# USE OF FOOD AND SPACE BY WHITE RHINOS

Adrian Morgan Shrader

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg, 2003

## DECLARATION

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

20th day of May 2003

## ABSTRACT

The manner in which herbivores respond to seasonal changes in the quality and availability of food resources is dependant on the herbivores' body size and digestive system. This study focused on how seasonal changes in the quality and availability of food resources influenced the foraging behaviour and movement of free ranging white rhinoceroses (body mass exceeding 1000 kg) in the Hluhluwe-Umfolozi Park, South Africa. Body size theory suggests that, because large herbivores tolerate lower quality food better than small herbivores, white rhinos should be relatively unselective grazers, selecting grassland types rather than grass species. In accordance with this prediction, I found that white rhinos selected mainly for grassland types throughout the study period. However, despite being non-ruminants of very large body size, white rhinos primarily fed on short to intermediate height swards of green grass throughout most of the study period.

The foraging of large herbivores can be seen as a trade-off between diet quality and quantity. To determine the trade-offs made by white rhinos during the dry season, I compared seasonal changes of dry matter intake and the intake of specific nutrients. As the greenness and nutrient content of grass declined late in the dry season, white rhinos responded by increasing their dry matter intake. Despite this response, the intake of crude protein, P and Na declined throughout the dry season. I suggest the possibility that instead of compensating for declines in nutritional gain through the adjustment of dry matter intake, white rhinos rely on fat reserves to help maintain them during periods of low food quality and availability.

A novel discovery of the study was that large scale movements, and possibly dispersal, of subadults, may be facilitated by individuals following companions or 'buddies' (either adult females or other subadults) into novel areas. This "buddy system” may be important in reducing the high costs potentially associated with dispersal.

For

My parents

Who, through their constant love and support,
have made this all possible.
This work is as much theirs as it is mine.

and the first

Dr. A.M. Shrader
(1906 –1989)

Who never quite understood what I
was going to do with a Zoology degree.

Well grandpa, with this and 20 Rand I'll be able to
get a cup of coffee almost anywhere.

In memory of

Marcel Viljoen
(1966–2001)

A close friend who’s influence on my life
was beyond compare and who’s presence
will never be forgotten...or replaced.

## ACKNOWLEDGEMENTS

“Success is not the result of spontaneous combustion; you must set yourself on fire.”
-Reggie Leach

In many ways, this quote describes the manner in which I was able to conduct and finish this PhD. The main difference, however, was that a lot of people helped provide the matches. The extent to which they helped is irrelevant, as without them I would never have been able to complete this mammoth task.

The first person I want to thank, and the one who made this whole thing possible, is my supervisor Prof. Norman Owen-Smith. Everything held within these pages has been directed and steered by his knowledge and encouragement. He was the one who convinced me to come to Wits to do a PhD. Something I suspect was just a cunning ploy that enabled him to visit and vacation in Umfolozi with his family over the course of the two years I was located in the reserve. Very smart Norman.

A very special thank you to KwaZulu-Natal Wildlife which, once again, allowed me to live and conduct my research within the Umfolozi Game Reserve. The help, assistance, and friendliness shown to me by members of the organisation was beyond the call of duty.

In the two years I lived in Umfolozi I came in contact with a very special group of people. These people allowed me to become part of their family and opened their hearts and doors to me. It seemed that whenever I required or needed help with something they were always more than willing to lend a hand and help sort out what ever needed to be done. Working with the staff in Umfolozi was incredible. Thank you firstly to Peter Hartely, Conservator Umfolozi, and his wife Rae for their friendship and enthusiasm with regard to my project. Thank you also for the open

invitation to come and watch all the Sharks' and Boks' rugby games. I don't know how I would have been able to maintain my rugby fix if it wasn't for you two. One of these days we'll have go see the lads play live.

Secondly, I want to thank Paul Haveman, Section Ranger Mbuzane, for all the assistance with regard to my project. Thank you also for the numerous (too many to count in fact) beers, dinners and guitar lessons. It was nothing but a pleasure being able to work within your section and get to know you. Thank you my friend.

There were also many people within the reserve that did not directly assist with the project but who's friendship was a great bonus. Thank you to Alyson Potter for the great chats and numerous cups of tea and coffee while I kept her from doing her work. Mike and Robyn Reed for the dinners, chats and guitar sessions. Thanks also to Mike for the use of the trails office on rainy days when I needed to do office work. Janet Webb for the amazing pizza and the opportunity to head back to the Wilderness Area and my old stomping grounds. Thanks also to Dave and Erika Robinson, Craig and Andrea Reed, Sam and Tyron Hudson, San-Mari Ras, Dale Airton, the 'Wicked witches of the west'; Karen, Liz and Colette and the numerous other people I know I've forgotten. The memories are many, I can not thank you enough.

Over the years that I conducted this study, I had the great pleasure of working with many people at the Hluhluwe Research Centre. They were always willing to answer my many questions and were always quick to provide any help, information, and the data I needed. The many maps contained within this thesis are just my data overlaying their hard work. Thanks to Dave Balfour (Regional Ecologist Northern Zululand / Co-ordinator for Ecological Advise, Zululand), Owen Howison (Ecologist), Ruth Howison and Caiphus Khumalo.

One of the main reasons that this project was able to start as smoothly, and as early in 1999 as it did, was due the extremely short time it took to implant the radio transmitters into the horns of the ten rhinos. I'm sure that I would still be trying to find rhinos to utilise in the study if it had not been for the interest and support of the Game Capture Unit for KwaZulu-Natal Wildlife. A very special thanks goes to Mark Cooke, Head of Game Capture, for the interest he expressed in this study, and for his extremely generous offer to cover all the expenses related to the darting of my study animals.

Mark, however, did not do it alone and it would be criminal if I didn't thank the rest of the Capture unit, who's professionalism and efficiency is mind blowing to behold. A very generous thank you to Quition Rochat, second in command of Game Capture; Selven Naidoo, Rhino Capture Officer; Eugine Geen, Administrative Officer Game Capture; Vere van Heerden, helicopter pilot extraordinar; Lance van der Bank, cadet; and the rest of the capture team; Zephania Siphiwe Buthelezi, Bonga Bekithemba Maziya, James Kulu Mbokazi, Zephania Fanon Mkhwanazi, Philemon Silwanempi Ndwandwe, Bhekizizwe Hezekia Nzuza, Mpiyonke Zungu, Jabulani Jetro Mhlenyama, Champion Elia Manqele, Sifiso Bongumusa Zunga and lastly Thembinkosi Mfanukhona Xulu.

The technique used to implant the transmitters into the horns of the rhinos was designed by Brain Beachcamp, National Parks Game Capture (see Appendix I). My thanks go out to Brain for coming down to Umfolozi for a couple of days, implanting the transmitters into the first five of my rhinos and in the process showing me exactly how the technique was done. Also, a special thanks for leaving his equipment in my trust when he left so that I could finish off the remaining five rhinos.

Thank you to Zarius Marx at Nova Dental Laboratory Supplies for donating the dental acrylic which was used in the implantation of the transmitters. Debbie Osberg for the illustrations used in the paper (see Appendix I), Peter Morkel and Mike Knight for their input.

It goes without saying that I am no rocket scientist when it comes to computer programming. When I got hold of a Psion, which I was to program and use as a data logger...well I was, to say the least, completely hopeless. However, thankfully, there are people who love programming computers and are extremely good at it, nogal. In an attempt to solve my problems I turned to Psion, South Africa and was put in contact with Mr. James Murry. I can not say 'Thank you' enough to James as he put up with all my stupid questions, wrote the entire 'rhino' program (see Appendix IV), and then sent it on to me within hours of me explaining what I needed. With a couple of revisions (ok, so no-one's perfect) he got the program up and running and I was able to collect the bite rate data. Thank you James.

Before I even started the field work, I had to complete a project proposal that turned out to be better written, almost as long, and have damn near as many references as my MSc. During the seemingly thousands of revisions I need to thank Angela Gaylard, Randal Arsenault and Dr. Rob Knell, who took time to answer my questions and wade through the various versions of the proposal. A special thanks to Rob who acted as my statistical sounding board and guiding light during that early stage.

When I first started my field work, one of the trickiest aspects was determining the bulk density of the rhino bites and then collecting the various different sized clippings. I want to thank Claire Deveraux for taking sometime out of her busy ten day vacation in Umfolozi (which consisted of mainly bird watching and sun bathing) to lend a hand, give suggestions and help with the initial bulk density clippings. Thank you Claire, I promise next time I won’t make you work.

When it came to the analysis of the data there were a few people that, through their help and guidance, made my life a hell of a lot easier. First and foremost is Dr. Joseph Ogutu. A fellow Kenyan, whose understanding of mathematics and statistics is at a level I could never even hope to achieve. No amount of thanks will ever convey how much I appreciated the many hours he spent writing SAS code, and all the advice on the many different statistical tests that were and were not used in the study. Remember, if there are problems with a data set, it is invariably mine. Asante sana rafiki yangu. Thanks also to Dr. Jackie Galpin who was always there and willing to help clarify any statistical questions I had.

Thanks to Professor Mary Scholes for her help in directing me with regard to the chemical analysis of my grass samples. It is through her that I met Silas Gwangwa, who did a fantastic and professional job of milling all 103 grass samples. Thanks also to Michael Chetty and his lab at the Institute for Commercial Forestry Research (ICFR), Pietermaritzburg for the professional way in which they conducted the chemical analysis on the grass samples.

Thanks to Craig McCloughlin, who spent many hours teaching me how to use ArcView, gave me his phone number so I could phone him late at night, and basically made it possible for me to create the home range maps found in Appendices II and III.

While I was conducting my research I had the great pleasure of being able to help the Center for Reproduction of Endangered Species, at the San Diego Zoo, to establish their white rhino study within the Umfolozi Game Reserve. All the best to Ron Swaisgood and Nancy Czekala with their study and Angela White with her field work. It was great getting to know you all (or Ya’ll as we say in Texas). Thanks to

Angela and Ron for the company over the last few months I was in the Reserve. Thanks Ron for all the cooking and then for passing on your recipes to me (I never knew you needed a recipe to make a Tuna Melt, but now I do). Thanks to Angela for all the chats, friendship and the Lattes in the middle of the bush. Oh, and you are wrong. Baja Mex is NOT as Good as Tex Mex. Trust me.

Thank you also to Thadaigh Baggallay and Allisyn Hudson for allowing me to head back to Umfolozi, tag along with them as they collected their data, thus allowing me to collect the percentage overlap data I so desperately needed. Thanks also for the dominoes. “Chicken take a hang, take a same old same old!”

A very special thanks must go to my girlfriend Caroline, who put up with two years of me being away from her while I was in the field. Upon returning she then dealt with my various ups and downs and was there to share my triumphs. Thanks also to her for looking over the chapters, putting in her two cents worth and all the references on whales. Quite simply...Thank you sweetie.

Thanks also to the lads (Grant, Matty, Paddy, Sean and Toby), friends who watched me go through this crazy journey, were always there to support me, helped take my mind off work and even took time out of there busy Johannesburg lives to make a couple of trips down to Paradise. Nothing quite like ‘pride rock’ and a couple of cold beers, hey lads? And despite their poor taste in rugby sides, I’m not sure what I would have done without their friendship. Thanks to Brother Daryl, who right at the end gave me numerous lifts into Wits on weekends and public holidays so I could work. Thanks mate. A ‘better late than never’ thank you to Dr. John Harder (Ohio State University) who, early in my university/scientific carrier, gave invaluable advice and thus started me off of this crazy journey. Thanks also to Stephanie Johnson who did absolutely nothing but asked if I would put her in here anyway.

Thanks also to Rush, Neil Young, Ben Harper, Travis, Tom Petty, Landscape Prayers, Richard Thompson, Karma/Henry Ate, Michael Tomlinson, America, James Taylor, Gordon Lightfoot, Tananas, Tony Cox, Watershed, Sugardrive, Fetish, Lenny Kravitz, Michelle Branch, Dr. Zoo, Sheryl Crow, U2, Troublemakers, Radney Foster, Garth Brooks, Clint Black, Alan Jackson and many others who's music helped get through the main hours of data loading and figure making.

Lastly, the 'Thank yous' would not be complete if I failed to mention my guard and friend Mr. Godfrey Zondo. Throughout the two years of the study, Godfery walked every kilometre I did, put up with my crazy schedule, my various moods, and became my appointed Zulu instructor. Yabonga Kakulu Godfery, and may your years of rhino tracking be many.

Adrian M. Shrader
16 December 2002
Johannesburg, South Africa

**CONTENTS** **Page**

## LIST OF FIGURES

### Chapter 1

### Chapter 2

**Chapter 3**

**Chapter 4**

**Conclusion**

**Appendix I**

**Appendix II**

## LIST OF TABLES

### Chapter 2

**Chapter 3**

**Chapter 4**

**Appendix IV**

# CHAPTER 1

## Introduction

### AIMS AND OBJECTIVES

Broad Aim

To determine how food resources influence the movements of white rhinos and hence potentially their dispersal.

Objectives

1. To determine how declines in the quality and availability food over the dry season influence the use of different grassland types by white rhinos.
2. To determine how the selection of grass swards within the different grassland types influences the intake rate and nutritional gain of white rhinos.
3. To determine how resource conditions influence larger scale movements of white rhinos and possibly dispersal.

### THE NEED FOR THE STUDY

In 1986, KwaZulu Natal Wildlife instituted a management policy for white rhinoceroses (Ceratotherium simum) in the Hluhluwe-Umfolozi Park (HUP), South Africa (28° 20’ S, 31° 51’ E). This policy, termed the ‘Sink management policy’, was based on the recommendations of a study conducted by Owen-Smith (1973, 1981). Owen-Smith (1973, 1981) recorded that white rhino population size was regulated through the dispersal (i.e. one way movement of an animal away from its home range to establish a new home range; Stenseth 1983) of individuals from areas of high rhino density into areas of low rhino density. Prior to the enclosure of HUP with a ‘rhino-proof fence’, white rhinos dispersed into areas beyond the reserve boundaries (Owen-

Smith 1973, 1981). With the completion of the fence in 1965, however, white rhinos were prevented from dispersing outside of the reserve. Thus, in an attempt to facilitate the process of dispersal within the enclosed reserve, Owen-Smith (1973, 1981) suggested that areas of low white rhino density, termed vacuum zones (or dispersal sinks), be established within the boundaries of HUP (Owen-Smith 1981, Maddock 1992).

In line with these recommendations, the sink management policy divides the southern section of HUP, the Umfolozi Game Reserve (UGR), into two areas; a central core (approximately 258 $km^2$) and surrounding vacuum zones (approximately 368 $km^2$ ; Fig 1). In the core, the white rhino population is not manipulated and thus allowed to grow (Maddock 1992). In the low density vacuum zones, however, all catchable white rhinos (primarily subadults and solitary adults) are removed on an annual basis. It is through these removals that the vacuum zones are maintained as areas of low white rhino density. The idea behind the sink management policy is that once food resources in the core are depleted by the white rhino population, individuals (mainly subadults and a few adult males) will disperse from the core into the surrounding vacuum zones. Due to the lower density of white rhinos in the vacuum zones, it is hypothesised that there will be a greater availability of food resources which may entice dispersing rhinos to stay (Owen-Smith 1973, 1981). Individuals which settle in the vacuum zones are then removed and sold in the annual game auction to other parks and zoos. Thus, by managing white rhinos through the use of the sink management policy the natural process of population regulation for the white rhinos, dispersal, is allowed to operate within the enclosed reserve.

Prior to this study, the management staff of HUP raised concerns about how well the sink management policy was working. Management questioned whether white rhinos, found within the vacuum zones, were in fact residents or whether they had made excursions into the vacuum zones to utilise the available food resources. The main questions asked by management were; 1) What factors influence the movement, and ultimately the dispersal, of white rhinos?, and 2) How do white rhinos find the artificially created vacuum zones within HUP? Management felt that, with answers to these questions, they would be better able to manage a long term viable white rhino population within HUP, while at the same time limiting any negative effects to the biodiversity of the park that may arise due to a large white rhino population (i.e. habitat degradation due to over grazing). Thus, in an attempt to address these questions, this study was initiated.

### *Rationale for the approach*

The most common factor which influences the movement, and possibly dispersal, of large herbivores is the search for food resources (Leuthold and Sale 1973, Western 1975, Sinclair 1983, McNaughton 1990, Turner et al. 1993, Scoones 1995). The white rhino provides a favourable species with which to study both foraging and movement under free-ranging conditions because, 1) data can be recorded in close proximity to individuals, 2) bites and steps are easily observed and 3) bite sizes can be determined from where a rhino has grazed.

Foraging and movement data were gathered primarily from subadult white rhinos, because 1) subadults are not restricted to specific home ranges or territories, and thus more likely to move during the study period, and 2) subadults are the main age class that disperse (Owen-Smith 1973, 1988). Along with the movements of the seven subadults used in the study, the foraging and movements of three adult females were also monitored. This was done as it was felt that the foraging of adult females, along with movements made within their home ranges, and the periodic excursions outside of their home ranges (Owen-Smith 1975), would give some insight into the factors which influence movement.

## LITERATURE REVIEW

### *Optimal foraging theory*

A conceptual framework that has been used to examine the foraging behaviour of large herbivores is provided by optimal foraging theory. Optimal foraging theory generally assumes that 1) an animal's fitness is dependent on its foraging behaviour, 2) that there is a heritable component to foraging behaviour, and 3) that a currency can be identified that links foraging behaviour with fitness (i.e. protein or energy; Pyke 1984). According to optimal foraging theory an animal should seek to maximise its long-term average intake of energy, or limiting nutrients, through a tradeoff between the gains and the associated costs (Stephens & Krebs 1986).

