense vegetation, the specific individuals encountered while tracking was random and not guaranteed on a daily basis. When encountered they were approached from downwind to minimise disturbance and allow time for individual identification.

**Data analysis**
All data points were checked for independence by ensuring no more than two GPS locations were recorded for each individual rhino or group on one day, working on the
assumption that the animals logged position was not influenced by its position during previous observations (Swihart & Slade 1985). At most, activity recorded in the morning and afternoon of the same day could be classed as independent providing the time in between was more than six hours (Shrader & Owen-Smith 2002), and not spent sleeping. The decimal degree GPS co-ordinates for each rhino were re-projected to Universal Transverse Mercator (UTM) [WGS84, Zone 36S] using Manifold System 7, Professional Edition (CDA International Ltd. 2006). Ten localities per individual or group are considered minimum for the estimation of range size (Conway & Goodman 1989), although more recent research into ideal sample sizes for home range analysis of black rhinos suggests a minimum of 35 localities should be adhered to (Lent & Fike 2003). The data collected in this study was sufficient by these guidelines.

Home ranges (HR) and utilisation distributions (UD) were constructed using a local convex hull (LoCoH), nonparametric kernel method, which generalizes the minimum convex polygon (MCP) method (see Getz & Wilmers, 2004, for technical methodology). The Adaptive LoCoH (a-LoCoH) method was used as it generally performs better than the ‘Fixed number of points’ (k-LoCoH) and ‘Fixed radius’ (r-LoCoH) methods (Getz et al. 2007). The a-LoCoH method creates hulls from a maximum number of nearest neighbours, to a point where the sum of their distances from the root point is less than or equal to a distance measure $a$. This measure ($a$) should be approximately the distance between the two most distant points in the data. This was used initially to determine an appropriate value of $a$ for each dataset (individual rhino and season) analysed, and was subjectively adjusted following the ‘minimum spurious hole covering’ (MSHC) approach of Getz & Wilmers (2004), to optimise the HR estimations. For each rhino, a-LoCoH was used to generate HR from all GPS data, as well as a wet and dry seasonal UD. Home range areas were taken as the area covered by the 100% isopleths, with the core area of utilisation determined by the 50% isopleths. LoCoH analyses were all run using the web-based version of the software (http://locoh.cnr.berkeley.edu/).

For this analysis the rhinos that did not show much independent movement during the study period were grouped together. The movements of the calf (calf 7) were always in
close proximity to the mother (Cow 1) as he was still a yearling (≤ 1 year old) for most of the study period, so they were classed as a pair for this analysis. The two sub-adults (Cow 3 and Bull 6) similarly were often located together and were therefore grouped for the purpose of range calculation. The remaining adult female (Cow 2) was periodically located with each of the above mentioned groups, and with bull 5, or on her own, so her range was calculated individually. Bull 5 was the only dominant male expressing territory marking (scraping, spray urination, dung kicking), so a minimum convex polygon (MCP) was applied to the dataset of his localities, as well as carrying out the a-LoCoH to see how his ranging area compared to the females. The MCP approach is the recognised method for measuring male territory sizes, and this was calculated by generating a convex hull around all bull 5 GPS locations, using Manifold (CDA International Ltd 2006). The ranges of each rhino/pair were compared for the year, and split into dry (Apr – Sep) and wet (Oct – Feb) seasons for further comparison.
RESULTS

A total of 572 independent localities for four rhinos (once cow 3 and bull 6 data were pooled) were recorded throughout the study period (Figure 3.2a).

Figure 3.2 The α-LoCoH annual ranges and utilisation distributions of the Pafuri rhinos with core areas in red, gradually fading to yellow with decreasing activity (see Table 3.1 for sample sizes).
Despite the labelling by the LoCoH software of the results as Home Range (HR) and Utilisation Distribution (UD), the term “annual range” is thought to be more accurate, as one year is not sufficient to determine an animal’s true home range (Pienaar et al. 1993). From these calculations of HR and UD of the Pafuri rhinos, it is immediately evident that the entire population focussed their movements primarily around the south-western sector of the study area.

The MCP placed around the $a$-LoCoH of Bull 5 (Figure 3.2b), to allow comparisons with the more conventional methods for calculating territory size, calculated a total territory size of 44.8 km$^2$. The bull exhibited three areas of core activity from the $a$-LoCoH HR (29.9 km$^2$), with the primary core comprising 3.65 km$^2$ of the HR. The 20% isopleth expressing highest activity within his territory, was an area surrounding the tar road that he would patrol on regular occasions while marking his territory with scraping and spraying every 5 metres. The 50% isopleth shows his activity focussing around the Punda Maria Sandveld that the rhinos preferred in the wet season (Chapter II, this study).

Cow 1 was seen to range as far west as the fence that leads to the military corridor (Figure 3.2c), which is an area that was rarely utilised by the other rhinos. Her core areas of activity fell within the Punda Maria Sandveld (1.78 km$^2$) and the Baobab/ Mopane Shrubveld, which was possibly a wet versus dry season difference in utilisation (Figure 3.3). The HR of cow 1 (25.4 km$^2$) was a similar size to that of bull 5 (Table 3.1), which could be due to their movements around the landscapes frequently triangulating between permanent water sources.

Cow 2, who was often pursued by bull 5 during the study period, appeared to develop her range (Figure 3.2d) primarily within the territory of the bull. The HR of cow 2 was the smallest in this study (17.0 km$^2$), which could be due to the unusual area of inactivity in the centre of her range. Her core area (2.95 km$^2$) was slightly larger than that of cow 1, but also focused in a similar area. The most interesting of the ranging areas was that of cow 3 and bull 6 (Figure 3.2e), who covered a greater area than all the other rhinos.
combined (84.1 km$^2$), with a core area (12.71 km$^2$) approaching the size of the entire HR of cow 2. This extensive ranging behaviour is not unusual for sub-adults however (Owen-Smith 1973; 1988).

Table 3.1 The annual range (100% isopleth) and core area (50% isopleth) for each rhino, including a wet and dry season breakdown (km$^2$).

<table>
<thead>
<tr>
<th>RHINO</th>
<th>$n$</th>
<th>ANNUAL RANGE (HR)</th>
<th>CORE AREA</th>
<th>$n$</th>
<th>DRY SEASON RANGE</th>
<th>$n$</th>
<th>WET SEASON RANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bull 5 ($a = 15000$ m)</td>
<td>253</td>
<td>29.9</td>
<td>3.65</td>
<td>120</td>
<td>21.0</td>
<td>133</td>
<td>19.9</td>
</tr>
<tr>
<td>Cow 1 &amp; calf 7 ($a = 10000$ m)</td>
<td>90</td>
<td>25.4</td>
<td>1.78</td>
<td>37</td>
<td>16.3</td>
<td>53</td>
<td>11.6</td>
</tr>
<tr>
<td>Cow 2 ($a = 8000$ m)</td>
<td>85</td>
<td>17.0</td>
<td>2.95</td>
<td>34</td>
<td>14.3</td>
<td>51</td>
<td>12.2</td>
</tr>
<tr>
<td>Cow 3 &amp; Bull 6 ($a = 19000$ m)</td>
<td>144</td>
<td>84.1</td>
<td>12.71</td>
<td>96</td>
<td>65.4</td>
<td>48</td>
<td>50.9</td>
</tr>
</tbody>
</table>

(a - the distance between two most distant GPS points in each dataset)

The seasonal variation was as expected, with dry season ranges being slightly larger than those of the wet season (Table 3.1; Figure 3.3), due to the decline in available forage and water. All of the rhinos appeared to focus their wet season activity around the Punda Maria Sandveld region, as is evident from the bold striped areas of each map in Figure 3.3. The dry season core areas of all the rhino ranges shifted to the Mopane Shrubveld, apart from the sub-adults who remained in the Sandveld and adjoining Baobab/ Mopane Veld. The dry and wet season core areas of utilisation are directly correlated with the landscape preferences revealed in Chapter II of this study. What is also evident from these maps is the utilisation by all the rhinos of the northern sector of Pafuri in the dry season. As the wet season commenced they did not range as far north very often. Despite the extreme ranging areas of cow 3 and bull 6 and the very clear shift in their dry and wet season locations (Figure 3.3d), their core areas of utilisation for the dry and wet season overlapped, suggesting there was potentially a perennial resource that attracted them to this area.
Figure 3.3 The wet and dry season ranging areas of the Pafuri rhinos, overlaying the five landscapes available (including permanent water sources and the original rhino boma site in red on the data point map).
DISCUSSION

The use of the a-LoCoH nonparametric kernel method for calculating home ranges produced some interesting images, potentially due to the fact that it is more adept at locating geographical features such as rivers, lakes, inhospitable terrain, and incorporating these into the analyses. This method is superior to parametric kernel methods as it draws on the spatial structure of data that is often affected by hard boundaries and areas of exclusion (Getz et al. 2007), such as lakes and mountains. Our findings in this study differed notably from some of the previous research on ranging and territory establishment of white rhinos (Owen-Smith 1972; Owen-Smith 1973; Owen-Smith 1988; Pienaar et al. 1993; White et al. 2007), in that the ranges established by the Pafuri rhinos were larger than those previously reported. This was as expected, due to the low density of only six rhinos in a 203 km$^2$ area (0.03 rhinos/km$^2$).