Initially optimal foraging models were aimed at explaining the relationships between carnivores and their food resources (i.e. great tits, Krebs et al. 1977). These models, however, did not apply well to the foraging of large herbivores, as herbivores do not feed on discrete, high quality prey, but on readily available, low quality food. Owen-Smith and Novellie (1982) proposed an optimal foraging model for large herbivores which focused on the selection of different food types by a short-term optimiser. This 'clever ungulate' model attempted to identify an optimal dietary range for a large herbivore, which varied for different nutrients and with foraging tactics (i.e. time-minimiser, where an animal forages only long enough to obtain minimum energy requirements (Schoener 1971, Ward 1992), verses energy maximiser, where an animal forages so as to maximise its long-term energy intake (Stephens and Krebs

1986)). Model predictions differed from the observed foraging behaviour of kudus. However, the model provided heuristic insight into how nutrients, diet breadth, spatial heterogeneity of plants and the cues used by large herbivores to locate food may influence foraging.

Belovsky (1978, 1981, 1984, 1986), applied linear programming models to patch selection of several herbivore species. Linear programming models predict dietary outcomes, at the level of broad food types, based on the intersection of constraint lines, which are determined by physiological, anatomical and energetic characteristics of the foragers (Belovsky 1978). Through the use of his linear programming model, Belovsky (1986) concluded that most generalist herbivores are not time minimisers, but energy maximisers. However, flaws in the biological basis of the model become apparent, 1) regarding digestive constraints (Hobbs 1990), 2) the high success of the model appeared statistically unlikely (Hobbs 1990; Huggard 1994) and 3) the model was circular due to the constraint lines being estimated from the average values of the governing parameters (Owen-Smith 1996).

The use of optimal foraging theory in foraging studies in no way attempts to prove that organisms are optimal (Krebs et al. 1983; Parker and Maynard Smith 1990), but provides a functional approach to explain foraging patterns of herbivores, including diet selection, patch selection and movements (Bailey et al. 1996). Optimality can be useful in foraging studies in helping to identify the upper limit of potential performance (Owen-Smith 2002).

Classical optimal foraging theory suggests that herbivores should accept food types and food patches in an all or nothing manner. Thus, acceptance should be dependant on the benefits obtained from consuming a food type or feeding in a patch, outweighing the costs of searching for a more profitable food type or patch (Stephens and Krebs 1986). Studies, however, indicate that large herbivores do not completely reject inferior food types or patches, but forage in a graded manner in which inferior food types and patches are utilised less frequently than preferred ones (Owen-Smith and Novellie 1982, Wilmshurst et al. 1995, van Wieren 1996, Illius et al. 1999, Fortin et al. 2002). Many suggestions have been made as to why herbivores have such varied diets, including variation between animals, discrimination errors in selecting optimal food types or patches, and sampling (Wilmshurst et al. 1995, Illius et al. 1999), along with the varied nutritional requirements of the herbivores (Belovsky 1978, McNaughton 1988, 1990, Van Soest 1994, Fortin et al. 2002).

### *Patch selection*

For herbivores, the potential energy which can be obtained in different food patches is to some degree dependent on patch features (i.e. availability and quality of food resources; Hanley 1984, Ungar and Noy-Meir 1988, Illius and Gordon 1993). Availability (quantity and distribution) of food can effect the foraging of herbivores through the mechanics of food-gathering (Ungar and Noy-Meir 1988, Illius and Gordon 1993). Food quality (physical and chemical characteristics of food) can effect foraging through a herbivore's selective grazing of plants or through differences in the digestion rate of different food items (Ungar and Noy-Meir 1988).

Where a herbivore eats and what food it selects can be influenced by a number of factors. Herbivores may use cues gathered prior to or while grazing, such as the intake rate of dry matter, bite mass, bite rate, sward height, biomass, grass colour and olfactory cues, to determine patches in which to forage (Duncan 1975 (as cited in Owen-Smith 1982), Black and Kenney 1984, Illius et al. 1992, Illius & Gordon 1993, Distel et al. 1995, Gordon et al. 1996, Illius et al. 1999). Black and Kenney (1984) suggested that sheep, given a choice of two patches in which to feed, selected the patch in which they were able to eat at a faster rate. Distel et al. (1995) recorded a similar pattern for cattle and hence suggested that the cattle used intake rate or bite rate within a patch as a cue for patch selection. Illius et al. (1992), however, suggested that grass height, and not intake rate, was a good indicator of patch selection by sheep. However, as on average the selection of tall swards result in higher intake rates, it is possible that sheep may use sward height as a cue of potential long term increase in intake rate (Illius & Gordon 1993). Duncan (1975 as cited in Owen-Smith 1982) recorded that topi (Damaliscus lunatus) seemed to alter their seasonal habitat preferences to favour grassland types that allowed them to maximise their intake of green leaves. The topis' selection for green leaf increased with increasing grass biomass, but there was no clear relationship between preference and the protein content of the green leaf (Owen-Smith 1982). Langvatn & Hanley (1993) indicated that red deer (Cervus elaphus) feeding in patches of Timothy grass (Phleum pratense) offering varying intake rates of digestible protein and digestible dry matter, utilised patches in relation to the intake rate of digestible protein.

As a herbivore feeds, it depletes the food resources in a patch, thus reducing the benefits gained from the patch. Charnov (1976) proposed the marginal value theorem to address the question of when a herbivore should leave a patch. The marginal value theorem, suggests that an animal should leave a patch once the benefits gained within the patch (i.e. intake rate or energy gain) decline to where they equal the benefits gained from a new patch, taking into account the costs of moving to the new patch. As giving up time is dependant on the rate of depletion of the patch, the model predicts that animals should spend more time in higher quality than in low quality patches.

Laca et al. (1993) recorded that cattle, feeding on patches of ryegrass created by mowing, adjusted the time spent feeding in a patch in relation to the distance between patches. In accordance with the marginal value theorem, cattle increased the time spent feeding in a patch as the distance between patches increased. Jiang and Hudson (1993) suggested that, during favourable conditions, wapiti (Cervus elaphus) stopped feeding in grassland patches after the bite rate in a feeding station dropped below seasonal expectations. Later in the seasonal cycle, when conditions were less favourable, wapiti stopped feeding in patches when the bite rate dropped below seasonal expectations in two consecutive feeding stations. The decision to leave a feeding station, however, was not determined by seasonal expectations of bite rate but rather by the lateral neck angle of the wapiti reaching a critical point, suggesting a biokenetic explanation (Jiang and Hudson 1993).

### *Diet selection*

Large grazers forage in grasslands that exhibit spatial and temporal variability in forage quality and availability through the seasonal cycle (O'Reagain 2001). It has been suggested that the maximisation of both energy and nutrients are likely to be achieved by foraging tactics which maximise the intake of digestible plant tissues (Illius et al. 1992, Illius and Gordon 1993, van Wieren 1996). In most graminoids, the majority of digestible dry matter is found in green leaves while the stem is comprised mainly of fibre (McDonald et al.1981). As grasses mature and grow, the stem to leaf ratio increases which increases the amount of fibre found in each plant (Dove 1996). Thus, as grass matures, quality declines. Increases in plant fibre can lead to increased handling and digestion times for herbivores (Janis 1976, Illius and Gordon 1992, 1993). On short, high quality swards, herbivores can obtain high bite rates but low instantaneous intake rates, while on tall, low quality swards the opposite is observed with herbivores obtaining low bite rates but high instantaneous intake rates (Fryxell 1991, Wilmshurst et al. 1995, Wilmshurst et al. 2000).

Fryxell (1991) suggested that, herbivores would maximise intake of energy by foraging on swards of intermediate height and maturation stage. By foraging in these swards, Fryxell suggested that herbivores would optimise dry-matter intake and energy digestibility. Other authors (McNaughton 1988, 1990, Murray 1995), have suggested the possibility that the selection of grass of intermediate height and greenness may provide the best combination of minerals needed for growth, gestation and lactation. Wilmshurst et al. (1995) tested Fryxell's (1991) model by monitoring the patch selection of wapiti in experimental pastures where the biomass of different patches was manipulated through mowing. Wilmshurst et al. (1995) found that, as predicted by Fryxell's (1991) model, that daily rate of energy gain was greatest for wapiti in patches of intermediate biomass and fibre. Wilmshurst et al. (1999) indicated that wildebeest (Connochaetes taurinus) in the Serengeti national park, Tanzania, selected habitats in which to feed based on grass height and greenness, selecting habitats with green grass of short to medium heights. However, within habitats, wildebeest selected select feeding areas based on grass greenness and not sward height.

### *Influence of physical features*

A second aspect which can influence a herbivore's potential energy gain in different patches are the physical features of the herbivore (i.e. body size and digestive system (i.e. ruminant vs. non-ruminant); Demment and Van Soest 1985, Illius and Gordon 1992, 1993). For ruminants, daily food intake declines as fibre content of ingested plant material increases (Bell 1971, Janis 1976, Foose 1982). This decline is a result of the slower passage rate of fibrous material through the rumen, as fibrous material takes longer to break down to a size where it will pass out of the rumen and into the remainder of the digestive tract (Bell 1971, Janis 1976, Foose 1982).

In comparison, non-ruminants do not have structures which restrict the passage rate of food particles through their digestive tract. Thus, it has been suggested that the passage rate of fibrous material for non-ruminants can be nearly twice that of ruminants (Bell 1971, Foose 1982, Illius and Gordon 1992). On high fibre diets, this faster passage rate allows non-ruminants to eat more food, and thus obtain more nutrients per day from abundant low-quality food than ruminants (Foose 1982, Duncan et al 1990). The ability for non-ruminants to obtain more nutrients per day may outweigh their reduced digestive efficiency compared to ruminants (Duncan et al 1990, Illius and Gordon 1992).

Bell (1971) and Jarman (1974) proposed that the allometric scaling of metabolic rate influences the food quality requirements of mammalian herbivores, and thus their food selection. The Bell-Jarman principle (Geist 1974) states that, due to their higher metabolic rates, small herbivores require more energy and protein per day per unit body mass than large herbivores. To achieve these requirements, small bodied herbivores select food types of high quality, while large herbivores can survive on food types of a higher fibre and lower protein content. Demment and Van Soest (1985) expanded these ideas further by showing that the reason why large herbivores should be better able to process and survive on poor quality food is because 1) metabolic requirements scale with body weight raised to the power of three-quarters ($W^{0.75}$) and 2) gut volume increases linearly with body weight ($W^{1.0}$). Hence they suggested that large herbivores are better able to meet their metabolic requirements on low quality food due to a greater extent of cell wall digestion resulting from increased retention times.

Jarman (1974) suggested that there is a general relationship between body size and food selection. Due to high quality food requirements, small herbivores tend to be selective feeders, selecting for plant parts. Larger herbivores, however, due to their ability to survive on lower quality food, tend to feed relatively unselectively. The degree to which herbivores can be selective is limited largely by mouth size (Jarman 1974, Hanley 1982). Smaller herbivores can respond to seasonal declines in quality by selecting for green leaves, while avoiding stems and senescent leaves (O'Reagain and Schwartz 1995). Due to their broad mouths, large herbivores find it difficult to select for plant parts. This difficulty, however, is compensated by the higher dietary tolerance of large herbivores.

### *Functional response*

Throughout the seasonal cycle, the availability of food resources in patches changes due to plant growth and decay, and consumption. As food availability changes, so may a herbivore’s intake rate. Holling (1959, 1965) termed the relationship between a predator’s intake rate and the availability of food the functional response. Holling (1959, 1965) identified three forms of functional response, termed Type I, II, and III. In a Type I response, intake rate increases linearly with increasing food availability until it hits a maximum limit where it levels off. This response is typical of filter feeders, where food is available in fine particles that can be ingested rapidly, thus handling time is negligible. In a Type II response, intake increases with increasing food availability, but then gradually decelerates into a plateau where intake does not continue to increase with increasing food availability. Type II responses are the result of animals having to pause to handle food items prior to continuing their search for new food items, thus search time and handling time do not overlap. In a Type III response, the relationship between food availability and intake rate is sigmoidal, with a slow increase in intake rate at low food availability. This response is found when normally selected prey types become difficult to find and thus effectively unavailable at low densities.

Holling's (1959, 1965) models, however, do not biologically reflect the foraging of large herbivores. In an attempt to model the foraging of large herbivores, Spalinger and Hobbs (1992) generated three models which addressed the influence that different spatial and morphological characteristics of plants have on intake rate of large herbivores. In the first situation ('Process 1'), plants are dispersed and hidden, thus herbivores must move and search for the next food item. In the second situation ('Process 2'), plants are dispersed but are easily detected by the herbivore, thus herbivores do not need to move to search for food. The final situation ('Process 3') most closely resembles the foraging of herbivores, where plants are concentrated such that each bite adjoins the next one.

Spalinger and Hobbs (1992) suggested that, despite the intake rate of large herbivores frequently resembling a Type II functional response (Gross et al. 1993a,b, Fryxell and Doucet 1993, Wilmshurst et al. 1995, Bergman et al. 2000), underlying constraints differ between predators and herbivores. Spalinger and Hobbs (1992) that large herbivores feed on food which is found in bite size clusters concentrated within patches (i.e. grass swards, bushes and trees). For each bite, handling time (i.e. time required to pluck, chew, and swallow food) may take only a few seconds. As a herbivore feeds, search time between bites is negligible and can overlap with the handling time of the previous bite. Thus, for herbivores, search time and handling time are not mutually exclusive as suggested for predators by Holling (1959, 1965). Over short time scales, when resources are abundant, a herbivore's search time is minimal within food patches and thus intake rate is regulated by handling time. However, when resources are sparse within patches, intake rate will be regulated by the time required to search for bites (Farnsworth and Illius 1996, 1998). Over longer time scales, intake will be influenced by the herbivores digestive system (ruminant or non-ruminant) and the fibre content of the different food types ingested, both of which influence passage rates (Owen-Smith 2002).

### *Intake rate*

Intake rate of large grazers is dependant on sward structure and the ingestive behaviour of the animal (Distel et al. 1995, Bergman et al. 2000). Herbage height, bulk density (herbage weight per unit volume) and biomass have been shown to be important sward determinants of intake rate within a patch (Black and Kenney 1984, Laca et al. 1992, Shipley et al. 1994, Bergman et al. 2000). Intake rate, however, is also influenced by bite mass, as larger bites result in higher intake rates (Hodgson 1985, Spalinger et al. 1988, Gross et al. 1993a, Laca et al. 1994).

Assuming that a herbivore attempts to maximise its intake rate across different bite masses, herbivores may compensate, to some extent, for changes in bite mass by changing bite rates (Black and Kenney 1984, Wickstrom et al. 1984). However, increases in bite rate cannot fully compensate for declines in bite mass (Hodgson, 1985, Wickstrom et al. 1984), as constraints such as mouth volume and chewing rate make the cropping of new grass directly compete with chewing of grass already within the mouth (Laca and Demment 1991, Spalinger et al. 1988, Spalinger and Hobbs 1992).

For herbivores, maximum bite rate is determined by mouth morphology (tooth size, jaw musculature) and the mechanics of food consumption (cropping and chewing processes; Shipley et al. 1994). Maximum bite rate seems to scale allometrically with body mass. For example, moose (Alces alces) achieve a maximum bite rate of only 25 bites/min, while smaller kudu (Tragelaphus strepsiceros) and mule deer (Odocoileus hemionus) obtain a maximum of 45 bites/min (Owen-Smith 2002). For even smaller impala (Aepyceros melampus; Cooper and Owen-Smith 1986) and sheep (O'Reagain and Owen-Smith 1996), maximum bite rate is about 60 bites/min, while Thompson’s gazelle (Gazella thomsoni) have been found to achieve bite rates as high as 78 bites/min (Bradbury et al. 1996). Shipley et al. (1994), suggested that maximum bite rate is constrained by pendulum movements of the lower jaw which are dependant on the allometric scaling of jaw length ($M^{-0.17}$).

### *White rhino foraging*

Due to their large size, white rhinos should be able to utilise a wider range of vegetation components (i.e. grassland types and grass species) than is possible for smaller herbivores (Owen-Smith 1988). Thus as the dry season progresses and plants senesce, white rhinos should be able to survive on low quality food available in a wide range of grassland types, but should still prefer high quality food.

Owen-Smith (1973, 1988) recorded that white rhinos utilised four broad grassland types throughout the annual cycle in the Umfolozi Game Reserve. In the summer rainy season, when there was a high availability of short green grass, white rhinos foraged primarily in short grasslands dominated by Digitaria argyrograpta, Panicum coloratum, Urochloa mossambicensis and Sporobolus nitens. At the start of the dry season, as the rate of short grass regrowth slowed and the grass turned brown, white rhinos utilised woodland grasslands containing Panicum maximum, where green grass was still available. Later in the dry season as the woodland grasses senesced and turned brown, white rhinos shifted and foraged mainly in accessible Themeda grasslands. By the end of the dry season, when the accessible Themeda grasslands had been depleted through utilisation, white rhinos moved into the more remote Themeda grasslands on hillslopes.

Analysis of whole plant samples of selected grass species in the Umfolozi Game Reserve (Downing 1972) indicated that short grasslands offer protein levels that can average up to twice that of other grasslands (e.g. Themeda). As white rhinos may spend a large portion of the annual cycle foraging in short grasslands (Owen-Smith 1973, 1988, Shrader 1998), they thus seem to concentrate their foraging on the most nutritious grasslands (Owen-Smith 1973). From these findings, Owen-Smith (1973; 1988) suggested that food resources may influence the movement of white rhinos between grassland habitats, and hence possibly their dispersal.

### *Movement*

Many factors, or combination of factors, like the search for mates (Sinclair 1983), habitat composition and spatial arrangement of habitats within a landscape (Dunning et al. 1992), and man-made disturbances (Stephenson et al. 1996), can influence the movement of large herbivores. However, probably the most common factor which influences movement is the search for food resources (Leuthold and Sale 1973, Western 1975, Sinclair 1983, McNaughton 1990, Turner et al. 1993, Scoones 1995).

Scoones (1995) suggested that seasonal movements of herds of communal cattle between foraging areas in southern Zimbabwe were dependent on the availability of grazing resources. As the dry season progressed, cattle shifted from upland foraging areas to lower riverine and drainage areas as the quality and availability of food resources in the upland areas decreased. Leuthold and Sale (1973) suggested that elephants in the Tsavo National Park, Kenya, moved over considerable distances in response to localised rainfall. On the basis of circumstantial evidence, they assumed that the primary factor influencing these movements was a change in the food supply due to the rains (i.e. flushes of green vegetation).

Throughout the annual cycle, the utilisation of different parts of an animal's home range may vary in response to changing seasonal conditions and the resulting spatial variation in resources (Owen-Smith 1975, Fryxell 1991, Tufto et al. 1996). When conditions are favourable, and food and water resources readily available, an animal may restrict its movements to a small portion of the home range, termed the core (Owen-Smith 1975). As conditions become worse, either through seasonal changes or the depletion of resources, an animal may move out of the core and utilise a larger area, which defines its home range. More mobile animals, however, may not remain within one home range throughout the year, but may traverse an area, termed the annual range (Jewell 1966). This annual range may include seasonal home ranges, migration routes, and temporary excursions outside the normally occupied area.

Tufto et al. (1996) recorded that, during the summer, female roe deer (Capreolus caprlus) partially expanded their home range in response to declines in the availability of food resources (i.e. deciduous browse and dicotyledonous ground flora). Owen-Smith (1975) recorded that adult female white rhinos utilised their home ranges to different extents depending on seasonal conditions. When green grass and surface water were readily available, individual adult females restricted their movements to the core of their home ranges (approximately 6-8 km$^2$). However, as the quality of the food resources declined, the adult female's movements expanded to where they utilised 10-15 km$^2$. With the start of the rainy season in September-October, the quality of the food resources increased, and the adult females restricted their foraging primarily to the home range core (Owen-Smith 1975). There were occasions, however, when adult females made excursions outside of their home ranges (Owen-Smith 1973). During the dry season, when the availability of surface water declined, adult females made temporary excursions outside of their home ranges in search of water. Adult male white rhinos primarily restrict their movements to specific mutually exclusive territories (0.75-2.6 km$^2$). However, similar to adult females, adult males may make excursions outside of these areas in search of water during the dry season (Owen-Smith 1975).

Subadult white rhinos of both sexes differ from adults with regard to their movement patterns (Owen-Smith 1975). Unlike adults, subadults do not restrict their movements primarily to specific home ranges or territories, but may move over large areas. At about 4 years of age, subadults establish temporary home ranges (2-7 km$^2$), and remain in an area for a short period of time, before moving or dispersing elsewhere. Subadult white rhinos continue to move until they reach socio-sexual maturity (Owen-Smith 1975). For females, socio-sexual maturity occurs at first parturition around 7 years of age, while males become solitary and settle within a territory (1-2.5 km$^2$) between 10 and 12 years of age (Owen-Smith 1975).

### *Dispersal*

Dispersal is probably one of the most important processes in the life history of many animals (Greenwood 1980, Dobson 1982). For many species, dispersal is conducted through the one-way movement of individuals away from their natal areas (Holekamp 1986, Woollard and Harris 1990, Beaudette and Keppie 1992). For most mammals, dispersal is usually male biased, while for birds, females tend to be dispersers (Greenwood 1980, 1983, Holekamp and Sherman 1989). White rhinos differ in that both male and female subadults disperse (Owen-Smith 1973).

For large herbivores, dispersal may be influenced through 1) the decline of resources (i.e. food and water) below a critical level (Owen-Smith 1973, Grant 1978, Dobson 1979), and 2) possibly through a reduction in access to food, shelter or mates due to competition from conspecifics (Lomnicki 1978, Dobson 1982, Moore and Rauf 1984, Waser 1985). Dispersal, however, may not just be limited to one of these causes, but may be a combination of the two (Dobson 1982, Dobson and Jones 1985, Hansson 1991).

Owen-Smith (1973) suggested that the dispersal of subadult white rhinos was possibly in response to declines in the availability of food and water resources. However, social pressures such as territoriality may also play a role with regard to subadult males (Owen-Smith 1973). As both male and female subadults disperse, it is possible that either one factor influences the dispersal of both sexes (i.e. food resources), or that separate factors influence the two sexes.

### *Thesis structure (a note for readers and reviewers)*

This thesis has not been written in the traditional ‘thesis’ fashion set out by the University, but follows a style where the majority of the chapters have been written as individual papers. Thus, each chapter (except the Introduction and Conclusion) contain an Abstract, Introduction, Methods, Results, Discussion and References. From writing in this fashion there is some degree of repetition between the chapters (i.e. study area and references), for which I apologise.

My initial goal in writing-up was to submit each chapter to peer reviewed journals as they were finished. I was able to do this for two chapters before time become a limiting factor. These two chapters have been included in their published format as chapter 4 and in Appendix I.

The introduction of the thesis (Chapter 1) lists the broad aim and objectives, gives the rationale behind my approach, provides a literature review on aspects of foraging and movement and explains the reason why the study was conducted. Chapters 2 and 3 address the foraging aspects of white rhinos (i.e. diet selection and intake rate respectively). Chapter 4 reproduces the paper 'The role of companionship in the dispersal of white rhinoceroses (Ceratotherium simum)' (Behavioral Ecology and Sociobiology **52**:255-261), which was published in 2002. After this paper appeared on the Behavioral Ecology and Sociobiology web site, Nature contacted me and did an article about the 'buddy system' which appeared on their web site (www.nature.com/nsu/) on 8 July 2002. This article resulted in other articles about the buddy system being written for 'National Geographic Kids' magazine (January/February 2003) and for at least 8 different web pages (including SOS Rhino, and the German edition of Scientific American, Wissenschaft-online). Web articles were from at least five different countries and in at least three different languages. Lastly, the conclusion (Chapter 5) sums up the findings of the study, provides a conceptual model on the mechanism behind the dispersal of white rhinos and addresses the implications of the 'buddy system' to the management of white rhinos in the Hluhluwe-Umfolozi Park.

There are four appendices which cover 1) a manuscript on methods which was published prior to the thesis being submitted and 2) aspects of the study that did not fit into the central chapters. Appendix I contains the paper, 'A new method for implanting radio transmitters into the horns of black and white rhinoceroses' (Pachyderm **30**:81-86), which was published in 2001. Appendix II contains the home range maps of the 10 study animals monitored during the study. Appendix III lists the code for the 'Rhino' bite rate computer program for the Psion Organiser II. Appendix IV contains the estimates of crude protein, P and Na from short, woodland and Themeda grasslands utilised to generate estimates of nutritional intake in Chapter 2.

It is my hope that, by writing in this fashion, the thesis is more concise and the information more accessible.

# REFERENCES

Bailey, D.W., J.E. Gross, E.A. Laca, L.R. Rittenhouse, M.B. Coughenour, D.M. Swift and P.L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**:386-400.

Beaudette, P.D. and D. M. Keppie. 1992. Survival of dispersing spruce grouse. Canadian Journal of Zoology **70**:693-697.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American **225**:86-93.

Belovsky, G.E. 1978. Diet optimisation in a generalist herbivore: the moose. Theoretical population biology **14**:105-134.

Belovsky, G.E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology **62**:1020-1030.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. The American Naturalist **124**:97-115.

Belovsky, G.E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia **70**:35-52.

Bergman, C.M., J.M. Fryxell and C.C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of Wood Bison. Functional Ecology **14**:61-69.

Black, J.L. and P.A. Kenney. 1984. Factors affecting diet selection by sheep. II height and density of pasture. Australian Journal of Agricultural Research **35**:565-578.

Bradbury, J.W., S.L. Vehrencamp, K.E. Clifton, and L.M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. Ecology **77**:2237-2255.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology **9**:129-136.

Cooper, S.M. and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. Oecologia **68**:446-455.

Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist **125**:641-672.

Distel, R.A., E.A. Laca, T.C. Griggs and M.W. Demment. 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. Applied Animal Behavioural Science **45**:11-21.

Dobson, F.S. 1979. An experimental study of dispersal in the California ground squirrel. Ecology **60**:1103-1109.

Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour **30**:1183-1192.

Dobson, F.S. and W.T. Jones. 1985. Multiple causes of dispersal. The American Naturalist **126**:855-858.

Dove, H. 1996. The ruminant, the rumen and the pasture resource: nutrient interactions in the grazing animal. *in* J. Hodgson and A.W. Illius, editors. The ecology and management of grazing systems. CAB international, Oxon, UK.

Downing, B.H. 1972. A plant ecological survey of the Umfolozi Game Reserve, Zululand, Unpublished PhD thesis. University of Natal, Pietermaritzburg, South Africa.

Duncan, P. 1975. Topi and their food supply. Unpublished PhD Thesis. University of Nairobi.

Duncan, P., T.J. Foose, I.J. Gordon, C.G. Gakahu and M. Lloyd. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia **84**:411-418.

Dunning, J.B., B.J. Danielson and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Farnsworth, K.D. and A.W. Illius. 1996. Large grazers back in the fold: generalizing the prey model to incorporate mammalian herbivores. Functional Ecology **10**:678-680.

Farnsworth, K.D. and A.W. Illius. 1998. Optimal diet choice for large herbivores: an extended contingency model. Functional Ecology **12**:74-81.

Foose, T.J. 1982. Trophic strategies of ruminant vs nonruminant ungulates. Unpublished PhD thesis. University of Chicago, USA.

Fortin, D., J.M. Fryxell and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Ecology **83**:970-982.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Fryxell, J.M. and C.M. Doucet. 1993. Diet choice and the functional response of beavers. Ecology **74**:1297-1306.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. American Zoology **14**:205-220.

Gordon, I.J., A.W. Illius and J.D. Milne. 1996. Sources of variation in the foraging efficiency of grazing ruminants. Functional Ecology **10**:219-226.

Grant, P.R. 1978. Dispersal in relation to carrying capacity. Proceedings of the National Academy of Science, USA **75**:2854-2858.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Greenwood, P.J. 1983. Mating systems and the evolutionary consequences of dispersal. Pages 116-131 *in* I.R. Swingland and P.J. Greenwood, editors. The ecology of animal movement. Oxford Press, Clarendon, UK.

Gross, J.E., N.T. Hobbs, and B.A. Wunder. 1993a. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? OIKOS **68**:75-81.

Gross, J.E., L.A. Shipley, N.T. Hobbs, D.E. Spalinger and B.A. Wunder. 1993b. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology **74**:778-791.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. Journal of Range Management **35**:146-151.

Hanley, T.A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in coastal montane coniferous forest. Journal of Applied Ecology **21**:423-436.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society **42**:89-103.

Hobbs, N.T. 1990. Diet selection by generalist herbivores: a test of the linear programming model. Pages 395-413 *in* R.N. Hughes, editor. Behavioural mechanisms of food selection. Springer-Verlag, Berlin, Germany.

Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. Proceedings of the Nutrition Society **44**:339-346.

Holekamp, K.E. 1986. Proximal causes of natal dispersal in Belding's ground squirrels (Spermophilus beldingi). Ecological Monographs **56**:365-391

Holekamp, K.E. and P.W. Sherman. 1989. Why male ground squirrels disperse. American Scientist **77**:232-239.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist **91**:293-320.

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada **45**:1-60.

Huggard, D.J. 1994. A linear programming model of herbivore foraging: imprecise, yet successful? Oecologia **100**:470-474.

Illius, A.W. and I.J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia **89**:428-434.

Illius, A.W. and I.J. Gordon. 1993. Diet Selection in mammalian herbivores: constraints and tactics. Pages 157-181 *in* R.N. Hughes, editor. Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell Scientific Publications, Oxford, UK.

Illius, A.W., D.A. Clark, and J. Hodgson. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. Journal of Animal Ecology **61**:183-194.

Illius, A.W., I.J. Gordon, D.A. Elston, and J.D. Milne. 1999. Diet selection in goats: a test of intake-rate maximization. Ecology **80**:1008-1018.

Jiang, Z. and R.J. Hudson. 1993. Optimal grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules. Evolutionary Ecology **7**:488-498.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and cecal digestion. Evolution **30**:757-774.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behavior **48**:215-267.

Jewell, P.A. 1966. The concept of home range in mammals. Symposia of the Zoological Society of London **18**:85-109.

Krebs, J.R., A.I. Houston and E.L. Charnov. 1977. Optimal prey selection in the great tit (Parus major). Animal Behaviour **25**:30-38.

Krebs, J.R., D.W. Stephens and W.J. Sutherland. 1983. Perspectives in optimal foraging. Pages 165-221 *in* A.H. Brush and G.A. Clark, editors. Perspectives in Ornithology: essays presented for the centennial of American ornithologists' union. Cambridge University Press, Cambridge, UK.

Laca, E.A. and M.W. Demment. 1991. Herbivory: the dilemma of foraging in a spatially heterogeneous food environment. Pages 30-44 *in* R.T. Palo and C.T. Robbins, editors. Plant defences against mammalian herbivory. CRC Press, Boca Raton, Louisiana, USA.

Laca, E.A., E.D. Ungar, N. Seligman and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science **47**:91-102.

Laca, E.A., R.A. Distel, T.C. Griggs, G. Deo and M.W. Demment. 1993. Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation. Pages 709-710. Proceedings of the XVII International Grassland Congress 1993.

Laca, E.A., E.D. Ungar, and M.W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. Applied Animal Behaviour Science **39**:3-19.

Langvatn, R. and T.A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. Oecologia **95**:164-170.

Leuthold, W. and J.B. Sale. 1973. Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. East African Wildlife Journal **11**:369-384.

Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. Journal of Animal Ecology **47**:461-475.

Maddock, A.H. 1992. The white rhino sink strategy in Hluhluwe Umfolozi Park. Unpublished Natal Parks Board report, South Africa.

McDonald, P., R.A. Edwards and F.D. Greenhalgh. 1981. Animal nutrition. Longman press, London, UK.

McNaughton, S.J. 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature **334**:343-345.

McNaughton, S.J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature **345**:613-615.

Moore, J. and A. Rauf. 1984. Are dispersal and inbreeding avoidance related? Animal Behaviour **32**:94-112.

Murray, M.G. 1995. Specific nutrient requirements and migration of wildebeest. Pages 231-256 *in* A.R.E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago, USA.

O'Reagain, P. J. 2001. Foraging strategies on rangeland: effects on intake and animal performance. *in* J. A. Gomide, W. R. S. Mattos and S. C. da Silva, editors. XIX International Grassland Congress. Brazilian Society of Animal Production. Sao Pedro, Brazil.

O'Reagain, P. J. and J. Schwartz. 1995. Coping with spatial and temporal variability:dietary selection and foraging strategies of animals on rangeland. Pages 407-423 *in* M. Journet, E. Grenet, M.-H. Farce, M. Thietez and C. Demarquilly, editors. Recent Developments in the Nutrition of Herbivores: Proceedings of the IVth International Symposium on the Nutrition of Herbivores. INRA Editions, Paris, France.

O'Reagain, P.J. and N. Owen-Smith. 1996. Effect of species composition and sward structure on dietary quality in cattle and sheep grazing South African sourveld. Journal of Agricultural Science, Cambridge **127**:261-270.

Owen-Smith, N. 1973. The behavioural ecology of the white rhinoceros. Unpublished PhD. Thesis, University of Wisconsin, Madison, USA.

Owen-Smith, N. 1975. The social ethology of the white rhinoceros Ceratotherium simum (Burchell 1817). Zeitschrift für Tierpsychologie **38**:337-384.

Owen-Smith, N. 1981. The white rhinoceros overpopulation problem, and a proposed solution. Pages 129-150 *in* P.A. Jewell, S. Holt and D. Hart, editors. Problems in Management of Locally Abundant Wild Mammals. Academic Press, New York, USA.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. Pages 360-404 *in* B.J. Huntley and B.H. Walker, editors. Ecology of tropical savannas. Springer-Verlag, Berlin, Germany.

Owen-Smith, N. 1988. Megaherbivores. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. 1996. Circularity in linear programming models of optimal diet. Oecologia **108**:259-261.

Owen-Smith, N. 2002. Adaptive herbivore ecology. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. and P. Novellie. 1982. What should a clever ungulate eat? The American Naturalist **119**:151-178.

Parker, G.A. and J. Maynard Smith. 1990. Optimality theory in evolutionary biology. Nature **348**:27-33.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics **15**:523-575.

Scoones, I. 1995. Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. Journal of Arid Environments **29**:221-237.

Schoener, T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics **2**:369-404.

Shipley, L.A., J.E. Gross, D.E. Spalinger, N.T. Hobbs and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. American Naturalist **143**:1055-1082.

Shrader, A.M. 1998. The utilisation of low density vacuum zones by white rhinos in the in Umfolozi Game Reserve. Unpublished MSc. dissertation. University of Natal, Pietermaritzburg.

Sinclair, A.R.E. 1983. The function of distance movements in vertebrates. Pages 240-258 *in* I.R. Swingland and P.J. Greenwood, editors. The ecology of animal movement. Oxford Press, Clarendon, UK.

Spalinger, D.E., T.A. Hanley, and C.T. Robbins. 1988. Analysis of the functional response in foraging in the sitka blacked-tailed deer. Ecology **69**:1166-1175.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Stenseth, N.C. 1983. Causes and consequences of dispersal in small mammals. Pages 63-101 *in* I.R. Swingland and P.J. Greenwood, editors. The ecology of animal movement. Oxford Press, Clarendon, UK.

Stephens, D.W. and J.R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, USA.

Stephenson, T.R., M.R. Vaughan and D.E. Andersen. 1996. Mule deer movements in response to military activity in southeast Colorado. Journal of Wildlife Management **60**:777-787.

Tufto, J., R. Andersen and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology **65**:715-724.

Turner, M.G., Y. Wu, W.H. Romme, and L.L. Wallace. 1993. A landscape simulation model of winter foraging by large ungulates. Ecological Modelling **69**:163-184.

Ungar, E.D. and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. Journal of Applied Ecology **25**:1045-1062.

Van Soest, P.J. 1994. Nutritional ecology of the ruminant. Second Edition. Cornell University Press, Ithaca, New York, USA.

van Wieren, S.E. 1996. Do large herbivores select a diet that maximizes short-term energy intake rate? Forest ecology and management **88**:149-156.