The MCP territory of bull 5 (44.8 km$^2$) was larger than the HR of 29.9 km$^2$ calculated by the a-LoCoH, as ranges correct for irregular excursions. The MCP method simply includes each of the outer points of the bulls range as the border of the territory, due to the fact that territories are generally fixed areas. This territory was substantially larger than the previously reported 0.75 – 2.6 km$^2$ in Hluhluwe-Umfolozi Game Reserve (density = 3 – 5.7 rhinos/km$^2$), South Africa (Owen-Smith 1988); 5 – 10 km$^2$ (0.7 rhinos/km$^2$) in Kyle Game Park (Condy 1973); 2.5 – 13.9 km$^2$ (0.6 – 1.8 rhinos/km$^2$) in Ndumu Game Reserve (Conway & Goodman 1989); and 6.2 – 13.8 km$^2$ (0.5 – 1.4 rhinos/km$^2$) in Kruger National Park (Pienaar et al. 1993). The difference in rhino densities in the other study areas accounts for the smaller territory sizes where competition for space is higher, particularly considering the fact that male territories do not overlap (Owen-Smith 1988). Bull 5 was the only dominant male in Pafuri so his territory could feasibly have covered the full 203 km$^2$ study area if he had wanted to.

When we compare this result with territory studies in similarly low rhino density areas, such as 14.6 – 50.4 km$^2$ (0.4 rhinos/km$^2$) in Matobo National Park (Rachlow et al. 1999); and 60 – 116 km$^2$ (0.23 rhinos/km$^2$) in Limpopo Province (Kretzschmar 2003), his territory size does not seem that excessive. Another distinction between our findings and previous studies is the fact that male territories are usually much smaller than female
ranges (Owen-Smith 1972; Pienaar et al. 1993; Rachlow et al. 1999), again primarily due to competition with other males which was not a factor in this study. The only range that the territory of bull 5 was smaller than, was that of the sub-adults (cow 3 and bull 6), who ranged an extensive 84.1 km² during the course of the year (this does not include their excursion across the Limpopo River into Zimbabwe, and occasional fence crossing into the military corridor on the western boundary).

The other female range sizes (17 km² for cow 2, and 25.4 km² for cow 1) were consistent with previous findings, such as 7.2 – 45.2 km² in KNP (Pienaar et al. 1993). It was also expected that dry season ranges would be larger than wet season ranges, due to the decreased availability and quality of forage and water (Owen-Smith 1988), and our results confirmed this. The change in range size was small for bull 5 (21 km² down to 19.9 km²) and cow 2 (14.3 km² down to 12.2 km²), but there was a difference of 4.7 km² seen in cow 1 and calf 7, with cow 3 and bull 6 decreasing their ranging area by 14.5 km² when the wet season commenced. Pienaar et al. (1993) found the opposite effect, with range sizes increasing in the wet season instead of the dry season. It was thought that this could be due to the wider range of available field water in the wet season, suggesting that the movement of the rhinos was not constrained by the few permanent water supplies.

The early wet season (Oct – Dec 2006) saw the first occurrence of all six rhinos inhabiting the same area, in the Punda Maria Sandveld after the first rains made post-burn green shoots abundant. This was evident from the wet season core areas of all rhinos in Figure 3.3. Unfortunately burn data was not recorded as this effect was only noted once the field season had concluded and analysis had commenced. From personal observations, this area was the first to benefit from the first substantial rains in November 2006, when grasses such as Brachiaria serrata and Stipagrostis uniplumis were suddenly available to the rhinos. The apparent influence of this burn on their subsequent landscape preferences and ranging behaviour can only be confirmed by comparing these results with the succeeding years.
When considering the wet and dry season ranges of the Pafuri rhinos, their movements can be correlated with water availability, in the absence of high quality forage. The distribution of drinking water during dry seasons in semi-arid landscapes places constraint on the foraging range of megaherbivores (Derry 2004), and grazers are influenced by this factor more than browsers (Smit et al. 2007). The seasonal springs, namely Mashikiri and Ndaekezane Spring, in the northern sector of Pafuri were regularly visited by the rhinos in the early dry season, when this study commenced. The utilisation of Ndaekezane Spring was clearly the only resource that attracted the rhinos to the most avoided Mixed Woodland landscape (see Chapter II, this study). By the late dry season however, these springs were drying up and the substantial permanent water of Mashisiti Spring and Palm Spring in the southern half of Pafuri clearly influenced their shift in range areas. There was some overlap evident of the wet and dry ranges of bull 5 and cow 2, but cow 1 occupied a totally separate area in the dry season versus the wet season. It could be due to the fact that her 3 month old calf was influencing her movements in the early dry season, if she was trying to avoid the areas frequented by the other rhinos, in particular bull 5. Dominant males are known to react aggressively towards new calves so the cows tend to seek solitude during the post-birth period (Owen-Smith 1988).

The extended ranging behaviour of cow 3 and bull 6 can possibly be explained by their youth, and the possibility that they were continuing to explore the entire area available to them after being released from the boma. Sub-adults are thought to take longer than adults to establish a home range (Owen-Smith 1988), as was evident in this study. Bull 6 did not have to be limited by territory establishment as he was too young (estimated 7 years old), and cow 3 did not have a calf to restrict her movements.
CONCLUSION

It appeared as if the landscape types were not the primary influence in the range and territory establishment of the Pafuri rhinos, as they were all seen to frequent the area of Pafuri that allowed the quickest and closest access to all five available landscapes (see Figure 3.3). It is possible there was a factor present in every landscape type that they benefited from, such as foraging in the Sandveld; drinking on the Floodplains; resting in the Mopane Shrubveld, and they therefore focused HR cores where the landscapes border each other. The lack of vegetation surveys makes it difficult to draw conclusions about the potential influence that feeding had on their movements, but the locations of water points appeared to have an influential impact on their movements around the study area. Herbivores can meet a lot of their water requirements from the liquid content of plant tissues (Owen-Smith 1988) and this is one of the reasons rhinos are not reported as being a water dependent species. It is feasible, however, that in semi-arid areas of notably low rainfall such as Pafuri, surface water availability is more influential in the ranging behaviour of these megaherbivores, than originally thought. The seasonal changes in range appeared to reflect this pursuit of available surface water, and confirmed our expectations that range size would increase in the dry season when food and water became limited.

The sizes of established ranges and territory, although large compared to many studies carried out in higher density areas (Owen-Smith 1988; Conway & Goodman 1989; Pienaar et al. 1993), were not unrealistically large when compared to studies carried out in areas of similar rhino density (Rachlow et al. 1999; Kretzschmar 2003). As expected with a new population, the initial ranges are large as there are few limiting factors such as competition for food and territory. It would be interesting to follow-up on this study to assess the difference between spatial utilisation now that they are settled and familiar with the area, in comparison to the post-reintroduction ranging behaviour. It is unlikely that the sub-adults would still be ranging quite as far as was seen during the study period, and the birth of two new calves in 2008 would suggest that the movements of the two cows will be affected by their need for post-birth privacy (Owen-Smith 1988).
Bull 6 should also be approaching adulthood, which will see the initiation of his territory establishment that is likely to cause conflicts with the well established bull 5, due to the extent of his territory and the fact that it encompasses most of the popular permanent water sources and preferred feeding areas.
REFERENCES


CHAPTER FOUR

WHITE RHINOCEROS DIETARY COMPOSITION IN PAFURI,
KRUGER NATIONAL PARK

INTRODUCTION
A vital aspect of assessing the suitability of reintroduction sites is the availability of substantial and high quality feeding areas. Habitat suitability is directly affected by food quality and availability (Muya & Oguge 2000), and food quality is directly affected by rainfall and soil nutrients (Arsenault & Owen-Smith 2002; Augustine et al. 2003; Verweij et al. 2006). Diet selection is a problem that animals need to solve, due to the varying degrees of nutritional value that the available food types hold (Emmans 1991), which directly affects survival rates and fecundity (Abaturov et al. 1995; Grant et al. 1995; Wrench et al. 1997). Herbivores have to make many choices on a daily basis, between numerous species of low to high nutritional value and even between the parts of these plants (Illius & Gordon 1987; Bartolomé et al. 1998). These biotic factors also affect the grazing distribution of large herbivores (Bailey et al. 1996). An understanding of the habitat requirements and use thereof, of large coexisting ungulate species, is also necessary in order to prevent negative habitat changes (Perrin & Brereton-Stiles 1999), such as overgrazing which can lead to soil erosion (Bailey et al. 1996; van Oudtshoorn 1999). Senft et al. (1987) suggest that four levels of ecological hierarchy are encountered by foraging large herbivores: feeding station; plant community; landscape system; and regional system. Melton (1987) confirms this by quantifying habitat selection at three spatial scales: selection for habitat types; area selection for grasses; and diet selection from the chosen areas.

Megaherbivores (plant-feeding mammals of adult body mass ≥1000 kg), despite needing to eat less food per day per unit of body mass than smaller ungulates, spend a greater proportion of their time foraging (Bell 1971; Owen-Smith 1988). This suggests that plant structure and distribution (Frank et al. 1998) can be a limiting factor on feeding rate by increasing the necessary foraging time. Large herbivores are capable of utilising high volumes of low quality feed (Bell 1971; Jarman 1974; Demment & Van Soest 1985; Illius &
Gordon 1987; Illius & Gordon 1993). This is fortunate as their daily intake requirements dictate that they do not have much time to be selective (Wegge et al. 2006), whereas small species, capable of foraging selectively, require forage of a higher quality.