Ward, D. 1992. The role of satisficing in foraging theory. Oikos **63**:312-317.

Waser, P.M. 1985. Does competition drive dispersal? Ecology **66**:1170-1175.

Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. East African Wildlife Journal **13**:265-286.

Wickstrom, M.L, C.T. Robbins, T.A. Hanley, D.E. Spalinger, and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management **48**:1285-1301.

Wilmshurst, J.F., J.M. Fryxell and R.J. Hudson. 1995. Forage quality and patch choice by wapiti (Cervus elaphus). Behavioral Ecology **6**:209-217.

Wilmshurst, J.F., J.M. Fryxell, B.P. Farm, A.R.E. Sinclair and C.P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology **77**:1223-1232.

Wilmshurst, J.F., J.M. Fryxell and C.M. Bergman. 2000. The allometry of patch selection in ruminants. Proceedings of the Royal Society London, Series B **267**:345-349.

Woollard, T. and S. Harris. 1990. A behavioural comparison of dispersing and non-dispersing foxes (Vulpes vulpes) and an evaluation of some dispersal hypotheses. Journal of Animal Ecology **59**:709-722.

# FIGURE CAPTION

Fig. 1. Position of white rhino vacuum zones (dispersal sinks) and central core area in the Umfolozi Game Reserve as established in 1997. (Scale 1: 200,000).

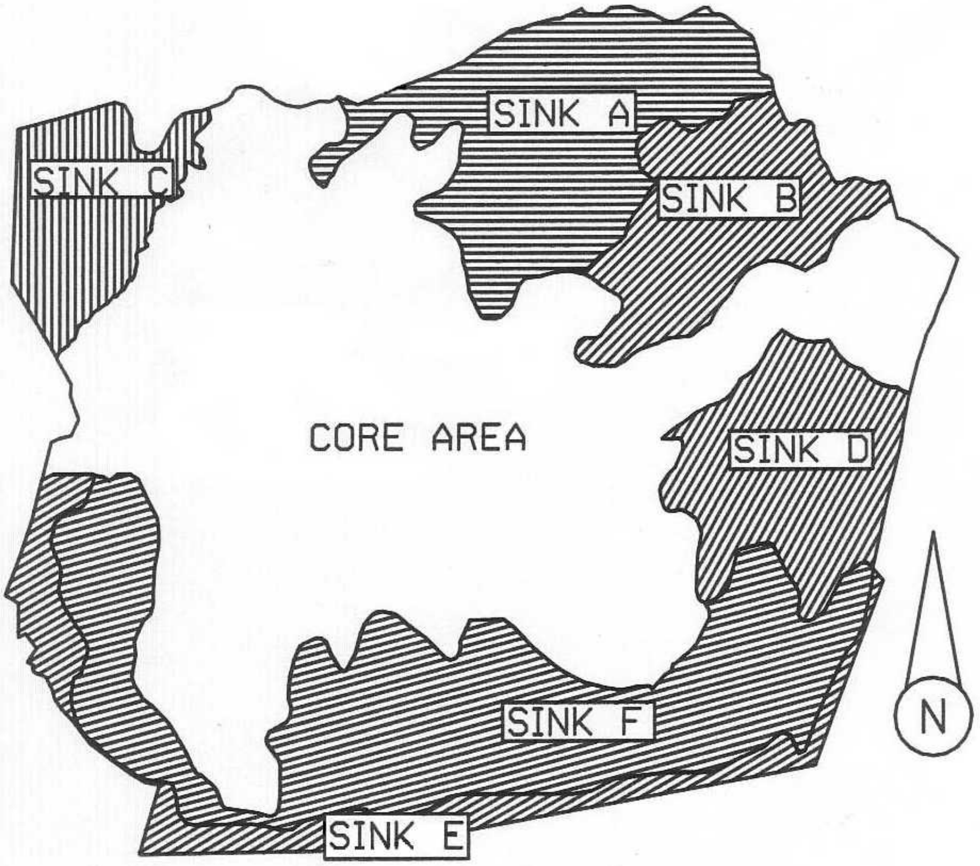

Fig. 1.

## CHAPTER 2

# Forage selection by a mega-grazer, the white rhinoceros (Ceratotherium simum)

*Abstract*. The selection of food resources is influenced by a herbivore's body size and digestive system. The predictions of body size theory suggest that a mega-grazer (i.e. body mass exceeding 1000 kg), like the white rhinoceros, should be relatively unselective, selecting grassland types rather than grass species. In accordance with these predictions, I found that white rhinos favoured short grasslands and neglected Themeda grasslands during the dry season. Themeda grasslands, however, became more utilised in the initial portion of the wet season when white rhinos responded to flushes of green grass. The seasonal utilisation of the different grassland types differed to patterns described in a previous study. However, compared to the previous study, the present study probably had a greater relative availability of food resources due to high rainfall and lower white rhinos density. This greater availability of food resources thus allowed white rhinos to feed in short grasslands throughout the dry season and neglect Themeda grasslands. Despite being non-ruminants of very large body size, white rhinos were similar to smaller ruminants in that they primarily fed on short to intermediate height swards of green grass throughout most of the study period. Results indicate that despite their higher tolerance of low quality food, large bodied herbivores select high quality food when it is available.

*Key Words: body size;* Ceratotherium simum*; diet selection; grazing; habitat use.*

# INTRODUCTION

Large grazers forage in grasslands that exhibit spatial and temporal variability in forage quality and availability through the seasonal cycle (O'Reagain 2001). Seasonal acceptability of different grassland types, grass species and sward structure is ultimately influenced by a herbivore’s body size and digestive system, which determines the efficiency with which different foods can be consumed and utilised (Demment and Van Soest 1985, Illius and Gordon 1992, 1993).

Bell (1971) and Jarman (1974) proposed that the allometric scaling of metabolic rate influences the food quality requirements of mammalian herbivores, and thus the level at which they select food (i.e. plant parts, plants, grassland types). The Bell-Jarman principle (Geist 1974) states that, due to their higher metabolic rates, small herbivores require more energy and protein per day per unit body mass than large herbivores. To achieve these requirements, small bodied herbivores must select for food types of high quality, while large herbivores can survive on food types of a higher fibre and lower protein content. Demment and Van Soest (1985) expanded these ideas further by showing that the reason why large herbivores should be better able to process and survive on poor quality food is because 1) metabolic requirements scale with body weight raised to the power of three-quarters ($W^{0.75}$) and 2) gut volume increases linearly with body weight ($W^{1.0}$). Hence they suggested that large herbivores are better able to meet their metabolic requirements on low quality food due to a greater extent of cell wall digestion resulting from increased retention times.

Jarman (1974) suggested that there is a general relationship between body size and food selection. Due to high quality food requirements, small herbivores tend to be selective feeders, selecting for plant parts. Larger herbivores, however, due to their ability to survive on lower quality food, can to feed relatively unselectively. The degree to which herbivores can be selective is limited largely by mouth size (Jarman 1974, Hanley 1982). Smaller herbivores can respond to seasonal declines in quality by selecting for green leaves, while avoiding stems and senescent leaves (O'Reagain and Schwartz 1995). Due to their broad mouths, larger herbivores find it more difficult to select for plant parts. This difficulty, however, may be compensated by the higher dietary tolerance of large herbivores.

Large herbivores achieve greater bite masses and hence intake rates on taller swards than on short swards (Black and Kenny 1984, Illius and Gordon 1987, Laca et al. 1992). Field studies, however, have indicated that large herbivores tend to prefer swards of intermediate height and biomass, even when tall swards of high biomass are available (Jarman 1974, McNaughton 1984, Langvatn and Hanley 1993, Wilmshurst et al. 1995, Wilmshurst et al. 1999). Van Soest (1994) indicated that protein content and digestibility of grass are usually negatively correlated with maturation stage. The forage maturation hypothesis (McNaughton 1984, 1986, Fryxell 1991) suggests that ruminants maximise dry matter intake and energy digestibility by feeding on swards of intermediate height and maturation stage, rather than on taller more mature swards. Fryxell (1991) suggested that the selection of intermediate swards should be more pronounced in ruminants than in non-ruminants, as daily intake is often more constrained by the digestion and passage of fibrous food through the rumen than through the hind-gut of non-ruminants (Bell 1971, Janis 1976, Foose 1982). Other authors (McNaughton 1988, 1990, Murray 1995), however, have suggested the possibility that herbivores select grass swards of intermediate height and maturation stage because these swards provide higher concentrations of minerals needed for growth, gestation and lactation than taller more mature swards.

Body size theory suggests that, as the dry season progresses and plants start to senesce, white rhinoceros (Ceratotherium simum), due to their large size, should be able to feed less selectively than smaller herbivores, and utilise a wide range of vegetation components and grassland types (Owen-Smith 1989). Melton (1987) recorded that, in relation to smaller African herbivores (e.g. buffalo Syncerus caffer, zebra Equus burchelli, wildebeest Connochaetes taurinus and waterbuck Kobus ellipsiprymnus), white rhinos in the Hluhluwe-Umfolozi Park, South Africa showed a lower degree of selection at a landscape (i.e. habitat types), community (i.e. feeding areas) and feeding station (i.e. grass species) spatial scales. As the dry season progressed, white rhinos became even less selective and utilised a wider array of habitat types, feeding areas and grass species.

In another study conducted in the Hluhluwe-Umfolozi Park, Owen-Smith (1973, 1988) documented how white rhinos changed their use of grassland types as the availability of food resources declined over the seasonal cycle. Seasonally, white rhinos transferred their feeding among four broad grassland types. In the summer wet season, when green grass was readily available, white rhinos fed primarily in short grasslands. At the start of the dry season, as grass senesced and started turning brown, white rhinos fed mainly in woodland grasslands, where green grass was still available. Later in the dry season, as the woodland grasses turned brown, white rhinos transferred most of their foraging to accessible Themeda grasslands on gentle terrain. By the end of the dry season, when the availability of food resources had declined in the accessible Themeda grasslands, white rhinos moved into and fed in Themeda grasslands on hillslopes.

The main objective of my study was to determine how the diet selection of a relatively unselective mega-grazer (i.e. body mass exceeding 1000 kg), the white rhino, would change during a period of resource limitation. Based on foraging theory, the observations from previous studies, and the predictions of body size theory, I hypothesised that 1) white rhinos would select for grassland types, and very little for specific grass species within the different grassland types, 2) as the dry season progressed, white rhinos would increase their utilisation of Themeda grasslands, while decreasing their use of short grasslands, and 3) early in the dry season, white rhinos would select for intermediate height swards of green grass, however, as the dry season progressed white rhinos would shift and utilise taller swards of brown grass.

## METHODS

### ***Study area***

The study was conducted in the western section of the 950 km² Hluhluwe-Umfolozi Park (HUP) in KwaZulu-Natal, South Africa (28° 20’ S, 31° 51’ E). The study area covered approximately 140 km² on the western side of HUP (Fig. 1). Rainfall was measured by the management staff using a permanent rain gauge situated in the western section of the park at the Mbuzane ranger station. Rainfall data used in my analysis included rainfall from 7 months prior to the study, so as to cover the previous wet season (October-February), which would influence the availability of food resources during the dry season. Rainfall was below average (545 mm) during the first seasonal cycle of the study (October 1998-September 1999), and above average (791 mm) during the second seasonal cycle (October 1999-September 2000), relative to the 690 mm long-term mean (1981-1998) for the western side of HUP (KwaZulu-Natal Wildlife, unpublished data).

Grassland composition of the study area (Fig. 2) was estimated from four 5 km transects located within the core of the study area, the 50 km$^2$ Gqoyeni basin (Fig 3).

The lengths of the segments through each grassland type were determined by recording GPS positions at the start and end of each grassland type along the separate transects. Boundaries of the different grasslands were delineated by changes in grass species composition. GPS positions were plotted using the GIS program Acrview 3.2 (Environmental Systems Research Institute, Inc. 1999) and the distance between the points determined. The total length of the transects that passed through each grassland type was then calculated by summing the individual lengths of each grassland type along the transects. These total distances were then divided by the total distance of all transects to determine the proportion of the study area occupied by each grassland type. Measurements of grassland type distribution along each transect were made three times during the study and the final proportions determined as the mean of these three estimates. Multiple measurements were taken as the transects were not permanently marked and thus the same pathway was not walked each time.

### *Data collection*

To monitor changes in the selection and utilisation of grassland types, grass species and grass sward structure, observations were made through the dry season months (May-August 1999; April-September 2000) and into the start of the wet season. This initial portion of the wet season (September-October 1999; October 2000) constituted the transitional period. September 2000 was considered part of the dry season, as the rains did not start until after data collection for this month had been completed.

White rhinos were located in the early morning and late afternoon, when they were most active (Owen-Smith 1973, 1988), and approached on foot from downwind.

Due to the poor eyesight of white rhinos, observations could be made from a distance of 10-40 meters. Data were gathered from subadults of both sexes (2.5-7 years) and from adult females (>7 years).

When a rhino was observed feeding, the area from which it had taken bites was marked visually in relation to landmarks. Once the rhino had moved a safe distance away, bites were located along the easily discernible (approximately 70 cm wide) feeding path. A set of ten successive bites constituted one feeding observation. The dimensions of each bite were determined as the furthest distances between the severed ends of grass leaves or stems. For each bite (typically 20 cm X 10 cm), the single or multiple grass species ingested were recorded, along with grass greenness, sward height and the broad grassland type in which the bites were taken. Percentage greenness and sward height were estimated subjectively from grass of the same species adjacent to each bite. Grass greenness was determined using Walker's (1976) eight point scale (0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100%). Prior to analysis, however, estimates of grass greenness were combined into four categories; very brown (0-10%), mainly brown (11-50%), mainly green (51-90%) and very green (91-100%). Sward height was measured using a ruler and then classified in one of three height categories (≤10 cm, 11-30 cm, or >30cm).

Grasslands were categorised as short, woodland, Themeda, Sandy, Cynodon, or Bothriochloa (Downing 1972, Owen-Smith 1973). Short grassland presented a short lawn-like cover dominated by Digitaria argyrograpta, Panicum coloratum, Urochloa mossambicensis and Sporobolus nitens. Woodland grasslands were found under tree canopies and consisted primarily of Panicum maximum and Enteropogon monostachyus. Themeda grasslands comprised primarily tall growing species dominated by T. triandra. Sandy grasslands were of medium height and were found on loose sandy soils, dominated by Eragrostis spp. and Aristida spp. Cynodon grasslands were lawn-like grasslands found on loose riverine sands, dominated by Cynodon dactylon and P. maximum. Bothriochloa grasslands consisted mainly of isolated patches of medium height grasses, including Bothriochloa insculpta, Aristida spp. and P. maximum. Since white rhinos fed primarily in short, woodland and Themeda grasslands during the study, the remaining grassland types were combined into an 'Other' category. During both years, portions of the study area were burnt during July and August. Burnt areas consisted primarily of Themeda grasslands, but also included sections of short, woodland and 'Other' grassland types. After the rains commenced (in September 1999 and October 2000), these burns provided areas of green grass flush.

Monthly utilisation of the different grassland types was estimated from the presence of white rhinos in the grassland types during the morning and afternoon sampling sessions. A white rhino was recorded as present if it was observed feeding in the grassland type during a sampling session. If a white rhino fed in more than one grassland type during a sampling session, the rhino was recorded as present in each of the grassland types. Observations, however, were not weighted (i.e. divided into 0.5 and 0.5, if a rhino fed in two grassland types), as only presence-absence data were recorded and used in the calculation. In total, white rhinos were recorded present in the different grassland types 221 times in 148 sampling sessions in 1999, and 223 times in 146 sampling sessions in 2000. For each month, the utilisation ($U_i$) of the different grassland types was determined as

$$U_i = \frac{o_i}{t_m}$$

where $o_i$ was the number of times white rhinos were recorded present in the $i^{th}$ grassland type, and $t_m$ was the total number of times white rhinos were recorded present in all grassland types during the month.

The utilisation of grass species, was estimated from feeding observations (i.e. 10 bites) recorded along the rhinos' feeding paths. In total, 810 feeding observations were recorded on 195 separate days over the two years. In each feeding observation, a 70 X 70 cm quadrat was placed over each of the ten bites measured along a rhino's feeding path. The 70 X 70 cm quadrat was used to represent the feeding station (approximately 1 metre wide) in which a white rhino could swing its head and feed without having to move its front feet (Bailey et al. 1996). Within each feeding station, the grass species freshly bitten, along with the other species present, were recorded.

The availability of grass in the different sward height and greenness categories within the short, woodland, Themeda and 'other' grassland types was recorded monthly within the study area. Sward height and greenness data were collected along the transects within the Gqoyeni basin (Fig 3). When the transects were walked, the categorical sward height and percentage greenness of the grass were estimated approximately every 50 m (N=8103) within each grassland type walked through. The dominant sward height in a metre square area was classified in one of the three sward height categories, while the percentage greenness of the grass was estimated using Walker's (1976) eight point scale and then combined into one of the four greenness categories (i.e. very brown, mainly brown, mainly green and very green).

The acceptability and dietary contribution of grass species in the different periods were determined from the combined data recorded in 1999 and 2000. Combined data were divided into three periods, based on changes in rainfall: 1) early dry (May 1999, April-May 2000), 2) late dry (June-August 1999, June-September 2000), and 3) transitional (September-October 1999, October 2000). Changes in the acceptability and dietary contribution of grass species were then determined between these three periods.

Acceptability and dietary contribution of each grass species was estimated from the grass species within the feeding stations (i.e. quadrats) recorded along the rhinos feeding paths. Each feeding station was considered an independent observation in which the white rhino either accepted or rejected the grass species present. The acceptance frequency ($A_i$) for each grass species was determined as

$$A_i = \frac{e_i}{p_i}$$

where $e_i$ was the number of quadrats in which the $i^{th}$ grass species was eaten, and $p_i$ was the total number of quadrats in which the $i^{th}$ grass species was present (Owen-Smith and Cooper 1987). Estimates of acceptability were determined only for grass species which were recorded as available in $\geq$20 quadrats.

To determine the dietary contribution of the different grass species in each period, the number of bites taken of each individual species was determined. Despite the width of the rhinos' mouths, 82% (N=8101 bites) of the bites recorded comprised a single grass species. In instances where more than one species was ingested, the bite was partitioned between the separate species (i.e. for 2 grass species ingested, each species was considered 0.5 of the bite). The dietary contribution ($C_p$) of each grass species in the three periods was then determined as

$$C_p = \frac{b_{ik}}{t_{bk}}$$

where $b_{ik}$ was the number of bites of the $i^{th}$ grass species recorded in the $k^{th}$ period, and $t_{bk}$ was the total number of bites recorded during the $k^{th}$ period.

### *Data analysis*

Seasonal changes in the feeding selectivity of white rhinos were quantified at the grassland type, feeding station and sward structure spatial scales. A ? $?^2$ test plus Bonferroni confidence intervals (Byers and Steinhorst 1984) was used to test whether white rhinos utilised grassland types and grass species in proportion to availability in each seasonal period. The expected number of rhino observations in each grassland type was generated by multiplying the proportional availability of each grassland type by the total number of rhino observations in each seasonal period (early dry N= 82 observations; late dry N= 181 observations; transitional= 101 observations). At the grassland type scale, the 'other' grassland type (2% of the study area) was not included in the analysis, as the expected number of rhino observations during each seasonal period were found to be less than five observations. Proportional availability of each grassland type was recalculated using only the total transect lengths from the short, woodland and Themeda grassland types.

Availability of grass species within the combined grassland types was estimated from the presence of each grass species in the feeding stations recorded along the rhinos' feeding paths. Proportional availability of each grass species was determined by dividing the number of times a species was recorded as present by the total records of occurrence of all species. Within each season, availability was determined only for grass species which were recorded as present $\geq$20 times. In the ? $?^2$ analysis, the number of times each grass species was eaten was compared to the expected use of the grass species. Expected use within each seasonal period was determined by multiplying by the total number of feeding stations for all grass species by the proportional availability of each grass species within the seasonal periods (early dry N= 1954 feeding stations; late dry N= 4249 feeding stations; transitional= 3137 feeding stations).

Overall selectivity at both the grassland type and feeding station levels was determined using the S index (McNaughton 1978)

$$S = \sum \frac{|P_{Ai} - P_{Ci}|}{2}$$

where for grassland types, $P_{Ai}$ was the proportional availability of the ith grassland type in the study area, and $P_{Ci}$ was proportional use of the ith grassland type, as estimated by the presence of white rhinos in each grassland type. For grass species within feeding stations, $P_{Ai}$ was the proportional availability of the ith grass species along the rhinos' feeding paths, and $P_{Ci}$ was proportions of the ith grass species eaten by white rhinos. S values range between 0 and 1, with 0 indicating selection equal to availability and 1 indicating maximum selectivity.

Ninety-five-percent binomial confidence limits were calculated for the acceptance frequencies of each grass species in the different periods. The different grass species were then listed in descending order of their initial acceptability estimates in the early dry period, to determine whether grass species could be categorised into discrete acceptance clusters (i.e. favoured and neglected species; Owen-Smith and Cooper 1987).

A 2-way ANOVA was used to analyse the variation in the daily dietary contribution of the different grass species ingested during the different periods. Categorical effects consisted of period (early dry, late dry and transitional) and grass species (P. maximum, T. triandra, D. argyrograpta, P. coloratum, Heteropogon contortus, E. monostachyus, S. nitens, U. mosambicensis and an 'Other' category). Grass species used in the analysis consistent of the 8 species which made up the majority of the white rhinos' diet in all three periods, while the remaining species were combined into a single 'Other' category. A Tukey honest significant difference test was used for post hoc comparisons.

Independent feeding observations were generated by separating the feeding data into days. Each day had to have a minimum of two observations (i.e. 20 bites) to be used in the analysis. Days in which only a single feeding observation was recorded were combined with the previous or following day. After combining, the total sample consisted of 155 days with 1395 replicates of the daily proportions of the eight grass species plus the 'other' grass species category.

The dietary contributions ($C_d$) of the different grass species for each day were then determined as

$$C_d = \frac{b_{ik}}{t_{bk}}$$

where $b_{ik}$ was the number of bites of the $i^{th}$ grass species recorded on the $k^{th}$ day, and $t_{bk}$ was the total number of bites recorded during the $k^{th}$ day. The 155 days were then divided into three periods: 1) early dry (May 1999, April-May 2000), 2) late dry (June-August 1999, June-September 2000), and 3) transitional (September-October

1999, October 2000), and differences between the periods analysed. Prior to analysis, the daily dietary proportions of the different grass species were arcsine transformed for normality. Analyses were performed using the statistical package Statistica 5.5 (StatSoft, Inc. 2000).

## RESULTS

### *Utilisation of grassland types*

Short grasslands contributed between a quarter and almost half of the observations of grassland type use in each month (Fig 4). Through the dry season months of both years (May-August 1999 and April-September 2000), woodland grasslands made up about a third of the observations. Just prior to the transitional period (i.e. in August 1999 and September 2000), the utilisation of woodland grasslands appeared to decline. The utilisation of *Themeda* grasslands by white rhinos remained fairly consistent, at just under a quarter of the observations each month. Use of the 'Other' grassland type was low for most of the study, but increased to approximately a fifth of the observations during the transitional period in both years (September-October 1999 and October 2000). With the start of the wet season (i.e. September 1999 and October 2000), the utilisation of green grass flush on burns contributed up to a third of the observations.

### *Selection of grassland types*

White rhinos were selective among grassland types in the early dry (??$^{2}$= 24.77, df= 2, P<0.001), late dry (? $^{2}$= 49.15, df= 2, P<0.001) and transitional periods (? $^{2}$= 11.16, df= 2, P=0.004). In the early and late dry periods, white rhinos significantly favoured short grasslands, showed marginally non-significant selection for woodland grasslands and neglected Themeda grasslands (Table 1). In the transitional period, white rhinos continued to significantly favour short grasslands, and utilised woodland grasslands a little less than in proportion to their availability, but increased their use of Themeda grasslands such that these grasslands were utilised almost in proportion to availability. The increase in the use of Themeda grasslands during the transitional period may have been the result of the white rhinos responding to flushes of green grass on burnt Themeda grasslands. Overall selectivity for grassland types by white rhinos was low throughout the study period. Selectivity was similar throughout the early dry (S= 0.27) and late dry (S= 0.24) periods, but declined with the start of the rains in the transitional period (S= 0.14).

### *Acceptability of grass species*

I drew a basic division between grass species with acceptance frequencies greater than 0.5, and those with acceptance frequencies less than 0.5 using the acceptance frequencies from the early dry period (Fig 5). Within these two divisions, I subdivided grass species further between: 1) five species where acceptance frequency was >0.67 in the early dry period (P. maximum, H. contortus, Panicum deustum, Digitaria eriantha, D. argyrograpta), 2) three species where acceptance ranged between 0.50 and 0.67 (Dactyloctenium spp., Sporobolus ioclados, S. nitens,), 3) six species where acceptance was between 0.30 and 0.50 (U. mosambicensis, C. plurinodis, T, triandra, E. monostachyus, P. coloratum, Eragrostis spp.), 4) two species with acceptance between 0.10 and 0.30 (B. insculpta, Eragrostis superba), and 5) one species which had an acceptance of <0.1 (Aristida spp.; Fig 5).

All eight species which had an acceptance greater than 0.5 during the early dry period remained above 0.5 through the late dry period (Fig 5). However, among these, the short grass species P. coloratum, Dactyloctenium spp., S. ioclados and S. nitens showed lowered acceptances (i.e. <0.5) in the transitional period (September-October 1999 and October 2000), when rhinos largely fed on green grass flushes on burns. The acceptance of both T. triandra and E. monostachyus increased significantly between the early and the late dry seasonal periods, and then further in the transitional period. The acceptance of B. insculpta fell to below 0.1 during the late dry period, while E. rigidior was not eaten during the transitional period despite being frequently available.

Throughout the study period, the acceptance of D. argyrograpta was significantly greater than the acceptance of other short grassland species (i.e. S. ioclados, S. nitens, U. mosambicensis and P. coloratum; Fig 5). In woodland grasslands, the acceptances of P. maximum and P. deustum were significantly greater than the acceptance of E. monostachyus in the early and late dry season periods. However, in the transitional period, no differences were recorded between the acceptances of the three woodland species. In Themeda grasslands, during the early and late dry season periods, the acceptance of both H. contortus and D. eriantha was significantly greater than the acceptance of T. triandra. During the transitional period, despite the significant increase in the acceptance of T. triandra during this period, the acceptance of H. contortus remained significantly greater than the acceptance of T. triandra.

### *Diet contribution*

White rhinos consumed a minimum of 42 different grass species during the study period. Only four uncommon grass species recorded in feeding sites were not consumed by white rhinos: Diplachne eleusine, Tristachya leucothrix, Trachypogon spicatus and Eleusine coracana. Twelve to fourteen species constituted approximately

95% of the diet in the different seasons during the study, while approximately 75% of the diet was made up of 6 to 8 species (Table 2). Forbs made up only 1% of the food ingested. Eight grass species constituted the core of the grass species eaten over the three periods: P. maximum and E. monostachyus, both woodland grass species; T. triandra and H. contortus, both Themeda grassland species; and the short grassland species D. argyrograpta, P. coloratum, S. nitens and U. mosambicensis.

The contribution of the different grass species eaten by white rhinos differed significantly ($F_{16,1368}=4.45$, $P<0.0001$) between the three periods. The contribution of P. maximum to the diet was significantly lower in the transitional period than in either the early dry ($\bar{x}=0.33$, $P<0.0001$) or late dry periods ($\bar{x}=0.22$, $P=0.03$). During the transitional period, when white rhinos fed on flushes of T. triandra on burns, the contribution of T. triandra was significantly greater than in both the early dry ($\bar{x}=0.06$, $P<0.01$) and late dry periods ($\bar{x}=0.11$, $P<0.05$).

Seasonal utilisation of the different grass species reflected the seasonal utilisation of the different grassland types. In the early dry period, when white rhinos utilised mainly woodland and short grasslands, three-fourths of the white rhinos' diet comprised woodland (P. maximum and Dactyloctenium spp.), or short grassland species (D. argyrograpta, U. mosambicensis and S. nitens). In the late dry period, while white rhinos continued to feed mainly on woodland (P. maximum, and E. monostachyus) and short grass species (D. argyrograpta, P. coloratum, and S. nitens), the dietary contribution of Themeda grassland species increased (T. triandra and H. contortus). After the start of rains in the transitional period (i.e. September 1999 and October 2000), the utilisation of woodland grasslands declined, and white rhinos fed mainly on lawn-forming grass species D. argyrograpta and P. coloratum and species flushing on the burns (T. triandra, H. contortus and E. superba).

### *Selection of grass species*

As with grassland types, white rhinos selected for specific grass species throughout the early dry (?$^2$= 245.34, df= 16, P<0.001), late dry (?$^2$= 475.64, df= 22, P<0.001) and transitional periods (??$^2$= 366.65, df= 20, P<0.001). Throughout the study, white rhinos utilised most grass species encountered along their feeding paths in proportion to availability (Table 3). In the early dry period, white rhinos favoured P. maximum, while neglecting P. coloratum, U. mosambicensis, T. triandra, Eragrostis superba and Aristida spp. (Table 3a). During the late dry period, white rhinos continued to favour P. maximum, but also selected for the green, lawn-forming Heteropogon contortus found in Themeda grasslands. The utilisation of T. triandra increased to where it was used in proportion to availability, while Eragrostis superba, Aristida spp., Eragrostis rigidior and B. insculpta were neglected (Table 3b). In the transitional period, white rhinos favoured D. argyrograpta, H. contortus and T. triandra. The selection of P. maximum declined to where it was used in proportion to availability, while P. coloratum, E. superba, Aristida spp. and E. rigidior were neglected (Table 3c). Overall selectivity of grass species by white rhinos remained consistently low throughout the study period (early dry S= 0.16, late dry S= 0.13 and transitional S= 0.16).

### *Selection of sward structure*

Very green and mainly green grass were available later into the dry season in 2000 than in 1999 (Fig. 6a). Throughout the study period, white rhinos utilised the greenest grass in proportions greater than availability in each month (Fig. 6 a and b). In the early dry period (April-May 2000) white rhinos fed only on green grass swards and neglected the small amount of brown grass available. During the late dry period (June-August 1999 and June-September 2000), as the availability of green grass declined, use of green grass by white rhinos was about twice the proportional availability of green grass. As the availability of green grass increased during the transitional period, white rhinos predominately fed on swards of green grass.

White rhinos also utilised the different sward height categories in proportions which differed from availability (Fig. 7 a and b). Throughout the study period, white rhinos preferentially fed on short (<10 cm) and intermediate swards (11-30 cm), while neglecting tall swards (>30 cm). During the early dry period, use of both short and intermediate height swards was about twice the respective availability of these height classes. In the late dry season, white rhinos showed strongest selection for intermediate height. In the transitional period, with the high availability of short swards of new growth, white rhinos again concentrated their use on short and intermediate height swards.

## DISCUSSION

White rhinos were found to select for grassland types throughout the study period. These findings are similar to the predictions of body size theory (Bell 1971, Jarman 1974) and the findings of a previous study (Melton 1987), which had suggested that, due to their large body size and wide mouths, white rhinos should be relatively unselective grazers, selecting primarily for grassland types. White rhinos, however, differed from expectations in that they did not utilise grassland types in the pattern previously observed by Owen-Smith (1973, 1988). Instead of increasing their utilisation of Themeda grasslands as the dry season progressed, white rhinos preferred short grasslands throughout the dry season and neglected Themeda grasslands. Fryxell

(1991) suggested that ruminants, due to daily passage rates being constrained by the digestion and slow passage rate of fibrous food through the rumen, should show a greater degree of selection for swards of intermediate height and greenness than non-ruminants. Somewhat at odds with these suggestions, however, white rhinos, despite being extremely large bodied non-ruminants, were found to have a high degree of preference for green grass swards of short to intermediate height throughout the study period.

Overall selectivity for grassland types by white rhinos in the present study was found to be lower than what was previously reported for the dry season by Melton (1987; Table 4). Selection values from the two studies, however, cannot be directly compared, as habitat levels were defined differently in each study. Melton (1987) defined habitats based on tree species composition, while I used grassland types defined by grass species composition. Melton (1987) also reported that habitat selection of white rhinos was low during the dry season. However, it is unlikely that the small difference between the wet and dry periods reported by Melton (1987) was significant. In the present study, white rhinos were more selective for grassland types during the dry season than in the transitional period. These findings indicate that white rhinos fed relatively unselectively on the new growth and green grass flushes available during the transitional period.

The utilisation of the different grassland types differed from what was recorded previously by Owen-Smith (1973, 1988). In the previous study, the use of short grasslands by white rhinos declined after April to where there was little use of these grasslands by the end of the dry season in September (Fig 8). As the dry season progressed, white rhinos increasingly shifted their feeding into Themeda grasslands on flat areas, and later to the more remote Themeda grasslands found on hillslopes.

Owen-Smith's study (1973, 1988) area was located in the western section of HUP, and partially over-lapped the present study area. The area in which Owen-Smith estimated seasonal change in the usage of grassland types did not represent woodland areas. Thus, to compare my findings to Owen-Smith's, I generated estimates of grassland type utilisation for short and Themeda grassland types, and excluded woodland grassland use. As in the previous study, the relative use of short grasslands by white rhinos declined to its lowest point at end of the dry season in September (Fig 8). However, the use of short grasslands by white rhinos was proportionally greater throughout the present study than in the previous study, even during September. White rhinos utilised Themeda grasslands proportionally less through the dry season than in the previous study, and did not, at any stage, utilise the more remote Themeda grasslands on hillslopes available in the study area.

Variation in the use of the different grassland types between the two studies is probably due, in part, to Owen-Smith's (1973) study being conducted during a period of generally low rainfall. Conditions during Owen-Smith's study included a low supply of food resources, coupled with a high rhino density of 5.7 rhinos/km$^2$ compared to approximately 2 rhinos/km$^2$ in the present study (KwaZulu-Natal Wildlife unpublished data). Under those conditions, heavy utilisation of the food resources probably caused the white rhinos to shift seasonally between the different grassland types as the availability of food resources declined (Owen-Smith 1973, 1988). In the present study, white rhinos most likely had a greater relative availability of food resources. This higher availability allowed white rhinos to feed extensively in short grasslands throughout the dry season, while neglecting Themeda grasslands.

Among the eight grass species, which made up the largest proportion of the species selected by white rhinos, five are considered to be of high grazing value to cattle (P. maximum, T. triandra, D. argyrograpta, P. coloratum and U. mosambicensis), H. contortus is considered to be of average grazing value, S. nitens has a low grazing value, while the grazing value of E. monostachyus is unknown (van Oudtshoorn 1999). The high acceptance of H. contortus was possibly the result of it forming short lawn-like patches, which remained green late into the dry season. Among common grass species, only B. insculpta and E. rigidior, two species considered to be of average grazing value to cattle, and Aristida spp., considered to be of poor grazing value (van Oudtshoorn 1999), were strongly neglected. Throughout the study period, white rhinos accepted some grass species considered to be of low grazing value to cattle (i.e. Melinis repens, Cymbopogon plurinodis, and Perotis patens). However, combined, these species only constituted about 3% of the grass species selected by the white rhinos. These findings suggest that white rhinos primarily selected high quality grass species within the grassland types.

Selectivity for grass species during the present study appeared lower than the values reported by Melton (1987; Table 4). However, as with grassland type selection, these values are not directly comparable. In the previous study, selection for grass species was derived from faecal analysis and related to regional availability of these species. In the present study, the availability of grass species was determined from feeding stations along the rhinos' feeding paths. By restricting measurements to the rhinos' feeding paths, my measurements may only reflect the selection of grass species available within the feeding patches utilised by white rhinos, and not the selection of species available within each grassland type.