The white rhino is known to be an area-selective, as opposed to species-selective, bulk grazer (Owen-Smith 1988) that is adapted for fast intake of high volumes of food required to support its large body size (Owen-Smith 1973). As a result, they can experience difficulties obtaining maximum quality from a highly fibrous, low nutrition diet of predominantly C4 grasses (Perrin & Brereton-Stiles 1999). Grazing mammals have been shown to enhance nutrient cycling in their environments (Georgiadis & McNaughton 1990; McNaughton et al. 1997; Frank et al. 1998; Augustine et al. 2003; Jacobs & Naiman 2007; Anderson et al. 2007), however, in the dry season grasses become dormant and available forage is severely depleted (Sinclair 1975). During this time grasses become more fibrous and protein levels drop (Owen-Smith 1982), with perennial grass quality declining before that of annuals (Prins 1988). Grazers are at a greater disadvantage than browsers at this time due to the drop in nutritive quality specifically of grasses (Wegge et al. 2006). The green leaves of grasses hold the highest proportion of protein and as such are more digestible (Prins 1988), but protein content varies between species, age of plant and soil in which it is growing. Perennial grasses produce more leaf material than annual grasses (Kretzschmar 2003), and perennials benefit from early, shorter rains faster than annuals (Prins 1988), making them potentially preferable grasses to grazers. Young plants and those that grow in shaded areas also have a tendency for higher protein and lower cell wall component concentrations (Kretzschmar 2003), making them more palatable forage. Perrin and Brereton-Stiles (1999) found that white rhinos avoided a small number of unpalatable species, yet still showed no preference for the highly palatable species and merely consumed species in accordance with their availability.

Grass species are characterised by their perenniality, palatability and grazing values (van Oudtshoorn 1999), to provide an indication of their value to grazing herbivores. The perenniality of a species describes the ability to produce high amounts of leaf material, which is the most valuable part of the plant to grazers (Owen-Smith 1973). Perennial
species produce the highest amount of leaf material as annual grass species utilise most of their resources for seed production (van Oudtshoorn 1999; Kretzschmar 2003). Perennial grasses are however more susceptible to extreme drought conditions and can struggle to recover, whereas annual species thrive after fires that often follow in extreme dry conditions (Smit et al. 2007). Grazing values are non-seasonal ratings assigned to grasses under normal growing conditions, based on subjective assessments of various factors such as perenniality, palatability, nutritive value, growth vigour, leaf production and digestibility (van Oudtshoorn 1999; Kretzschmar 2003). These characteristics are applied on a national scale by van Oudtshoorn (1999), but grass species can vary between areas, depending on local conditions and climate. This should be taken into account when interpreting the value of grass species to herbivores following this classification system.

It is fundamental when assessing animal movements and habitat preferences that an understanding of the food resources supporting herbivores through the crucial dry season is focal (Owen-Smith 2002). The majority of feeding studies today assess preferences shown by the focal animal by comparing observed feeding habits and species consumed, to those available to the animal (Laurie 1982; Bartolomé et al. 1998; Perrin & Brereton-Stiles 1999; Macandza et al. 2004; Shrader et al. 2006), utilising the well-used ‘feeding station’; ‘feeding-minutes’; and ‘feeding track’ methods (Hall-Martin et al. 1982). However, dry season studies do not often allow for suitable animal observations or efficient grass species identification, and low rainfall areas exacerbate this problem. Faecal analysis has progressed noticeably in the last 70 years (Baumgartner & Martin 1939) and advanced as a preferred tool for assessing herbivore feeding habits and diet quality (Sparks & Malechek 1968; Vavra & Holechek 1980; Holechek et al. 1982; Wrench et al. 1997; Maia et al. 2003) by identification of grass leaf blade cuticular fragments (Davies 1959; Carrière 2002) of the species within the faeces, using anatomical features (Metcalfe 1960; Stewart 1965; Stewart 1967; Ellis 1979; Ellis 1981; De Jong et al. 2004; Wegge et al. 2006). It is most advantageous under field conditions that make direct animal observations difficult, such as in thick vegetation; with study animals nervous of human presence; and in very dry habitats (Holechek et al. 1982). All of which were issues in the current study, and hence this alternative technique was adopted.
According to Prins (1988), grasses are favoured depending on their moisture content, suggesting that annuals and weak perennials will be more popular. Yet Kretschmar (2003) suggests that perennials will be favoured as they produce more leaf material than the other grasses. It was expected that, due to the fact that rhinos are known to graze on species according to their availability, if there is a seasonal change in species consumed it will be for moderate grazing value species and annuals during the late wet season when they are well developed and abundant. Perennial species will be their primary forage during the dry season, with an increase in the consumption of low grazing value species towards the late dry season when options become severely depleted.
METHODS

Study Area

The study was conducted in Pafuri, in the far northern section of the Kruger National Park (KNP), South Africa (22°23'S, 031°08'E). The study area covers 203 km² of KNP, bordered by Mozambique to the east, Zimbabwe to the north, with the Luvuvhu River forming the natural boundary between Pafuri and the rest of the park to the south. The area has a reputation for low rainfall and high temperatures (Tinley 1981), with long term average annual rainfall at 466 mm (Zambatis 2003). The dry season of the study period saw much lower rainfall than the long term average, yet the wet season showed a marginal increase (Figure 4.1).

Field data collection

The study period extended from February 2006 to February 2007. Rhinos were tracked on foot daily with the aid of spoor and discontinuous radio-tracking (Harris et al. 1990), using a Communications Specialist R-1000 handheld receiver and AWT ‘H’ Two-element Yagi antenna. Radio transmitters have an average lifespan of 9 to 13 months (Pienaar & Hall-Martin 1991) but this varies widely, depending on battery life, field conditions and animal behaviour. Once a signal was received from the radio transmitter in the horn of the animal, it was triangulated (Kenward 1987) in order to confirm a more precise location, and then followed until the animal was located. This facility was available for
3-9 months of the study period until the final transmitter failed. The feeding path of the animal was then backtracked in order to collect information on the grass species available, and those grazed. At the first sign of freshly grazed grass a 0.7 x 0.7 m quadrat was used to represent a ‘feeding station’, that is the approximate area a white rhino will swing its head while feeding, without having to move its feet (Bailey et al. 1996; Shrader 2003). Five quadrats, approximately 3 to 5 m apart, comprised one ‘feeding path’ or transect. Within each feeding station the number of grazed and ungrazed tufts of each grass species eaten was recorded, measured as the distance between the tips of the index finger and thumb as this is roughly equivalent to the width of the white rhino mouth (Owen-Smith 1973). When it was possible to carry out more than one transect in a day, these were spaced approximately 30 m apart along the path of the animal.

The method of faecal analysis (Stewart 1967; Sparks & Malechek 1968; Vavra & Holechek 1980; Holechek et al. 1982; Wrench et al. 1997; Maia et al. 2003; Wegge et al. 2006) provides a suitable alternative as a more thorough means to determine the primary dietary composition of the study animals. When fresh dung was located along the animal’s path a sample of approximately a handful was collected by hand from the centre of three boluses to avoid any potential impact from sun, rain, dung beetles, etc. These samples were placed in paper bags, returned to camp and air dried for at least 24 hours, out of direct sunshine. Once dry, samples were boxed and stored in a dry room until return to the laboratory for microhistological analysis, at the conclusion of the field season.

**Faecal analysis**

Once in the lab the samples were individually fed through a grinding mill fitted with a 1 mm sieve (Wegge et al. 2006) and transferred to individual sealed plastic jars. The lab protocol followed was that outlined by Stewart (1967). One gram of dry ground dung was weighed and placed in a 10 ml test tube, to which 4 ml of 55% Nitric Acid was added. This test tube was then placed in a 600 ml beaker, on a hot tray, containing 350 ml of boiling water, and left for 3 minutes under a ventilation hood. Thereafter the sample was made up to 100 ml with water and returned to the heating plate in a beaker
until boiling (Stewart 1967). As the liquid started to boil (approximately 6 minutes later) it was removed from the heat and poured through a 0.425 mm and 0.300 mm sieve. A pinch of the pulp remaining in the 0.300 mm sieve was removed with a spatula and placed in a drop of glycerol (for preservation purposes) on a microscope slide and covered, ready for microscopy.

Slides were examined under a Leitz HM-LUX3 light microscope using 100X or 400X magnification (Rogerson et al. 1976; Bartolomé et al. 1998). Fifty fragments per sample were identified to grass species level as this is considered sufficient to reveal the grasses comprising 10% of the diet (Macandza et al. 2004). This was done with the aid of a leaf anatomy identification key of the dominant grass species in the study area, obtained from a microphotograph reference collection compiled by Roger Ellis (1981), as well as some reference samples collected from the study area. An anatomical description of the individual grasses was used in combination with the visual aid (Metcalfe 1960; Stewart 1965). Fragments of similar sizes were identified to avoid biases based on the less digestible grass species remaining in slightly larger fragments and therefore being more noticeable. Any species that could not be immediately identified was noted and a detailed description of its characteristics recorded. The characteristics used to distinguish between species were found on the abaxial layer of the leaf epidermis and comprised of silica bodies, stomata, long cells, short cells and presence or absence of hairs (Macandza et al. 2004). The shapes and sizes of these features differ significantly among certain grass species and can therefore be used as a means to identify individual grasses present in the faeces, using the previously compiled key and microphotographs (Metcalfe 1960; Stewart 1965; Stewart 1967; Ellis 1979; Ellis 1981).

Unidentifiable fragments were photographed and a description written for later identification, prior to analysis. The identified fragments were recorded on spreadsheets and combined into an overall database at the end of sampling, ready for statistical analysis.
Data analysis

Site-based acceptance

Acceptance indices are used to calculate the likelihood of animals feeding on particular species when they are available nearby (Owen-Smith & Cooper 1987). Site-based acceptance was calculated following Owen-Smith and Cooper (1987) with slight modifications due to the data collection method allowed by the particular field conditions. Instead of using 30 minute feeding intervals, as per the original calculation, one transect or ‘feeding path’ was used as representative of an approximately equivalent site distinction. It was not possible to carry out feeding observations in this study, but each feeding path similarly represented an independent feeding unit, as they were not repeated on the same rhino or group in one day. When more than one feeding path was surveyed in one day, the results were averaged, as feeding paths 30 m apart are not considered independent of each other. Site-based acceptance (SA) per grass species was calculated by dividing the number of feeding paths in which the species was eaten, by the number of feeding paths in which the species was present.

Site availability was calculated by dividing the number of feeding paths that the species was present within, by the total number of feeding paths recorded. Data for the entire study season were pooled for these calculations due to the low number of feeding surveys carried out per season. The frequency of acceptance per grass species was calculated by dividing the number of feeding stations in which the species was eaten by the number of feeding stations in which the species was present.

Dietary composition

Grass species preference and avoidance could not be determined due to the lack of data on available and consumed species from field vegetation surveys. To determine the species composition of the diet from the faecal samples, the frequency of each grass species was calculated as a percentage of the total fragments identified. For subsequent analyses, all raw data were checked for normality and analysed accordingly. The relationship between all grass species consumed and the frequency of occurrence within faecal samples per season was tested using a one-way ANOVA, with grass species as the
dependent variable and season as the independent variable. Season was split into four categories directly reflecting the dry and rainy seasons during the study period (Figure 4.1): Early dry (April-June); Late dry (July-Sep); Early wet (Oct-Dec); and Late wet (Jan-Feb). Homogeneity of variances was tested using Cochran’s C, and normality of residuals using a Shapiro-Wilk test.

Seasonal changes in diet composition, quantified at the grass species level, were further investigated according to grazing value and perenniality in order to interpret any significant differences shown here. Grazing value was categorised into High; Moderate; and Low according to van Oudtshoorn (1999) and perenniality split into Annuals; Weak perennials; and Perennials. A one-way ANOVA was utilised with grazing value/perenniality as dependent variables and season as the independent variable. A bootstrap (Efron & Tibshirani 1993) macro was run, using Statistica v.8 (StatSoft 2007) on the perenniality versus season for the Annuals in the Early Wet and Late Wet seasons, as these data were not normally distributed.
RESULTS

Site-based acceptance

In total, only 12 vegetation transects were carried out due to difficulties locating the study animals early enough in the day to allow time for many feeding surveys, as well as complications with positive grass species identification and confirmed fresh grazing in one of the driest areas of the KNP. Of the 12 feeding paths surveyed during the study season, 10 grass species were identified (Table 4.1). *Urochloa mosambicensis*, *E. cenchroides*, *S. pappophoroides*, *P. maximum* and *B. insculpta* were all equally accepted species, with an acceptance value of 1 (SA >0.5). When the frequency of acceptance of the above mentioned species was calculated per feeding station, the differences in acceptability could be further broken down, as there was more variation in species consumption between feeding stations than between feeding paths. *Tragus berteronianus*, *A. adscensionis*, and *P. patens* all showed SA values of 0, due to being available but never consumed, giving them a ranking of rejected (SA <0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>Site Acceptance</th>
<th>Frequency of acceptance</th>
<th>Site Availability</th>
<th>Ranking</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>(n = 10)</em></td>
<td>(SA)</td>
<td><em>(n = 60)</em></td>
<td><em>(n = 12)</em></td>
<td></td>
</tr>
<tr>
<td><em>Panicum maximum</em></td>
<td>1</td>
<td>1</td>
<td>0.33</td>
<td>Accept</td>
</tr>
<tr>
<td><em>Bothriochloa insculpta</em></td>
<td>1</td>
<td>1</td>
<td>0.08</td>
<td>Accept</td>
</tr>
<tr>
<td><em>Urochloa mosambicensis</em></td>
<td>1</td>
<td>0.97</td>
<td>0.67</td>
<td>Accept</td>
</tr>
<tr>
<td><em>Schmidtia pappophoroides</em></td>
<td>1</td>
<td>0.86</td>
<td>0.42</td>
<td>Accept</td>
</tr>
<tr>
<td><em>Enneapogon cenchroides</em></td>
<td>1</td>
<td>0.80</td>
<td>0.25</td>
<td>Accept</td>
</tr>
<tr>
<td><em>Digitaria eriantha</em></td>
<td>0.67</td>
<td>0.91</td>
<td>0.25</td>
<td>Intermediate</td>
</tr>
<tr>
<td><em>Brachiaria serrata</em></td>
<td>0.5</td>
<td>0.25</td>
<td>0.17</td>
<td>Intermediate</td>
</tr>
<tr>
<td><em>Tragus berteronianus</em></td>
<td>0</td>
<td>0</td>
<td>0.17</td>
<td>Reject</td>
</tr>
<tr>
<td><em>Aristida adscensionis</em></td>
<td>0</td>
<td>0</td>
<td>0.17</td>
<td>Reject</td>
</tr>
<tr>
<td><em>Perotis patens</em></td>
<td>0</td>
<td>0</td>
<td>0.08</td>
<td>Reject</td>
</tr>
</tbody>
</table>

*Panicum maximum* and *B. insculpta* had the highest acceptance frequency when taking availability into account, although *B. insculpta* is only an accepted species due to it being consumed despite its low availability. The same influence would have applied to *P. patens* had it been consumed at all, as it was available in such low proportions. The high availability of *U. mosambicensis* could account for its rank of third, despite the high frequency of acceptance, as the SA calculations classify a species as more acceptable if
consumed when availability is low. Only *B. serrata* and *D. criantha* showed an intermediate acceptance value (SA 0.05 – 0.5) due to the low level of consumption combined with limited availability. Little more can be interpreted from these results due to the low number of feeding surveys carried out.

**Dietary composition:**

(i) Species composition

A total of 3850 grass fragments were identified from 77 faecal samples, collected from the six study animals over the course of the study period. Of the identified fragments, comprising 43 grass species consumed, the nine most consumed species comprised 50% of the annual diet. The top 20 consumed species made up 79% of the annual diet.

*Schmidtia pappophoroides* was consumed in significantly greater proportions than any other species (*F*[3, 73] = 4.301; *p* < 0.05) with three other species contributing significantly towards the annual diet composition (Table 4.2), namely *E. cenchroides* (*F* = 9.255; *p* < 0.0001); *C. ciliaris* (*F* = 8.502; *p* < 0.0001); and *S. uniplumis* (*F* = 22.868; *p* < 0.0001). The late dry season showed only a slight increase in consumption of *E. cenchroides* and *S. pappophoroides* with a much broader diet encompassing many more species (*n* = 40) than the early dry season (*n* = 28) as options were becoming more limited. The early wet season (*n* = 39) saw this broad general feeding continuing, apart from a distinct increase in the proportion of *S. uniplumis* in the diet, as rains started to fall and grass quality and choice slowly increased. The *Eragrostis spp.* were also seen to be increasing at this time. The late wet season showed little change, apart from the dominant species reverting to *S. pappophoroides* again.
Table 4.2  Seasonal frequencies of species eaten, in order of early dry season, most consumed species. (n = number of faecal samples analysed)