Selection values reported by Melton, however, seem high when compared, not only to the present study, but also to McNaughton's (1978) findings of grass species selection by wildebeest (S= 0.19), buffalo (S= 0.22), zebra (S= 0.32) and Thompson's gazelle (S= 0.34) during the dry season in the Serengeti National Park and Masai-Mara Game Reserve. Melton’s high values for species selection may be the result of difficulties associated in identifying grass species in faecal samples. These difficulties may have resulted in a higher representation of easily recognisable species and a lower representation of species difficult to identify. It is thus possible that when results from the faecal analysis were analysed using the S index (McNaughton 1978) high selection values were determined. Another factor which may have lead to these high values could be that availability in Melton’s study was measured at a broader scale (landscape level) than either the present or McNaughton’s (1978) study, which focused on the feeding station level. By looking at the landscape level, a large number of species that would be avoided by a herbivore are included in the analysis and thus higher S values would have been generated.

Results seem to suggest that white rhinos were relatively unselective at the grass species level. Instead of selecting for grass species, white rhinos may rather have selected for feeding patches, possibly based on grass greenness or species composition, and then fed relatively unselectively on grass species within these feeding patches. However, as I did not focus on the feeding patch scale, I am unable to determine the extent to which white rhinos selected for specific feeding patches within the grassland types.

A second factor, which may have contributed to the low selection of grass species, may be that white rhinos ingested a large number of different grass species encountered along their feeding paths. However, within each seasonal period, white rhinos showed significant preference for a few species (e.g. P. maximum and T. triandra), and also significant rejection of a few species (e.g. E. superba and Aristida spp.). As the S index is a measure of the selection of all species available, overall selectivity of grass species by the white rhinos was determined to be low, because use did not differ substantially from availability for most species.

The suggestion that white rhinos were relatively unselective with regard to grass species, however, is not entirely convincing. First, despite the white rhinos' wide mouths, 82% of the bites recorded (N= 8101) comprised a single grass species, suggesting some degree of selection of the individual bites. Second, despite the ingestion of a minimum of 42 different grass species, approximately 95% of the white rhinos' diet was comprised of only 12 to 14 species, while only 6 to 8 species comprised approximately 75% of the diet. As 5 of the 8 species which made up the core of the white rhinos' diet are considered to be of high grazing value to cattle and only one is considered to of low grazing value, findings suggest a degree of selection for specific grass species. Third, seasonal changes in the acceptability of the different grass species suggests that white rhinos reacted to changes in food quality by altering their preference for specific grass species. However, the extent to which these findings reflect the selection of specific grass species or possibly the selection of the different grassland types in which the species were found still needs to be determined.

Fryxell (1991) suggested that the effects of sward maturation (i.e. height, greenness, fibre content and biomass) would have a greater effect on the food selection of ruminants like wildebeest and buffalo than non-ruminants such as zebras and elephants (Loxodonta africana). However, despite being non-ruminants of very large body size, and thus having a higher tolerance of lower quality forage (Bell 1971, Jarman 1974), white rhinos generally favoured short to intermediate height swards of the greenest grass available throughout the study period. These findings are some what at odds with Fryxell's (1991) suggestion, but support Bell (1971) and Jarman

(1974) in indicating that, despite their higher tolerance of low quality food, large bodied herbivores should feed on high quality food when it is available.

In conclusion, results indicate that, despite their large body size, and thus an ability to utilise a wide range of vegetation components and grassland types, white rhinos were relatively selective feeders at the grassland type spatial scale. During the dry season, white rhinos selected for short grasslands and preferred a few grass species (i.e. P. maximum and H. contortus), while concentrating their foraging primarily on short to intermediate swards of green grass. As expected, late in the dry season, as the availability of green grass declined, white rhinos increased their use of tall swards of brown grass. The ability of white rhinos to remain selective throughout the dry season may have been the result of the higher relative food availability during the dry season, due to higher rainfall and low rhino density.

# REFERENCES

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**:386-400.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American **225**:86-93.

Black, J.L. and P.A. Kenney. 1984. Factors affecting diet selection by sheep. II height and density of pasture. Australian Journal of Agricultural Research **35**:565-578.

Byers, C. R. and Steinhorst, R. K. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management **48**:1050-1053.

Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist **125**:641-672.

Downing, B. H. 1972. A plant ecological survey of the Umfolozi Game Reserve, Zululand. Unpublished PhD Thesis, University of Natal., Pietermaritzburg, South Africa.

Foose, T.J. 1982. Trophic strategies of ruminant vs nonruminant ungulates. Unpublished PhD thesis. University of Chicago, USA.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. American Zoology **14**:205-220.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. Journal of Range Management **35**:146-151.

Illius, A.W. and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology **56**:989-999.

Illius, A. W. and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia **89**:428-434.

Illius, A. W. and I. J. Gordon. 1993. Diet selection in mammalian herbivores: constraints and tactics. Pages 157-181 *in* R. N. Hughes, editor. Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell Scientific Publications, Oxford, UK.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and cecal digestion. Evolution **30**:757-774.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behavior **48**:215-267.

Laca, E.A., E.D. Ungar, N. Seligman, and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science **47**:91-102.

Langvatn, R. and T.A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. Oecologia **95**:164-170.

Melton, D. A. 1987. Habitat selection and resource scarcity. South African Journal of Science **83**:646-651.

McNaughton, S. J. 1978. Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. Science **199**:806-807.

McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. The American Naturalist **124**: 863-886.

McNaughton, S.J. 1986. On plants an herbivores. The American Naturalist **128**: 765-770.

McNaughton, S.J. 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature **334**:343-345.

McNaughton, S.J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature **345**:613-615.

Murray, M.G. 1995. Specific nutrient requirements and migration of wildebeest. *in* A.R.E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago, USA.

O'Reagain, P. J. 2001. Foraging strategies on rangeland: effects on intake and animal performance. *in* J. A. Gomide, W. R. S. Mattos and S. C. da Silva, editors. XIX International Grassland Congress. Brazilian Society of Animal Production. Sao Pedro, Brazil.

O'Reagain, P. J. and J. Schwartz. 1995. Coping with spatial and temporal variability: dietary selection and foraging strategies of animals on rangeland. Pages 407-423 *in* M. Journet, E. Grenet, M.-H. Farce, M. Thietez and C. Demarquilly, editors. Recent Developments in the Nutrition of Herbivores: Proceedings of the IVth International Symposium on the Nutrition of Herbivores. INRA Editions, Paris, France.

Owen-Smith, N. 1973. The behavioural ecology of the white rhinoceros. Unpublished PhD Thesis, University of Wisconsin, .Madison, USA.

Owen-Smith, N. 1988 Megaherbivores. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. 1989. The megaherbivore syndrome: alternative life style or different time frame? Pages 441-457 *in* M. N. Bruton, editor. Alternative life-history life styles of animals. Kluwer Academic Publishers, Dordrecht, Netherlands.

Owen-Smith, N. and S. M. Cooper. 1987. Assessing food preferences of ungulates by acceptability indices. Journal of Wildlife Management **51**:372-378.

van Oudtshoorn, F. 1999. Guide to the grasses of southern Africa. Briza publications, Pretoria, South Africa.

Van Soest, P.J. 1994. Nutritional ecology of the ruminant. Second Edition. Cornell University Press, Ithaca, New York, USA.

Walker, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. South African Journal of Wildlife Resources **6**:1-32.

Wilmshurst, J.F., J.M. Fryxell and R.J. Hudson. 1995. Forage quality and patch choice by wapiti (Cervus elaphus). Behavioral Ecology **6**:209-217.

Wilmshurst, J.F., J.M. Fryxell, B.P. Farm, A.R.E. Sinclair and C.P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology **77**:1223-1232.

# FIGURE CAPTIONS

Fig. 1. Study area (140 km$^2$) within the Hluhluwe-Umfolozi Park, Kwa-Zulu Natal, South Africa.

Fig. 2. Composition of grassland types in the 50 km$^2$ Gqoyeni Basin.

Fig. 3. Location of the four 5 km transects established in the Gqoyeni Basin.

Fig. 4. Seasonal utilisation of the different grassland types by white rhinos in the present study. Proportions generated from the presence of white rhinos feeding within the different grassland types during the morning and afternoon sampling sessions.

Fig. 5. Acceptance (mean ±95% binomial CI's) of grass species by white rhinos during the early dry (May 1999, April-May 2000), late dry (June-August 1999, June-September 2000), and transitional periods (September-October 1999, October 2000). Grass species were P. max (Panicum maximum), H. con (Heteropogon contortus), P. deu (Panicum deustum), D. eri (Digitaria eriantha), D. arg (Digitaria argyrograpta), D. spp. (Dactyloctenium spp.), S. ioc (Sporobolus ioclados), S. nit (Sporobolus nitens), U. mos (Urochloa mosambicensis), C. plu (Cymbopogon plurinodis), T. tri (Themeda triandra), E. mon (Enteropogon monostachyus), P. col (Panicum coloratum), E. spp (Eragrostis spp.), B. ins (Bothriochloa insculpta), E. sup (Eragrostis superba), A. spp. (Aristida spp.), C. cil (Cenchrus ciliaris), C. gay (Chloris gayana), C. dac (Cynodon dactylon), C. vir (Chloris virgata), P. pat (Perotis patens), E. rig (Eragrostis rigidior), F. afr (Fingerhuthia africana).

Fig. 6. a) Availability and b) utilisation of grass in all three grassland types in the different grass greenness categories (i.e. very brown (0-10%), mainly brown (11-50%), mainly green (51-90%) and very green (91-100%)). Availability was estimated from the number of 1 $m^2$ quadrats recorded in the different height and greenness categories along the different transects each month in 1999 (April N=151, May N=153, June N=139, July N=156, August N=197, September N=162, October N=182) and 2000 (April N=186, May N=188, June N=174, July N=180, August N=175, September N=170, October N=182). Proportion of use was estimated from monthly bite mass observations recorded in 1999 (June N=42, July N=63, August N=57, September N=96, October N=73) and 2000 (April N=37, May N=85, June N=44, July N=43, August N=50, September N=40, October N=65).

Fig. 7. a) Availability and b) utilisation of grass in all three grassland types by white rhinos in the different sward height categories (i.e. $\leq$10 cm, 11-30 cm, and >30 cm). Samples sizes same as in Fig. 6.

Fig. 8. Comparison of the seasonal utilisation of short and *Themeda* grasslands by white rhinos in the present and previous study (Owen-Smith 1973). Areas indicate the mean monthly utilisation during Owen-Smith's (1973) study, while the line divides the mean monthly utilisation of the short (below the line) and *Themeda* grassland types (above the line) during the present study.

Table 1. Seasonal selection of grassland types by white rhinos. (* indicates significant (P<0.05) positive selection and # indicates significant (P<0.05) rejection of a grassland type relative to its availability.)

| Season | Grassland type | Available proportion | Observed proportion of usage | Bonferroni intervals of observed usage |
|---|---|---|---|---|
| Early Dry | Short | 0.24 | 0.39 | 0.26<P<0.52* |
| N=82 observations | Woodland | 0.28 | 0.40 | 0.27<P<0.53 |
| | Themeda | 0.48 | 0.21 | 0.10<P<0.32# |
| Late Dry | Short | 0.24 | 0.43 | 0.34<P<0.51* |
| N=181 observations | Woodland | 0.28 | 0.33 | 0.25<P<0.42 |
| | Themeda | 0.48 | 0.24 | 0.16<P<0.31# |
| Transitional | Short | 0.24 | 0.39 | 0.27<P<0.50* |
| N=101 observations | Woodland | 0.28 | 0.20 | 0.11<P<0.31 |
| | Themeda | 0.48 | 0.41 | 0.29<P<0.52 |

Table 3. Dietary contribution (proportion of bites) of grass species that made up approximately 95% of the species eaten by white rhinos during the different seasonal periods. Grass species are categorised into the grassland types in which they were most regularly found. However, some species (i.e. P. maximum and T. triandra) were found in more than one grassland type.

| Grassland Type | Grass Species | Early Dry N=25 (Days) | Late Dry N=89 (Days) | Transitional N=41 (Days) | Combined Seasons N=155 (Days) |
|---|---|---|---|---|---|
| Short | Digitaria argyrograpta | 0.11 | 0.10 | 0.16 | 0.12 |
| | Panicum coloratum | 0.04 | 0.10 | 0.11 | 0.09 |
| | Sporobolus nitens | 0.05 | 0.05 | 0.03 | 0.04 |
| | Urochloa mosambicensis | 0.08 | 0.02 | 0.05 | 0.04 |
| | Sporobolus ioclados | 0.02 | 0.04 | - | 0.02 |
| Woodland | Panicum maximum | 0.39 | 0.25 | 0.09 | 0.22 |
| | Enteropogon monostachyus | 0.04 | 0.07 | 0.03 | 0.05 |
| | Panicum deustum | 0.02 | 0.04 | 0.01 | 0.03 |
| | Dactyloctenium spp. | 0.06 | 0.03 | - | 0.02 |
| Themeda | Themeda triandra | 0.06 | 0.11 | 0.24 | 0.15 |
| | Heteropogon contortus | 0.05 | 0.05 | 0.09 | 0.06 |
| | Digitaria eriantha | 0.04 | 0.04 | 0.04 | 0.04 |
| Other | Eragrostis superba | - | 0.02 | 0.06 | 0.03 |
| | Eragrostis spp. | - | 0.03 | - | 0.02 |
| | Cenchrus ciliaris | - | - | 0.02 | 0.01 |

Table 3. Seasonal selection of grass species by white rhinos in the a) early dry, b) late dry and c) transitional periods. (* indicates significant (P<0.05) positive selection and # indicates significant (P<0.05) rejection of a grass species relative to its availability.) As in Table 2, grass species are categorised into the grassland types in which they were most regularly found.

a.

Early Dry N= 1954 feeding stations

| Grassland Type | Grass Species | Available proportion | Observed proportion of usage | Bonferroni intervals of observed usage |
|---|---|---|---|---|
| Short | Digitaria argyrograpta | 0.10 | 0.12 | 0.10 <P< 0.14 |
| | Panicum coloratum | 0.07 | 0.04 | 0.03 <P< 0.06# |
| | Urochloa mosambicensis | 0.11 | 0.09 | 0.07 <P< 0.10# |
| | Sporobolus nitens | 0.05 | 0.05 | 0.04 <P< 0.06 |
| | Sporobolus ioclados | 0.02 | 0.02 | 0.01 <P< 0.03 |
| Woodland | Panicum maximum | 0.26 | 0.37 | 0.34 <P< 0.41* |
| | Enteropogon monostachyus | 0.06 | 0.04 | 0.03 <P< 0.06 |
| | Panicum deustum | 0.02 | 0.02 | 0.01 <P< 0.03 |
| | Dactyloctenium spp. | 0.07 | 0.08 | 0.06 <P< 0.10 |
| Themeda | Themeda triandra | 0.10 | 0.07 | 0.05 <P< 0.09# |
| | Heteropogon contortus | 0.02 | 0.03 | 0.02 <P< 0.04 |
| | Digitaria eriantha | 0.03 | 0.04 | 0.02 <P< 0.05 |
| | Cymbopogon plurinodis | 0.01 | 0.01 | 0.001 <P< 0.01 |
| Other | Eragrostis superba | 0.03 | 0.01 | 0.002 <P< 0.02# |
| | Aristida spp. | 0.02 | 0.002 | 0.001 <P< 0.004# |
| | Eragrostis spp. | 0.02 | 0.01 | 0.006 <P< 0.02 |
| | Bothriochloa insculpta | 0.01 | 0.004 | 0.001 <P< 0.01 |

b.

Late Dry N= 4249 feeding stations

| Grassland Type | Grass Species | Available proportion | Observed proportion of usage | Bonferroni intervals of observed usage |
|---|---|---|---|---|
| Short | Digitaria argyrograpta | 0.10 | 0.12 | 0.10 <P< 0.13 |
| | Panicum coloratum | 0.13 | 0.11 | 0.10 <P< 0.13 |
| | Urochloa mosambicensis | 0.03 | 0.02 | 0.01 <P< 0.03 |
| | Sporobolus nitens | 0.05 | 0.05 | 0.04 <P< 0.06 |
| | Sporobolus ioclados | 0.04 | 0.04 | 0.03 <P< 0.05 |
| Woodland | Panicum maximum | 0.16 | 0.23 | 0.21 <P< 0.25* |
| | Enteropogon monostachyus | 0.07 | 0.07 | 0.06 <P< 0.08 |
| | Panicum deustum | 0.03 | 0.04 | 0.03 <P< 0.04 |
| | Dactyloctenium spp. | 0.03 | 0.03 | 0.02 <P< 0.04 |
| Themeda | Themeda triandra | 0.12 | 0.11 | 0.10 <P< 0.13 |
| | Heteropogon contortus | 0.03 | 0.05 | 0.04 <P< 0.06* |
| | Digitaria eriantha | 0.03 | 0.04 | 0.03 <P< 0.05 |
| | Cymbopogon plurinodis | 0.01 | 0.01 | 0.01 <P< 0.01 |
| Other | Eragrostis superba | 0.04 | 0.02 | 0.01 <P< 0.02# |
| | Aristida spp. | 0.04 | 0.01 | 0.01 <P< 0.02# |
| | Eragrostis rigidior | 0.02 | 0.01 | 0.003 <P< 0.01# |
| | Bothriochloa insculpta | 0.01 | 0.001 | 0.001 <P< 0.002# |
| | Eragrostis spp. | 0.04 | 0.03 | 0.02 <P< 0.04 |
| | Cynodon dactylon | 0.01 | 0.01 | 0.003 <P< 0.01 |
| | Chloris gayana | 0.004 | 0.004 | 0.001 <P< 0.008 |
| | Perotis patens | 0.004 | 0.004 | 0.001 <P< 0.004 |
| | Chloris virgata | 0.004 | 0.004 | 0.001 <P< 0.004 |
| | Cenchrus ciliaris | 0.004 | 0.004 | 0.001 <P< 0.007 |

c.