<table>
<thead>
<tr>
<th>Grass species</th>
<th>Early Dry</th>
<th>Mean ±SE</th>
<th>Late Dry</th>
<th>Mean ±SE</th>
<th>Early Wet</th>
<th>Mean ±SE</th>
<th>Late Wet</th>
<th>Mean ±SE</th>
<th>All</th>
<th>Mean ±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schmidtia pappophoroides</td>
<td>11.8%</td>
<td>5.88 ± 0.83</td>
<td>7.8%</td>
<td>3.88 ± 0.61</td>
<td>4.3%</td>
<td>2.17 ± 0.66</td>
<td>8.96%</td>
<td>6.39 ± 1.42</td>
<td>8.96%</td>
<td>4.48 ± 0.48</td>
</tr>
<tr>
<td>Enneapogon cenchroides</td>
<td>11.3%</td>
<td>5.63 ± 0.69</td>
<td>5.8%</td>
<td>2.88 ± 0.40</td>
<td>2.8%</td>
<td>1.39 ± 0.48</td>
<td>7.95%</td>
<td>3.39 ± 0.65</td>
<td>6.44%</td>
<td>3.22 ± 0.31</td>
</tr>
<tr>
<td>Cenchrus ciliaris</td>
<td>9.6%</td>
<td>4.81 ± 0.84</td>
<td>3.7%</td>
<td>1.84 ± 0.35</td>
<td>2.9%</td>
<td>1.44 ± 0.36</td>
<td>6.44%</td>
<td>3.00 ± 0.44</td>
<td>5.27%</td>
<td>2.64 ± 0.28</td>
</tr>
<tr>
<td>Eragrostis superba</td>
<td>9.3%</td>
<td>4.63 ± 0.71</td>
<td>9.7%</td>
<td>4.84 ± 0.72</td>
<td>7.7%</td>
<td>3.83 ± 0.78</td>
<td>5.27%</td>
<td>2.33 ± 0.85</td>
<td>7.95%</td>
<td>3.97 ± 0.39</td>
</tr>
<tr>
<td>Pogonarthria squarrosa</td>
<td>6.4%</td>
<td>3.19 ± 0.56</td>
<td>3.0%</td>
<td>1.48 ± 0.27</td>
<td>1.8%</td>
<td>0.89 ± 0.24</td>
<td>5.19%</td>
<td>0.33 ± 0.14</td>
<td>2.86%</td>
<td>1.43 ± 0.19</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>5.8%</td>
<td>2.88 ± 0.42</td>
<td>4.5%</td>
<td>2.24 ± 0.40</td>
<td>2.1%</td>
<td>1.06 ± 0.32</td>
<td>4.23%</td>
<td>1.72 ± 0.55</td>
<td>3.95%</td>
<td>1.97 ± 0.22</td>
</tr>
<tr>
<td>Bothriochloa insculpta</td>
<td>4.8%</td>
<td>2.38 ± 0.46</td>
<td>0.4%</td>
<td>0.2 ± 0.08</td>
<td>1.9%</td>
<td>0.94 ± 0.40</td>
<td>3.95%</td>
<td>1.22 ± 0.45</td>
<td>2.13%</td>
<td>1.06 ± 0.19</td>
</tr>
<tr>
<td>Ischaemum afrum</td>
<td>4.3%</td>
<td>2.13 ± 0.41</td>
<td>4.0%</td>
<td>2.4 ± 0.35</td>
<td>0.2%</td>
<td>1.39 ± 0.45</td>
<td>3.95%</td>
<td>1.83 ± 0.48</td>
<td>3.95%</td>
<td>1.97 ± 0.21</td>
</tr>
<tr>
<td>Panicum maximum</td>
<td>4.3%</td>
<td>2.13 ± 0.55</td>
<td>4.8%</td>
<td>2 ± 0.34</td>
<td>2.8%</td>
<td>0.11 ± 0.11</td>
<td>3.95%</td>
<td>0.83 ± 0.29</td>
<td>2.62%</td>
<td>1.31 ± 0.20</td>
</tr>
<tr>
<td>Aristida adscensionis</td>
<td>4.0%</td>
<td>2.00 ± 0.52</td>
<td>5.1%</td>
<td>2.56 ± 0.54</td>
<td>2.8%</td>
<td>1.39 ± 0.37</td>
<td>3.56%</td>
<td>2.33 ± 0.55</td>
<td>4.23%</td>
<td>2.12 ± 0.26</td>
</tr>
<tr>
<td>Brachiaria deflexa</td>
<td>3.6%</td>
<td>1.81 ± 0.37</td>
<td>4.6%</td>
<td>2.28 ± 0.38</td>
<td>4.4%</td>
<td>2.22 ± 0.53</td>
<td>3.27%</td>
<td>1.44 ± 0.38</td>
<td>3.95%</td>
<td>1.97 ± 0.21</td>
</tr>
<tr>
<td>Chloris gayana</td>
<td>3.5%</td>
<td>1.75 ± 0.48</td>
<td>1.7%</td>
<td>0.84 ± 0.22</td>
<td>1.4%</td>
<td>0.72 ± 0.30</td>
<td>2.94%</td>
<td>1.11 ± 0.39</td>
<td>2.13%</td>
<td>1.06 ± 0.17</td>
</tr>
<tr>
<td>Bothriochloa radicans</td>
<td>3.1%</td>
<td>1.56 ± 0.38</td>
<td>1.2%</td>
<td>0.6 ± 0.22</td>
<td>0.3%</td>
<td>0.17 ± 0.12</td>
<td>2.86%</td>
<td>0.83 ± 0.28</td>
<td>1.51%</td>
<td>0.75 ± 0.14</td>
</tr>
<tr>
<td>Echinochloa pyramidalis</td>
<td>2.9%</td>
<td>1.44 ± 0.30</td>
<td>2.1%</td>
<td>1.04 ± 0.32</td>
<td>2.4%</td>
<td>1.22 ± 0.42</td>
<td>2.68%</td>
<td>0.50 ± 0.26</td>
<td>2.08%</td>
<td>1.04 ± 0.17</td>
</tr>
<tr>
<td>Brachiaria mosambicensis</td>
<td>2.5%</td>
<td>1.25 ± 0.32</td>
<td>0.6%</td>
<td>0.28 ± 0.15</td>
<td>0.4%</td>
<td>0.22 ± 0.13</td>
<td>2.36%</td>
<td>2.50 ± 0.57</td>
<td>1.97%</td>
<td>0.99 ± 0.19</td>
</tr>
<tr>
<td>Digitaria eriantha</td>
<td>1.9%</td>
<td>0.94 ± 0.27</td>
<td>2.3%</td>
<td>1.16 ± 0.24</td>
<td>3.7%</td>
<td>1.83 ± 0.42</td>
<td>2.29%</td>
<td>2.72 ± 0.55</td>
<td>3.27%</td>
<td>1.64 ± 0.20</td>
</tr>
<tr>
<td>Perotis patens</td>
<td>1.8%</td>
<td>0.88 ± 0.27</td>
<td>0.7%</td>
<td>0.36 ± 0.16</td>
<td>0.0%</td>
<td>0.00</td>
<td>-</td>
<td>2.18%</td>
<td>0.17 ± 0.12</td>
<td>0.68%</td>
</tr>
<tr>
<td>Tragus berteronianus</td>
<td>1.6%</td>
<td>0.81 ± 0.26</td>
<td>1.5%</td>
<td>0.76 ± 0.27</td>
<td>2.0%</td>
<td>1.00 ± 0.34</td>
<td>2.13%</td>
<td>0.11 ± 0.08</td>
<td>1.35%</td>
<td>0.68 ± 0.14</td>
</tr>
<tr>
<td>Brachiaria xantholeuca</td>
<td>1.3%</td>
<td>0.63 ± 0.29</td>
<td>2.0%</td>
<td>1 ± 0.29</td>
<td>4.7%</td>
<td>2.33 ± 0.73</td>
<td>2.13%</td>
<td>0.61 ± 0.30</td>
<td>2.29%</td>
<td>1.14 ± 0.23</td>
</tr>
<tr>
<td>Aristida stipitata</td>
<td>1.0%</td>
<td>0.50 ± 0.24</td>
<td>1.9%</td>
<td>0.96 ± 0.23</td>
<td>0.6%</td>
<td>0.28 ± 0.16</td>
<td>2.08%</td>
<td>0.17 ± 0.17</td>
<td>1.04%</td>
<td>0.52 ± 0.11</td>
</tr>
<tr>
<td>Chloris roxburghiana</td>
<td>0.6%</td>
<td>0.31 ± 0.15</td>
<td>0.2%</td>
<td>0.12 ± 0.09</td>
<td>1.2%</td>
<td>0.61 ± 0.28</td>
<td>2.05%</td>
<td>0.72 ± 0.41</td>
<td>0.83%</td>
<td>0.42 ± 0.12</td>
</tr>
<tr>
<td>Eragrostis lehmanniana</td>
<td>0.5%</td>
<td>0.25 ± 0.17</td>
<td>0.8%</td>
<td>1.4 ± 0.35</td>
<td>3.6%</td>
<td>6.33 ± 0.75</td>
<td>1.97%</td>
<td>2.61 ± 0.70</td>
<td>2.36%</td>
<td>1.18 ± 0.25</td>
</tr>
<tr>
<td>Setaria sphacelata</td>
<td>0.5%</td>
<td>0.25 ± 0.14</td>
<td>0.7%</td>
<td>0.4 ± 0.20</td>
<td>0.8%</td>
<td>1.78 ± 0.57</td>
<td>1.51%</td>
<td>2.50 ± 0.76</td>
<td>0.70%</td>
<td>0.35 ± 0.10</td>
</tr>
<tr>
<td>Stipagrostis uniplumis</td>
<td>0.5%</td>
<td>0.25 ± 0.14</td>
<td>2.8%</td>
<td>0.36 ± 0.18</td>
<td>12.7%</td>
<td>0.39 ± 0.23</td>
<td>1.35%</td>
<td>0.39 ± 0.24</td>
<td>5.19%</td>
<td>2.60 ± 0.36</td>
</tr>
<tr>
<td>Chloris virgata</td>
<td>0.4%</td>
<td>0.19 ± 0.14</td>
<td>0.8%</td>
<td>0.4 ± 0.19</td>
<td>1.2%</td>
<td>0.61 ± 0.34</td>
<td>1.32%</td>
<td>0.39 ± 0.18</td>
<td>0.81%</td>
<td>0.40 ± 0.11</td>
</tr>
<tr>
<td>Sporobolus consimilis</td>
<td>0.4%</td>
<td>0.19 ± 0.10</td>
<td>0.7%</td>
<td>0.36 ± 0.15</td>
<td>1.1%</td>
<td>0.56 ± 0.41</td>
<td>1.17%</td>
<td>0.28 ± 0.14</td>
<td>0.70%</td>
<td>0.35 ± 0.11</td>
</tr>
</tbody>
</table>
Table 4.2 cont.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dactyloctenium aegyptium</th>
<th>Eragrostis trichophora</th>
<th>Panicum coloratum</th>
<th>Sporobolus ioclados</th>
<th>Eragrostis ciliaris</th>
<th>Setaria incrassata</th>
<th>Eragrostis rigidior</th>
<th>Brachiaria nigropedata</th>
<th>Sporobolus nitens</th>
<th>Cymbopogon excavatus</th>
<th>Cymbopogon plurinodis</th>
<th>Dactyloctenium giganteum</th>
<th>Themeda triandra</th>
<th>Fingerhuthia africana</th>
<th>Urochloa oligotricha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dactyloctenium aegyptium</td>
<td>0.3% 0.13 ± 0.13 0.0% 0.0% 0.00 - 0.0% 0.00 - 1.04% 0.00 - 0.05% 0.03 ± 0.03</td>
<td>0.0% 0.00 - 4.9% 2.44 ± 0.44 5.6% 2.78 ± 0.63 0.96% 1.44 ± 0.65 3.56% 1.78 ± 0.28</td>
<td>0.0% 0.00 - 3.8% 1.92 ± 0.40 2.4% 1.22 ± 0.30 0.91% 1.83 ± 0.61 2.68% 1.34 ± 0.22</td>
<td>0.0% 0.00 - 3.4% 1.72 ± 0.42 0.7% 0.33 ± 0.20 0.83% 1.44 ± 0.65 3.56% 1.78 ± 0.28</td>
<td>0.0% 0.00 - 3.2% 1.6 ± 0.40 3.7% 1.83 ± 0.54 0.81% 0.61 ± 0.30 2.18% 1.09 ± 0.21</td>
<td>0.0% 0.00 - 1.9% 0.96 ± 0.29 1.4% 0.72 ± 0.36 0.78% 0.44 ± 0.27 1.17% 0.58 ± 0.14</td>
<td>0.0% 0.00 - 1.6% 0.8 ± 0.32 1.7% 0.83 ± 0.35 0.70% 0.11 ± 0.11 0.96% 0.48 ± 0.14</td>
<td>0.0% 0.00 - 1.5% 0.76 ± 0.26 7.1% 3.56 ± 1.00 0.70% 1.67 ± 0.58 2.94% 1.47 ± 0.31</td>
<td>0.0% 0.00 - 1.4% 0.68 ± 0.29 2.0% 1.00 ± 0.41 0.70% 0.00 - 0.91% 0.45 ± 0.14</td>
<td>0.0% 0.00 - 1.0% 0.48 ± 0.20 2.0% 1.00 ± 0.44 0.68% 0.00 - 0.78% 0.39 ± 0.13</td>
<td>0.0% 0.00 - 0.6% 0.32 ± 0.15 0.0% 0.00 - 0.55% 0.00 - 0.21% 0.10 ± 0.05</td>
<td>0.0% 0.00 - 0.6% 0.28 ± 0.14 1.1% 0.56 ± 0.23 0.44% 0.22 ± 0.13 0.55% 0.27 ± 0.08</td>
<td>0.0% 0.00 - 0.6% 0.28 ± 0.15 0.3% 0.17 ± 0.17 0.23% 0.94 ± 0.33 0.70% 0.35 ± 0.10</td>
<td>0.0% 0.00 - 0.1% 0.04 ± 0.04 0.0% 0.00 - 0.21% 0.44 ± 0.32 0.23% 0.12 ± 0.08</td>
<td>0.0% 0.00 - 0.0% 0.00 - 0.2% 0.17 ± 0.12 0.05% 0.78 ± 0.27 0.44% 0.22 ± 0.08</td>
</tr>
</tbody>
</table>
(ii) Perenniality and grazing value

Weak perennials and perennial grass species were more common in the diet, along with moderate grazing value grasses (Table 4.3).

Table 4.3 The perenniality ratings and grazing values of the 20 most consumed species (proportions of each species within diet are listed in Table 4.2).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>PERENNIALITY</th>
<th>GRAZING VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schmidtia pappophoroides</td>
<td>Perennial</td>
<td>High</td>
</tr>
<tr>
<td>Eragrostis superba</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Enneapogon cenchroides</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Cenchrus ciliaris</td>
<td>Perennial</td>
<td>High</td>
</tr>
<tr>
<td>Stipagrostis uniplumis</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Aristida adscensionis</td>
<td>Annual</td>
<td>Low</td>
</tr>
<tr>
<td>Brachiaria serrata</td>
<td>Perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>Perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Panicum maximum</td>
<td>Perennial</td>
<td>High</td>
</tr>
<tr>
<td>Eragrostis tricophora</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Digitaria eriantha</td>
<td>Perennial</td>
<td>High</td>
</tr>
<tr>
<td>Eragrostis rigidior</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Pogonarthria squarrosa</td>
<td>Weak perennial</td>
<td>Low</td>
</tr>
<tr>
<td>Panicum coloratum</td>
<td>Perennial</td>
<td>High</td>
</tr>
<tr>
<td>Ischaemum afrum</td>
<td>Perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Eragrostis lehmanniana</td>
<td>Perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Brachiaria xantholeuca</td>
<td>Annual</td>
<td>Low</td>
</tr>
<tr>
<td>Eragrostis cilianensis</td>
<td>Annual</td>
<td>Low</td>
</tr>
<tr>
<td>Bothriochloa insculpta</td>
<td>Weak perennial</td>
<td>Moderate</td>
</tr>
<tr>
<td>Chloris gayana</td>
<td>Weak perennial</td>
<td>High</td>
</tr>
</tbody>
</table>

Little seasonal variation was seen in the perenniality category, as perennial grasses were consistently consumed in greater proportions (Table 4.4), with weak perennials contributing almost equal proportions to the diet throughout the year, apart from an increase in the early wet season. The annuals made up a small proportion of the diet (14.5% for the year; Figure 4.2) most likely due to their shorter season as palatable grasses in an area with very low rainfall.

Table 4.4 The percentage of grasses consumed each season, categorised by perenniality.

<table>
<thead>
<tr>
<th></th>
<th>Early Dry</th>
<th>Late Dry</th>
<th>Early Wet</th>
<th>Late Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual</td>
<td>11.4</td>
<td>16.9</td>
<td>16.8</td>
<td>11.7</td>
</tr>
<tr>
<td>Weak Perennial</td>
<td>40.1</td>
<td>37.6</td>
<td>47</td>
<td>36</td>
</tr>
<tr>
<td>Perennial</td>
<td>48.5</td>
<td>45.5</td>
<td>36.2</td>
<td>52.3</td>
</tr>
</tbody>
</table>

Weak perennials showed a peak in the early wet season (Table 4.4) with a sudden drop in the late wet (F [3, 73] = 3.116; p < 0.05), as the perennial grasses were seen to make a significant climb from the lowest consumption in the early wet season, to the
highest in the late wet (F = 6.537; p < 0.001). The annual species were consumed more in the late dry and early wet seasons, but this could be due to their availability being directly reliant upon rainfall and faster growth after fires.

Figure 4.2 The percentage contribution of each perenniality category to the overall occurrence within faecal samples.

When considering the species eaten in terms of their grazing value, a slight variation was evident between the seasons (Figure 4.3) as would be expected. Throughout the year the moderate grazing value grasses were consumed in higher proportions than the rest, with the frequency of low grazing value species being highest in the late dry season (21.1%) and lowest in the late wet season (10.3%).

Figure 4.3 The percentage consumption of the three levels of grazing value by season (ED – Early dry; LD – Late dry; EW – Early wet; LW – Late wet).
The ANOVA’s show that the consumption of low grazing value grasses was significantly low in the late wet season versus the peak in the late dry season ($F[3, 73] = 8.252; p < 0.0001$), and moderate grazing species consumption peaked significantly in the early wet season ($F = 5.019; p < 0.005$). High grazing value grasses were most evident in the late wet season when they almost equalled the proportion of consumed moderate graze (44.2 and 45.4% respectively). The consumption of high palatability grasses showed the greatest contrast from low rates in the early wet season, to the highest in the late wet ($F = 11.017; p = 0.0001$), which follows a similar pattern seen by the perennial grasses in Table 4.4.
DISCUSSION
The primary influences to consider when assessing the dietary composition of area-specific grazers such as rhinos, are availability, seasonality and grazing value of species. Grasses tend to be consumed according to their availability and palatability, which are directly affected by the season. White rhinos are known to focus their foraging time on moderate to high grazing value species, when available, but (as with all large herbivores) they can survive on less nutritious diets better than smaller species can (Owen-Smith 1988; Shrader et al. 2006). The seasonality of certain grass species, rendering them of lower grazing value at certain times of the year, also impacts the benefit of these grasses to the grazers.