Transitional N= 3137 feeding stations

| Grassland Type | Grass Species | Available proportion | Observed proportion of usage | Bonferroni intervals of observed usage |
|---|---|---|---|---|
| Short | Digitaria argyrograpta | 0.13 | 0.17 | 0.15 <P< 0.19* |
| | Panicum coloratum | 0.17 | 0.12 | 0.10 <P< 0.14# |
| | Sporobolus nitens | 0.05 | 0.03 | 0.03 <P< 0.05 |
| | Urochloa mosambicensis | 0.07 | 0.06 | 0.05 <P< 0.08 |
| | Sporobolus ioclados | 0.01 | 0.004 | 0.001 <P< 0.01 |
| Woodland | Panicum maximum | 0.07 | 0.09 | 0.07 <P< 0.10 |
| | Enteropogon monostachyus | 0.03 | 0.03 | 0.02 <P< 0.04 |
| | Panicum deustum | 0.01 | 0.01 | 0.01 <P< 0.02 |
| | Dactyloctenium spp. | 0.01 | 0.004 | 0.001 <P< 0.01 |
| Themeda | Themeda triandra | 0.19 | 0.23 | 0.20 <P< 0.25* |
| | Heteropogon contortus | 0.05 | 0.08 | 0.06 <P< 0.09* |
| | Digitaria eriantha | 0.03 | 0.04 | 0.03 <P< 0.05 |
| | Cymbopogon plurinodis | 0.01 | 0.01 | 0.002 <P< 0.01 |
| Other | Eragrostis superba | 0.11 | 0.07 | 0.05 <P< 0.08# |
| | Aristida spp. | 0.03 | 0.01 | 0.002 <P< 0.01# |
| | Eragrostis rigidior | 0.004 | 0 | 0 <P< 0# |
| | Bothriochloa insculpta | 0.004 | 0.01 | 0.001 <P< 0.01 |
| | Eragrostis spp. | 0.02 | 0.01 | 0.004 <P< 0.02 |
| | Cynodon dactylon | 0.02 | 0.01 | 0.01 <P< 0.02 |
| | Cenchrus ciliaris | 0.02 | 0.02 | 0.01 <P< 0.03 |
| | Fingerhuthia africana | 0.004 | 0.01 | 0.001 <P< 0.01 |

Table 4. Seasonal selection of grassland types and grass species, as represented by the S index, in the present and previous (Melton 1987) studies. In the present study, seasons are divided into early dry, late dry and transitional periods, while in Melton (1987) seasons were divided into winter (dry) and summer (wet).

| | Seasonal Period | Present Study S= | Melton (1987) S= |
|---|---|---|---|
| Grassland type | Early Dry (N= 82 observations) | 0.27 | Winter 0.07 |
| | Late Dry (N= 181 observations) | 0.24 | |
| | Transitional (N= 101 observations) | 0.14 | 0.11 |
| Grass species | Early Dry (N= 3317 feeding stations) | 0.16 | Winter 0.39 |
| | Late Dry (N= 7632 feeding stations) | 0.13 | |
| | Transitional (N= 5950 feeding stations) | 0.16 | 0.49 |

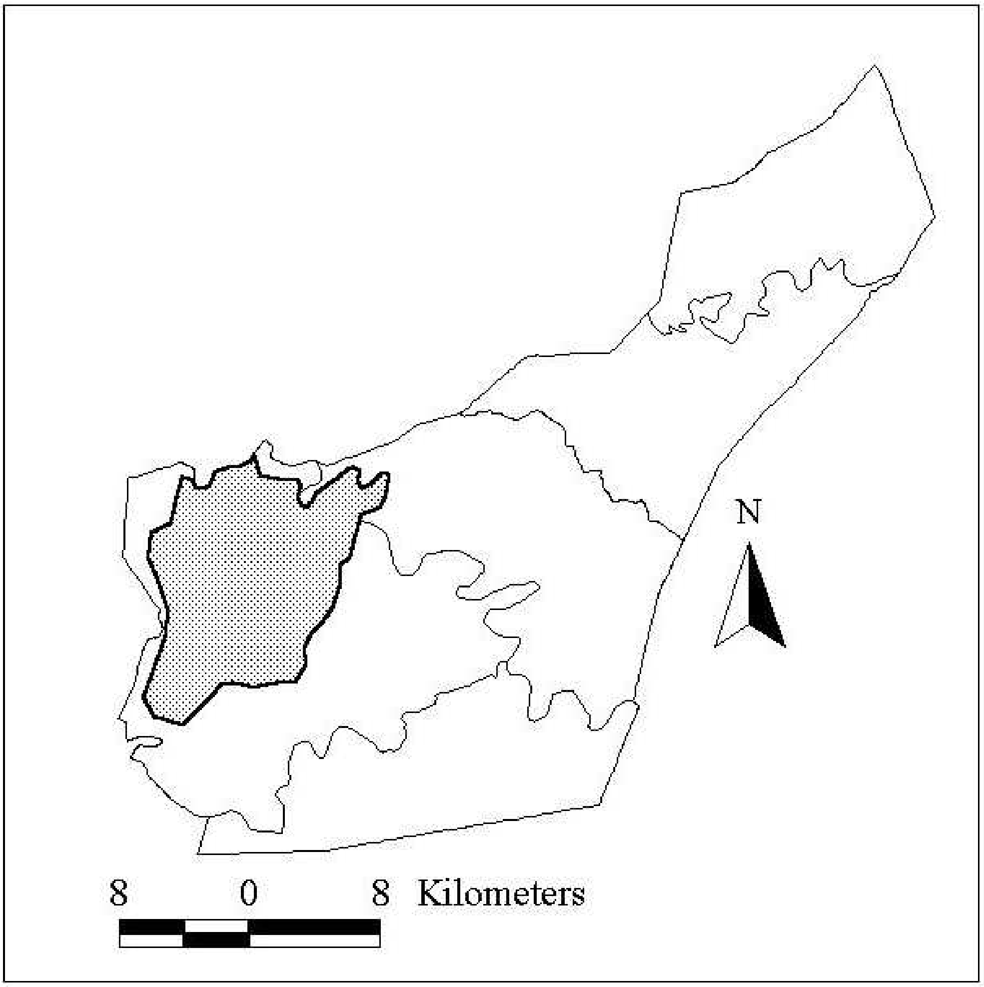

Fig. 1.

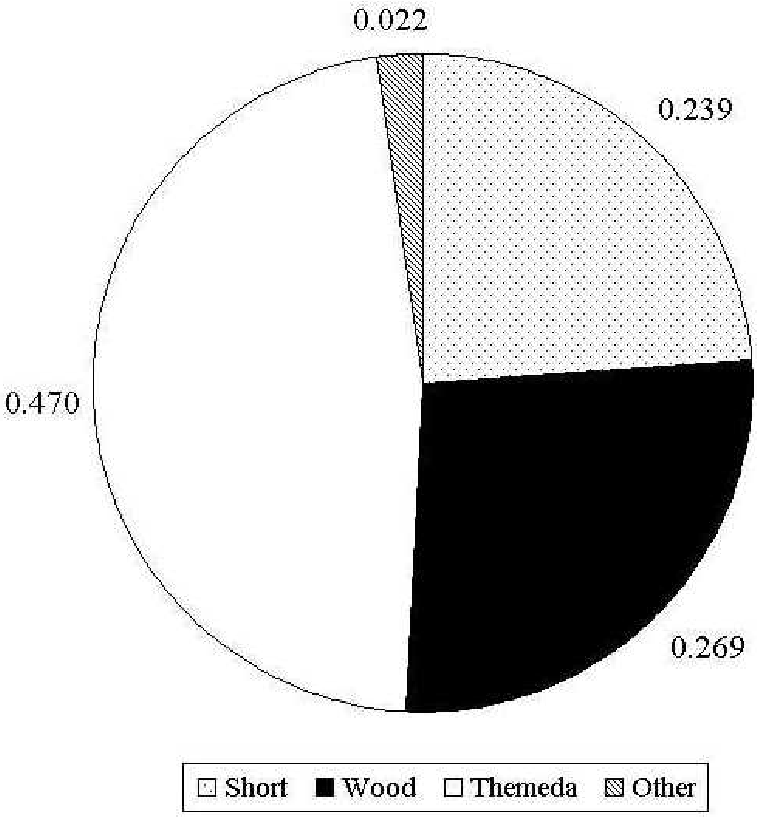

Fig. 2.

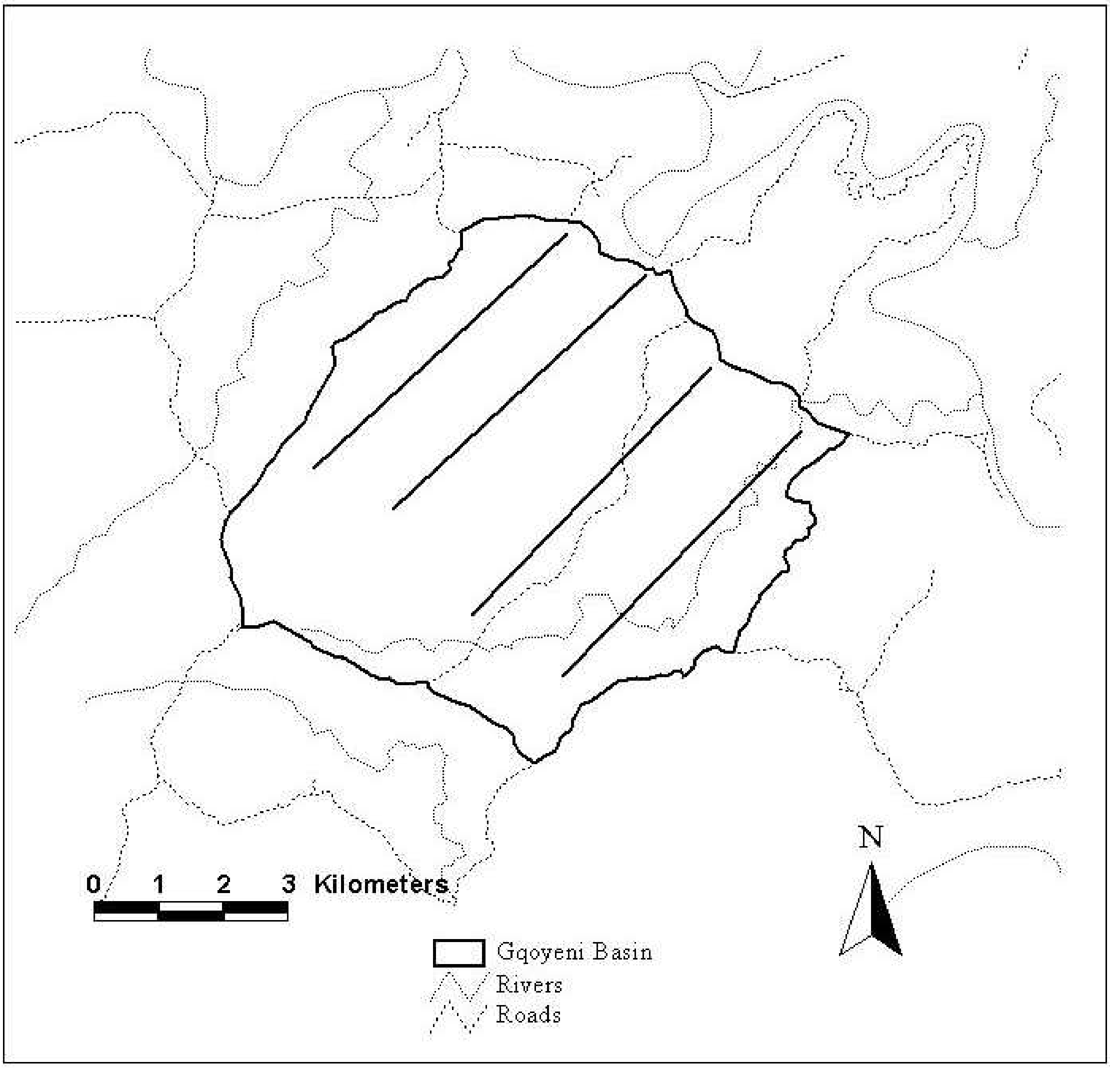

Fig. 3.

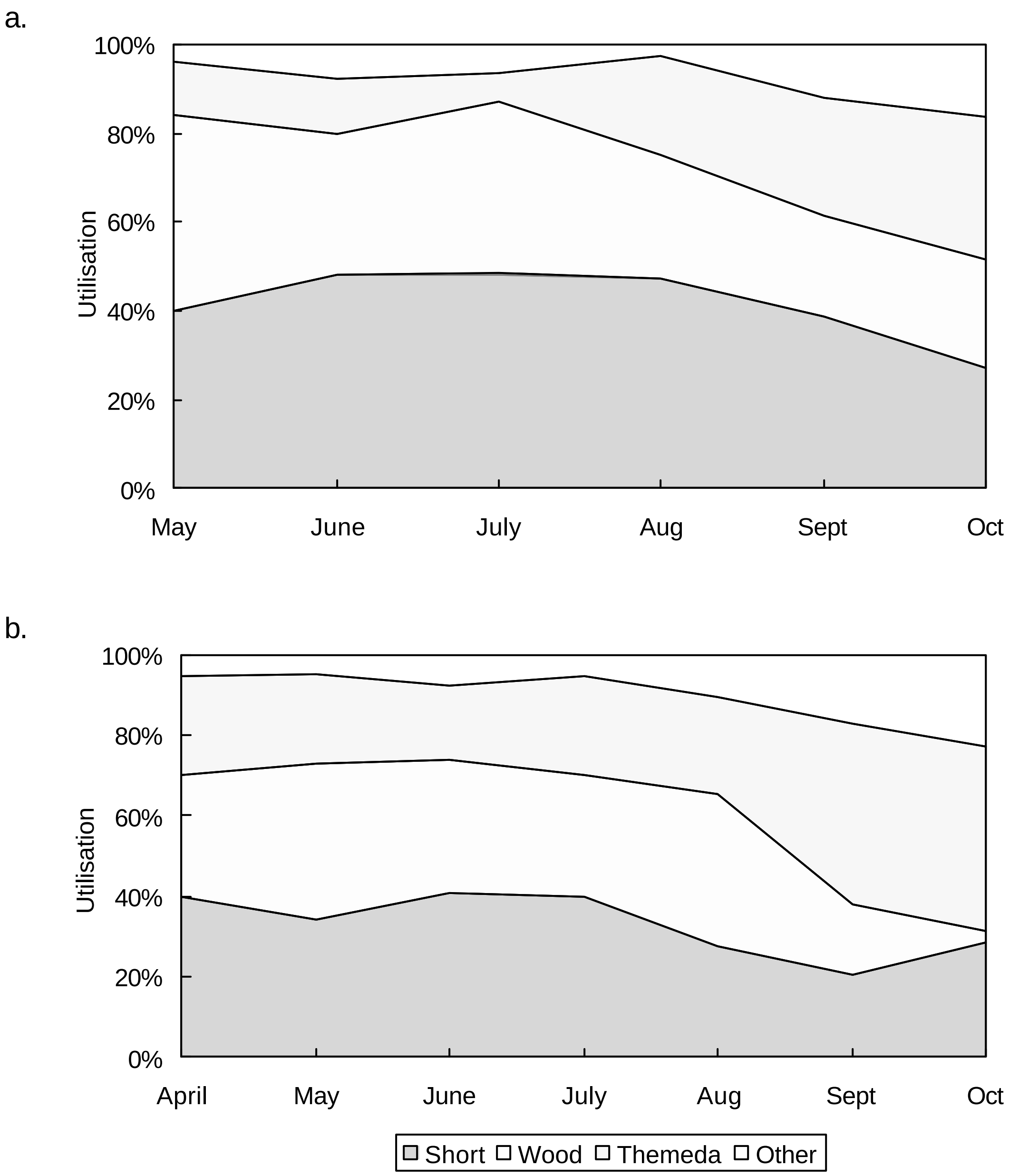
a.
100%
80%
60%
40%
20%
0%
Utilisation
May
June
July
Aug
Sept
Oct
b.
100%
80%
60%
40%
20%
0%
Utilisation
April
May
June
July
Aug
Sept
Oct
▨ Short ☐ Wood ☐ Themeda ☐ Other

Fig. 4.