Previous research in Hluhluwe-Umfolozi Park (Kwa-Zulu Natal) has shown white rhinos to graze primarily on Panicum maximum; Themeda triandra (seasonally); Panicum spp. (Owen-Smith 1988; Perrin & Brereton-Stiles 1999; Shrader et al. 2006); Urochloa mosambicensis; Digitaria spp. (Owen-Smith 1988; Shrader et al. 2006); and Chloris gayana (Page & Walker 1978). These grasses are all either short, nutritious species or they are taller more fibrous species, such as Themeda, that are consumed in the dry season when options are limited and the quantity consumed becomes more important as quality is reduced (Owen-Smith 1988; Perrin & Brereton-Stiles 1999; Shrader & Perrin 2006). Our results support these findings, apart from the notable lack of T. triandra in the diet (both from faecal analyses and field surveys), and the dominance of S. pappophoroides in the diet of the Pafuri rhinos. The reasons for this could be the preference shown by these rhinos for areas where T. triandra was not a common species (as it was primarily found in the area of the original boma site, that they quickly departed from post release), but where U. mosambicensis and S. pappophoroides were regularly the dominant field grasses (pers. obs.). The reputation of S. pappophoroides for tolerance of heavy grazing, as well as drought-resistance (van Oudtshoorn 1999) is no doubt accountable for the prevalence of this species in the diets of these herbivores. The low frequencies of U. mosambicensis in the diet from the faecal analyses (Table 4.2), despite being the most available and third most consumed species in the site-acceptance analysis (Table 4.1), can be attributed, to some extent, to seasonal influences. It was a favoured species in the late wet season, which was when the majority of vegetation surveys could be carried out, as the rains were
promoting fresh growth and grasses became easier to identify. It is potentially under represented overall due to the low levels of consumption in the dry months. It is also important to consider that, despite being present and consumed in 75% of the feeding paths surveyed, these only represented 7 days of grazing in the entire study season. The reasons for this low consumption level are unclear, as it is a weak perennial grass that is known to still be palatable when dry (van Oudtshoorn 1999), but not necessarily in its entire geographic range, and it is favoured by low rainfall areas (Kennedy et al. 2003), such as Pafuri. It is possible that overgrazing in the wet season decreased the availability of the species in the dry season. One other possible explanation for the under-representation of this species in the faeces is grass length, as shorter grass species may not appear in the faecal samples in the same proportions as the taller grasses even if consumed in the same proportions. This hypothesis would need to be tested further with concurrent field surveys for grass height comparisons. *Urochloa mosambicensis* exhibits low structural cellulose in relation to cell content, making it a highly nutritious grass when green (Owen-Smith 1973), which explains the almost 100% consumption of it in the areas where it was available (Table 4.1).

According to Du Toit (2005), white rhinos are known to show a preference for sweet grasses on clayey soils and will avoid the less palatable grasses that grow on sandy soils. However, many pioneer grass species of moderate to high grazing quality when young, such as *Dactyloctenium* spp., *Enneapogon cenchroides*, *Brachiaria deflexa*, *Chloris virgata* and *Sorghum bicolor*, can be found in sandy habitats, emphasising the importance of considering seasonal impacts when determining feeding preferences. Shadrer and Perrin’s (2006) findings that rhinos prefer the Sandy grasslands during the wet season, and repeatedly neglect *Themeda* grasslands regardless of season, were supported by the findings of this study. The Punda Maria Sandveld became the most frequented landscape by the rhinos in the early wet season (see Chapter II, this study), when the post-burnt ground was covered in fresh green shoots after the first rains. Unfortunately the impact of this burn on grass growth and subsequent diet selection of the rhinos is inconclusive as data were not collected on pre and post-burn vegetation. Field observations recorded the lack of moderate value grazing in this area in the dry season, hence the lack of interest by the rhinos. There was a substantial gap between the burn and first rains, but the growth that the rainfall
triggered was undoubtedly what attracted the rhinos to this area. It is also worthwhile noting that, out of the 18 most dominant grass species in their diets, 13 of these are characterised by their prevalence in Sandveld and sandy soils (van Oudtshoorn 1999), as well as nine species being common in disturbed places. This could indicate that further investigation into the veld condition be undertaken as a prerequisite for any long term conservation planning in the area. The peak in consumption of *S. uniplumis* in the early wet season could be explained by its status as an Increaser (II) grass. This means that it thrives in overgrazed areas and was possibly therefore more available after the heavy grazing in the resource depleted dry season, and it is also known to be a palatable species that is crucial in dry Sandveld ecosystems (van Oudtshoorn 1999). The *Themeda* grasslands occurring in the area of the original boma release site (Figure 1.2, Chapter I, this study), were rarely returned to after the reintroduction in 2005, which accounts for it only comprising 0.23% of the overall diet.

White rhinos have been known to favour the higher nutrient bottomlands and drainage lines where shade loving grasses, such as *Panicum maximum*, grow (Perrin & Brereton-Stiles 1999). Grasses growing in the bottomlands tend to have a higher protein content than those on uplands and sandy soils (Owen-Smith 1973). The Pafuri rhinos were regularly located feeding in and around drainage lines, close to waterholes and wallows, and along well used game paths heading to and from waterholes, where species such as *Panicum maximum, P. coloratum, Ischaemum afrum, Eragrostis tricophora* and *Digitaria eriantha* commonly occur.

Georgiadis and McNaughton (1990) found that nitrogen concentrations and exchangeable sodium and potassium levels in soils, increased by two to three times with an increase of herbivore activity around waterholes. It is possible that, despite the abundance of moderate grazing value species in the rhinos diet, and their apparent lack of sodic area and mineral lick utilisation, they may have gained sufficient nutrients by concentrating grazing around waterhole utilisation gradients (piospheres) when this was available (Derry 2004). The abundance and nutritive value of forage directly influences the rate of food intake by mammalian herbivores (Abatuov et al. 1995). Grazers in the Serengeti are known to select grazing areas by soil characteristics and subsequent nutritional values of plants (McNaughton 1988;
Fryxell et al. 2004). Other nutrients thought to be vital but possibly not available in palatable plants in great enough proportions for megaherbivores, are iodine, cobalt and selenium (Milewski & Diamond 2000). These nutrients are the ultimate metabolism catalysts, responsible for supplying metabolic energy, and are as such vital. Further research into the plant-herbivore nutrient cycling within Pafuri would be beneficial, particularly when considering that long term rainfall averages (Figure 4.1) see the area becoming drier, and also as a consideration when planning any future reintroductions.

The grazing value ratings assigned to grasses take basic nutrient levels into account, and it is clear from Figure 4.3 that rhinos will consume moderate grazing value species more, and avoid the low grazing value grasses when alternatives are available. The noticeable increase of high grazing value intake in the wet season is indicative of the improved quality of grasslands after the rains start to fall. This confirms our hypothesis that moderate grazing grasses will be dominant in their diets, as well as there being a marked increase in the level of low grazing species in their diets by the late dry season. This increase is most evident when comparing the frequency of low grazing value species consumption by season, as opposed to between ratings.

Palatability is one of the factors considered when classifying the grazing value of grasses. The other features of grazing value classification are production, nutritional value, growth vigour, digestibility, and habitat preference (van Oudtshoorn 1999). Digestibility is based on the fibre content but also considers plant secondary compounds, such as tannins (Ellis 1990), and minerals such as silica (O’Reagain & Mentis 1989; Massey et al. 2006). These compounds are not essential to the plants but are thought to act as a defence against herbivores (Feeny 1975), and are as such a vital feature when considering herbivore feeding selection. Grasses with tannin-like substances (TLS) in epidermal cells are associated with sour and savanna (such as Pafuri) grasslands, and the TLS are thought to increase in the epidermal cells in response to grazing, making the grasses toxic or reducing nutritional value (Ellis 1990). However, these TLS generally occur in low enough concentrations to not have detrimental effects on larger herbivores. Silica has been proposed as an anti-herbivore defence mechanism by reducing the digestibility of grass leaves through an increase of abrasiveness, which subsequently affects tooth wear (Herrera 1985;
Massey et al. 2006). It is thought that silica influences the flow of energy and nutrients through grazing ecosystems, and has been found to be true in the Serengeti ecosystem (McNaughton et al. 1985). These are all factors that should be considered in greater detail in future, when doing a thorough analysis of herbivore feeding preferences in respect to the suitability of a new habitat.

The perenniality data also confirms the hypothesis that perennial grasses will be consumed in higher proportions, particularly during the dry season. The only season that the perennials did not dominate was the early wet season, which saw a switch to the weak perennials. This situation fully corroborates the suggestions by Kretschmar (2003) that perennials are more frequently grazed due to the increased leaf production, but disputes the theory by Prins (1988) that annuals would be more frequently grazed due to the higher moisture content. The seasonality of grasses is controlled by the rain, and Frank et al. (1998) found that the movements of Serengeti grazers was determined spatially and temporally by rainfall. The diversity of species consumed in the dry season in this study was indicative of overgrazed veld conditions, and hence fewer species being consumed, but in greater proportions. Yet in the wet season the species availability increased, resulting in lower consumption of a more diverse range of species, as was seen with black rhinos in Kenya (Oloo et al. 1994). Annual rainfall is a primary influence in herbivore biomass (Arsenault & Owen-Smith 2002), and in an area of low rainfall such as Pafuri, the changes in dietary composition can be correlated with the start and end of the wet season.
CONCLUSION

The purpose of this study was to assess the diet selection of reintroduced rhinos into a new area that little was known about. Their feeding habits allow us to determine the likelihood of a population thriving in an area, along with the consideration of other factors. White rhinos are fortunate in that they are bulk grazers that can survive for long periods on less than ideal food (Bell 1971; Jarman 1974; Demment & Van Soest 1985; Illius & Gordon 1993), but that does increase the amount of grazing that they require. What this study achieved, was confirmation that these rhinos are succeeding in exploiting the less than ideal grasslands that they have found themselves in. Due to the low rainfall in Pafuri (Zambatis & Biggs 1995) and the reliance of grasslands and savannas upon rain (Georgiadis & McNaughton 1990; Jacobs et al. 1999; Kennedy et al. 2003; Anderson et al. 2007), there was some initial scepticism as to whether this area would be suitable for establishing a permanent, growing population of white rhinos. However, the ability of these rhinos to maintain a diet of predominantly moderate grazing value species, with high grazing value species, such as *Schmidtia pappophoroides, Cenchrus ciliaris, Panicum maximum* and *Digitaria eriantha*, dominant when readily available, suggests that the grass cover is sufficient to support this population at its proposed potential rate of increase [three cows with a 16 month gestation and calving interval of 2.5 to 3 years (Du Toit 2005) suggests a maximum of one birth per year].

However, despite their evident ability to maximise forage intake in an area with poor grass cover and species composition, there is still a possibility that years with lower rainfall than 2006/7, or a lack of burn areas will see the increase of disturbed and overgrazed areas in Pafuri. This would lower the overall quality of the field layer and needs to be considered for the ongoing management of this population. The fact that 2006/7 was a below average rainfall year and the rhinos still managed to maintain a dietary composition of moderate to high quality grass species, similar to those recorded in high rainfall areas, indicates the suitability of the area for this subpopulation of megaherbivores.
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CHAPTER FIVE

MANAGEMENT RECOMMENDATIONS

OBJECTIVE

The final aim of this study was to be able to recommend future management options to aid in continuing the success and expansion of this newly established rhino subpopulation in Pafuri. This information is primarily based on the results reported in the preceding chapters, but the format was thought to be more beneficial if following those management plans designed and utilised by various conservation organisations and park managers. As a consequence certain ecological aspects were not specifically covered by this study but are still considered crucial to the ongoing management of this species.

Habitat suitability

- Studies on the impact of white rhinos on the new habitat as well as potential competition with other grazers, should be carried out (Okita-Ouma et al. 2007). The only major competitor with rhinos for grazing, due to their utilisation of the short grass (Shrader 2003) ‘grazing lawns’, is the hippo (Verweij et al. 2006; Waldram et al. 2008). There is no risk of detrimental competition here as the rhinos in Pafuri were never recorded feeding anywhere near the rivers, and the hippos were rarely found far from the rivers.

- Other interactions between the impacts of rhino grazing and the surrounding ecosystem, are mostly beneficial. Such as the nutrient cycling promoted by the bulk grazing of these megaherbivores (McNaughton et al. 1997; Augustine et al. 2003).

- White rhinos are also known to open up grazing patches for other species, such as Impala, Zebra and Wildebeest (Waldram et al. 2008), due to their close-crop (Owen-Smith 1973) grazing techniques. Personal observations in Pafuri, saw the numbers of Zebra increasing impressively after their reintroduction as part of the large mammal reintroduction project in 2005. Zebra were frequently located in grazing areas recently departed by the rhinos when tracking.

- The other habitat suitability factors, such as available water and nutritional grazing, that this study focussed on, should be reassessed on an annual basis.
(as climate and rainfall charts are compiled and changes over time can be analysed), with the potential for compiling a ‘worst case scenario’ type management intervention, should conditions become more arid in this area of such low rainfall. Fortunately, the windmill controlled permanent water points that exist as part of the KNP management, occur in two locations in Pafuri which suggests that water should always be available regardless of possible drought conditions.

- Intensive vegetation surveys would enable a thorough, reliable and up to date assessment of exactly what grass species are seasonally dominant and in which areas. Changes to the field layers can be used to calculate the areas of highest grazing value availability in the dry season for these mega-grazers.
- A disease threat assessment (Okita-Ouma et al. 2007) should always be considered when dealing with endangered species reintroductions (Mathews et al. 2006), but this usually forms part of the pre-reintroduction planning phase.

### Carrying capacity

- Endangered species need to be managed for maximum growth (Brooks 1999).
- The Ecological Carrying Capacity of the area should be estimated and the rhinos should be managed at, or below, this threshold (Okita-Ouma et al. 2007).
- It is recommended that a minimum effective population size of 50 be adhered to for both black and white rhinos (Conway & Goodman 1989), but this is not always logistically and financially feasible. The carrying capacity would be the first step to assessing the suitability of Pafuri for a population of this size. Thereafter, the practicality and cost of further reintroductions can be considered.
- Genetic diversity (Primack 1998) of the population is a key factor to consider as inbreeding must be avoided at all costs. The current situation in Pafuri is not ideal, as the departure of one territorial bull left only one mature bull to sire all subsequent offspring. The behaviour of the male sub-adult (bull 6) needs to be monitored closely as his anticipated sexual maturity will alleviate gene pool concerns. At present the paternity of the first calf (calf 7) born in Pafuri is unknown as cow 1 was pregnant upon arrival, and it is unlikely that
bull 5 is the father (although the rhinos did all come from Satara and their group dynamics there were unknown). The birth of two new calves in Pafuri in 2008, although being a good sign for the suitability of this habitat for white rhinos, suggests that bull 5 is the father of both as he is the sole territory holder in the area. It is recommended therefore that further reintroductions be considered to minimise the loss of genetic diversity (Brooks 1999).

- Brooks (1999) recommended a founder population of 20 animals. Pafuri currently has 8 rhinos but the best case scenario will only see this population naturally increase to 11 in approximately 3 years with no further reintroductions (dependent upon every cow being sexually mature and conceiving by that stage). Without further reintroductions, bull 5 is highly likely to father at least 1 new calf when the females are once again in oestrus. The late age of sexual maturity in rhinos (6+ years in females and 10 – 12 years in males) (Owen-Smith 1988), and average calving interval of 2.5 – 3 years (Du Toit 2005), equates to a slow rate of natural population expansion from a small founder population. Reintroduction is the only alternative.

**MONITORING**

- Research, such as that undertaken in this study, can be used as a very effective monitoring tool, as well as increasing the security of the study animals.

- All rhinos should be easily and individually recognisable (Okita-Ouma et al. 2007) for monitoring purposes. Compilation of photo identikits are recommended, highlighting any distinguishing features of individuals such as ear tears, horn length and shape. Spoor can also be used as a means to identify individual rhinos (Alibhai et al. 2008) when tracking, if facilities such as radio telemetry are not available to make individual identification easier.

- Understanding landscape preferences and seasonal movements of all rhinos makes for easier identification and also facilitates an early, fast detection system if any unusual rhino activity/behaviour is observed, such as poaching activity or sick animals. Historical data on origins and movements of animals is also useful if available (Okita-Ouma et al. 2007).

- A standard age-class and body condition scoring system (Okita-Ouma et al. 2007) should be implemented to ensure that the health of the population is maintained.
PROTECTION

- It is essential that adequate, effective security exists within conservation areas (Brooks 1999; Okita-Ouma et al. 2007).
- Regular anti-poaching patrols must be undertaken, in conjunction with the information provided by the monitoring recommendations above.
- The Ntomeni Ranger Services cc. in Pafuri have maintained a zero-poaching threshold since their involvement in 2005.
- Anti-poaching patrols should be increased when new calves are in the area, as this tends to have an influence on the movements of the cow post-birth (Owen-Smith 1988), which could lead her into unsafe territory while she is avoiding areas of high rhino activity until the calf is a few months old.

CO-ORDINATION AND SUPPORT

- The establishment of a decision-making framework is essential for management of populations of endangered species. Pafuri has a very effective system already in place with the Joint Management Board (JMB) comprising the Makuleke Community Property Association (CPA), Wilderness Safaris, and KNP. All management decisions about this area and its occupants are considered by this board.
- Community involvement is also considered a key factor in the field of wildlife conservation today. If conservation of an area is in the best interest of the local community it is far more likely to succeed.
- As David Craig (of Lewa Conservancy, Kenya) says, neither the conservation area, nor their rhinos will prosper, unless we create a periphery of wealth around the park. Conservation-minded communities along borders and fences of national parks can play a vital role in security (conflict avoidance) and anti-poaching measures.
IN CONCLUSION

The establishment of a small population of white rhinos in Pafuri, Kruger National Park, has thus far been a success. The fact that the rhinos have not left the area (as the area is bordered by two rivers with intermittent to no flow in the dry season), which they are quite free to do, indicates that there is no specific driving force encouraging them to leave the area. There is abundant surface-water available, which this study has ascertained to be the primary factor influencing rhino movements across the landscape, and preferences for specific areas at different times of the year. The grass layer, although sparse and dry, has proven to be sufficient to maintain decent body condition (Owen-Smith, pers. comm.) for five mature rhinos through the crucial dry season. This assessment of habitat availability versus utilisation of the first population of white rhinos in Pafuri in over 100 years, suggests no reason why these rhinos should not establish a successful breeding nucleus in the area, with potential for long term expansion into other areas of the Great Limpopo Transfrontier Park. Considering the density of rhinos in areas such as Hluhluwe-Umfolozi GR and the southern region of KNP, an increase from 0.03 rhinos/km² to 0.25 rhinos/km² would still be below an average density, if the Pafuri population were to increase to 50 individuals. The crucial factor to consider here would be whether the grass cover will be sufficient for 50 rhinos in the dry season. This study would be inclined to suggest not, but there is nothing to stop the rhinos ranging further into KNP and the Great Limpopo Transfrontier Park should Pafuri prove to be unsuitable for a population of up to 50 individuals.
REFERENCES