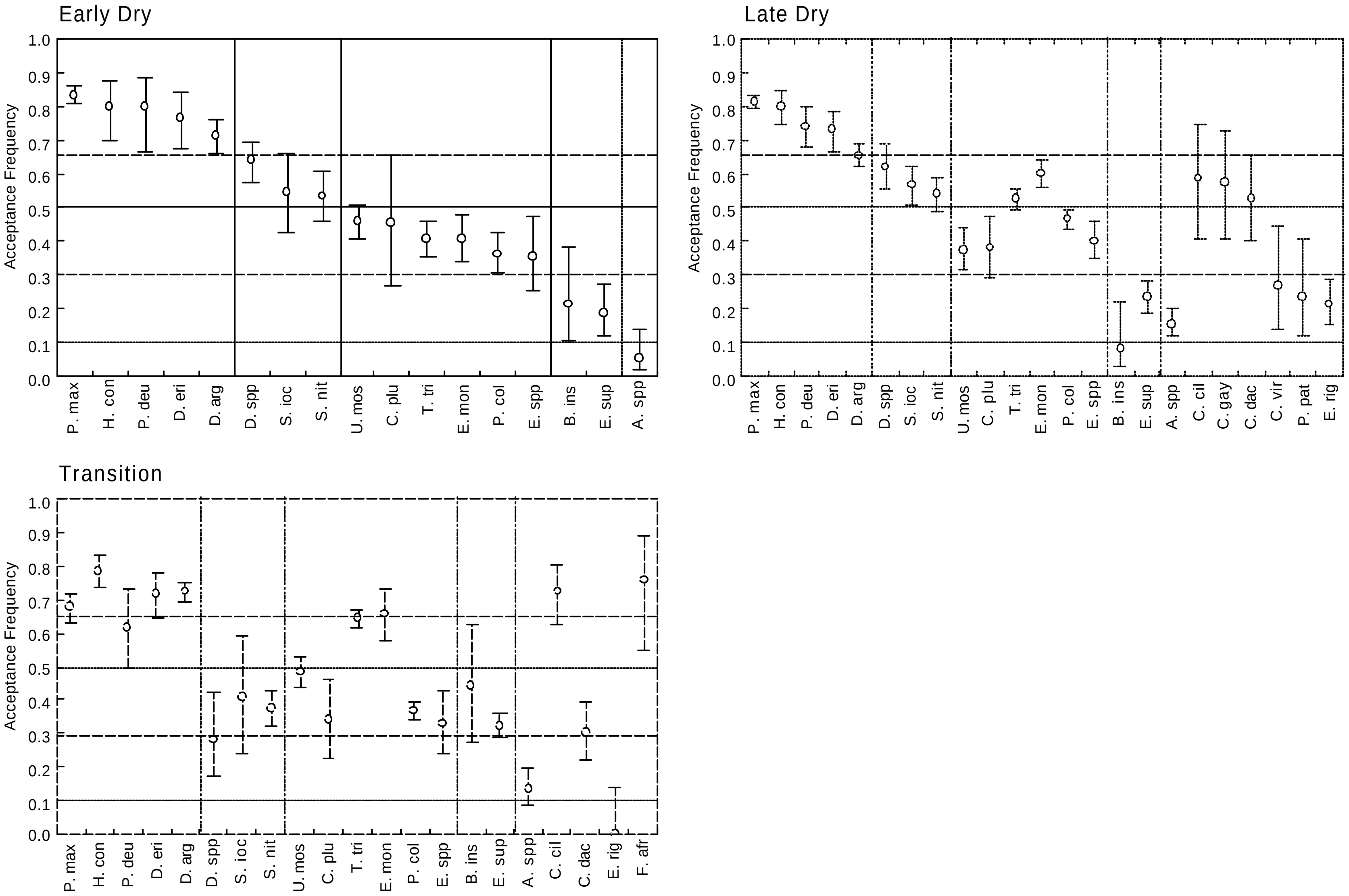
Early Dry
Late Dry
Transition
Acceptance Frequency
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
P. max
H. con
P. deu
D. eri
D. arg
D. spp
S. ioc
S. nit
U. mos
C. plu
T. tri
E. mon
P. col
E. spp
B. ins
E. sup
A. spp
C. cil
C. gay
C. dac
C. vir
P. pat
E. rig
F. afr

Fig. 5.

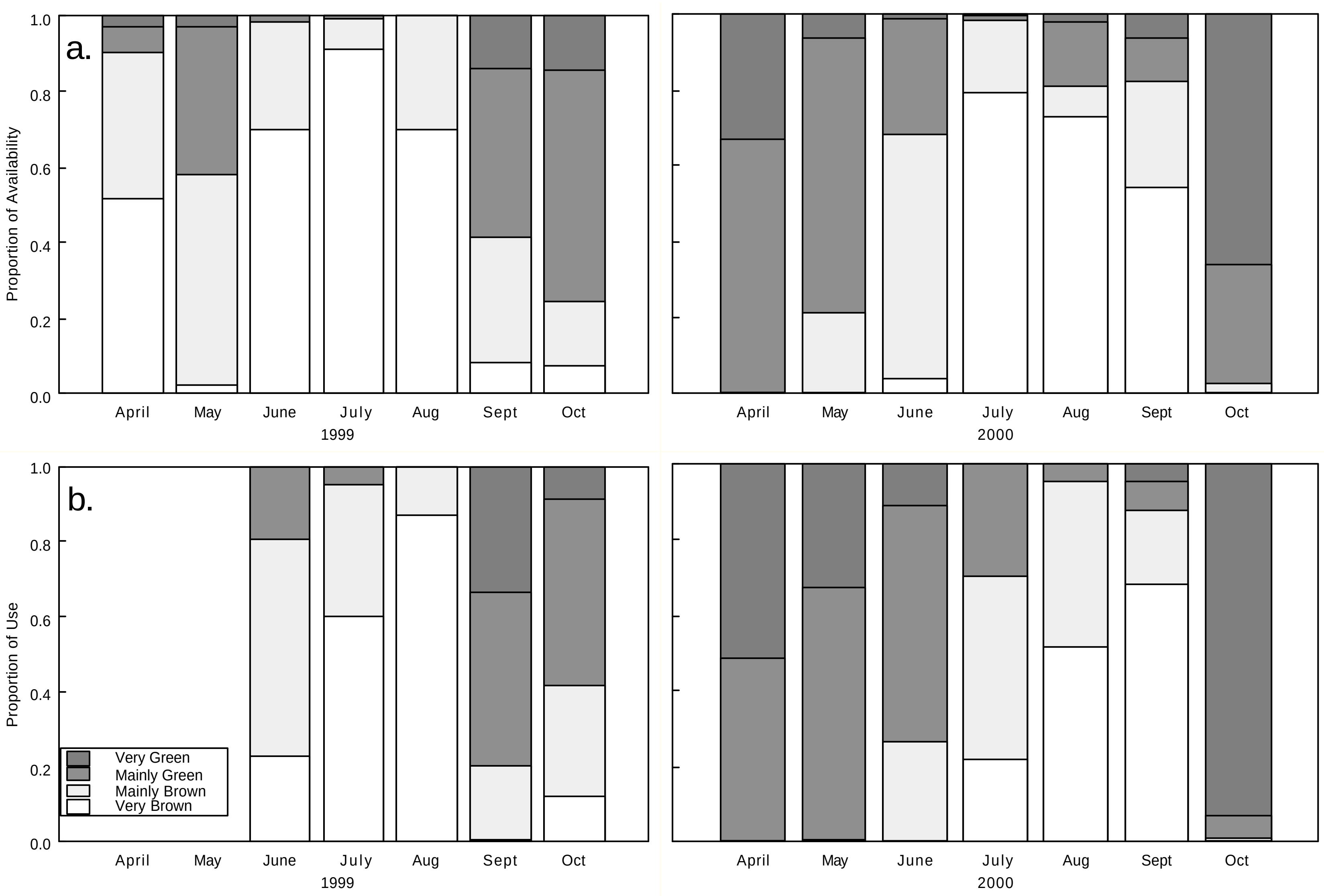
a.
b.
Proportion of Availability
Proportion of Use
1.0
0.8
0.6
0.4
0.2
0.0
April
May
June
July
Aug
Sept
Oct
1999
2000
Very Green
Mainly Green
Mainly Brown
Very Brown

Fig. 6 (a and b).

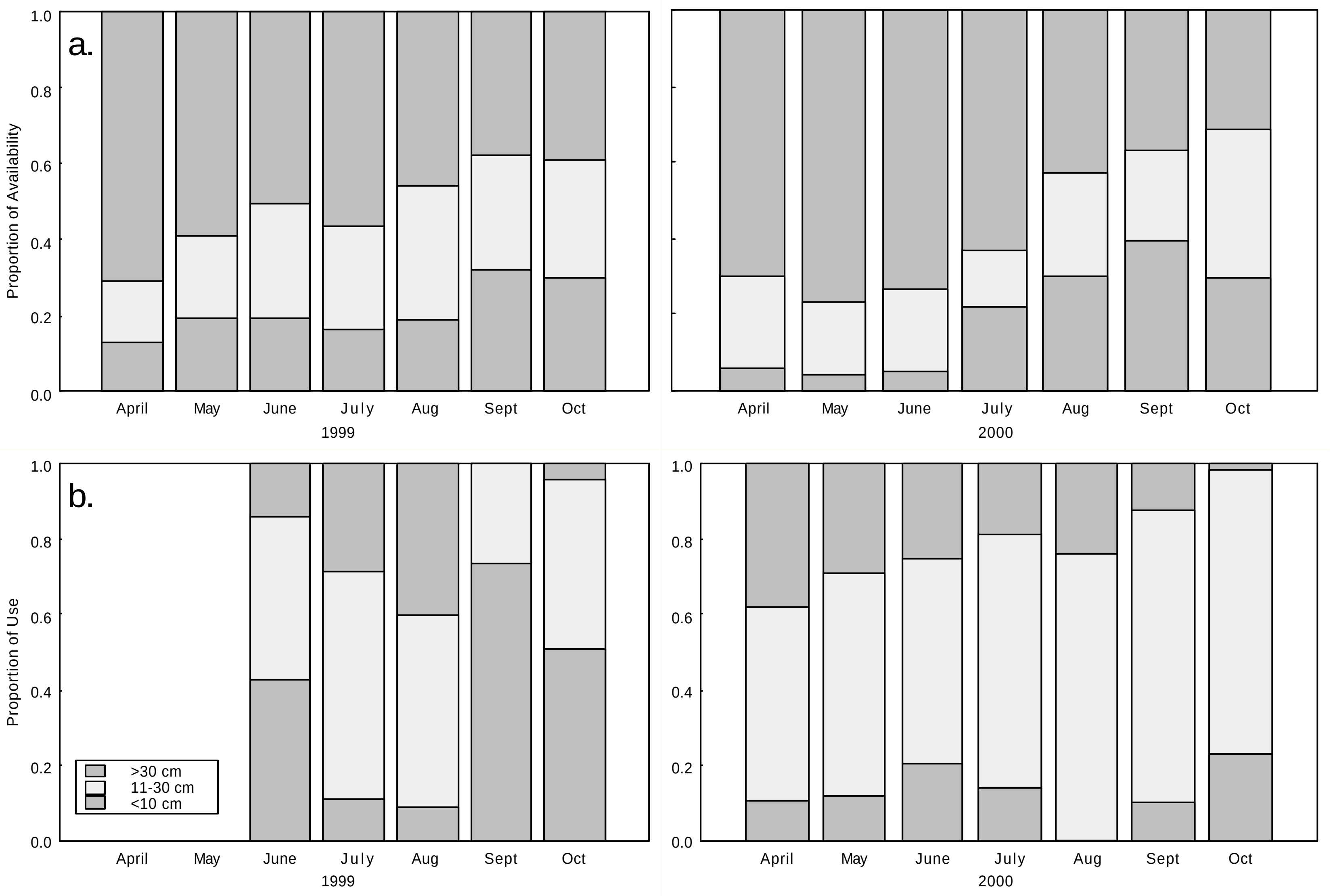
a.
Proportion of Availability
1.0
0.8
0.6
0.4
0.2
0.0
April
May
June
July
Aug
Sept
Oct
1999
2000
b.
Proportion of Use
>30 cm
11-30 cm
<10 cm

Fig. 7 (a and b).

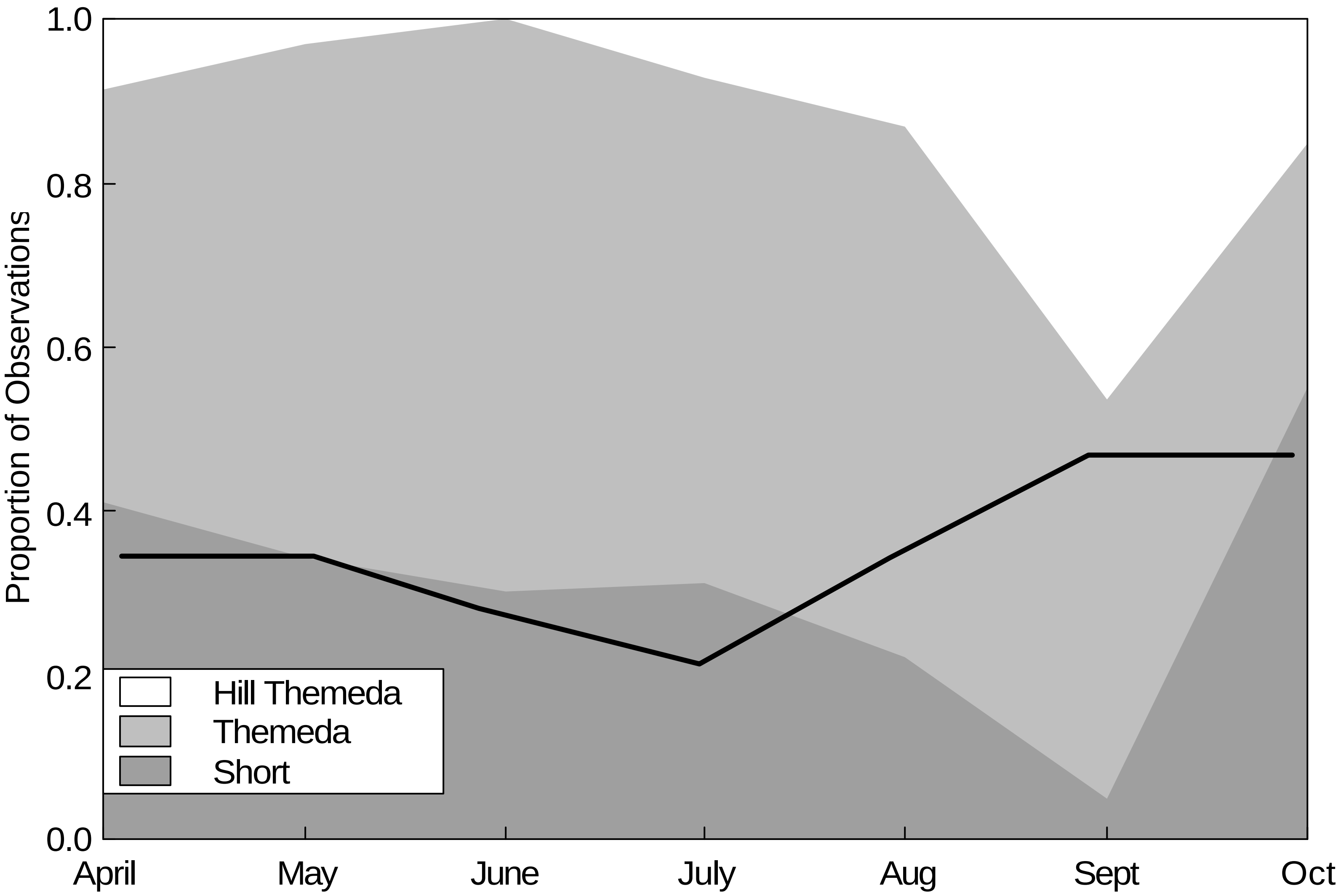
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of Observations
April
May
June
July
Aug
Sept
Oct
Hill Themeda
Themeda
Short

Fig. 8.

## CHAPTER 3

# Factors influencing food intake rate and nutrient gains of a mega-grazer, the white rhinoceroses (Ceratotherium simum), through the dry season

*Abstract.* The foraging of large herbivores can be seen as a trade-off between diet quality and quantity. I recorded changes in bite mass, bite rate, resultant intake rate, and intake rate of specific nutrients to determine the trade-offs made by the white rhinoceros (which exceeds 1000 kg in body mass), during the dry season in the Hluhluwe-Umfolozi Park, South Africa. Intake rate was determined largely by bite mass, and bite mass was determined by sward height. Maximum intake rate was approximately 120 g/min, which was at the upper end of the theoretical maximum for this body mass. A weak inverse relationship was recorded between bite rate and bite mass in the dry and early wet seasonal periods. As the greenness and nutrient content of grass declined late in the dry season, white rhinos responded by increasing their bite mass and intake rate. Despite these responses, intake of crude protein, P and Na declined throughout the dry season. I suggest the possibility that instead of compensating for declines in nutritional gain through the adjustment of dry matter intake, white rhinos rely on fat reserves to help maintain them during periods of low food quality and availability.

Key Words: Ceratotherium simum, *feeding ecology, food intake, large herbivores, white rhinoceros.*

# INTRODUCTION

Large mammalian herbivores forage within an environment that has a relatively high availability of low quality food (Illius and Gordon 1993, Senft 1989). Within this environment, the foraging of mammalian herbivores can be seen as a trade-off between diet quality and quantity (Illius et al. 2002). For African herbivores, this trade-off becomes readily apparent during the dry season with the decline in both food quality and availability. As the dry season progresses, digestible dry matter and nutrients decrease as plants senesce (Dove 1996), while the availability of food is depressed through consumption by herbivores.

How herbivores respond to seasonal declines in food quality and availability is dependent on a herbivore's body size and digestive system, as these determine the efficiency with which different foods can be consumed and utilised (Demment and Van Soest 1985, Illius and Gordon 1992, 1993). The Bell-Jarman principle (Geist 1974) states that, due to their higher metabolic rates, small herbivores require more energy and protein per unit body mass than large herbivores. To achieve these requirements, small herbivores must select for food types of high quality, while large herbivores can survive on food types of a higher fibre and lower protein content.

For ruminants, daily food intake declines as fibre content of ingested plant material increases (Bell 1971, Janis 1976, Foose 1982). This decline is a result of the slower passage rate of fibrous material through the rumen, as fibrous material takes longer to break down to a size where it will pass out of the rumen and into the remainder of the digestive tract (Bell 1971, Janis 1976, Foose 1982).

In comparison, non-ruminants do not have structures that restrict the passage rate of food particles through their digestive tract. Thus, it has been suggested that the passage rate of fibrous material through a non-ruminant's gut can be nearly twice that of ruminants (Bell 1971, Foose 1982, Illius and Gordon 1992). On high fibre diets, this faster passage rate allows non-ruminants to eat more food, and thus obtain more nutrients per day from abundant low-quality food than ruminants (Foose 1982, Duncan et al. 1990). The ability for non-ruminants to obtain more nutrients per day may outweigh their reduced digestive efficiency compared to ruminants (Duncan et al. 1990, Illius and Gordon 1992).

As food resources decline in quality and availability, herbivores may compensate by 1) widening their diet breadth to include previously avoided species, which may be less nutritious but offer higher intake rates than the rarer preferred species (Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Owen-Smith and Cooper 1989, Owen-Smith 1994, 1997), 2) increasing their daily dry matter intake by increasing daily foraging time and possibly the proportion of foraging time spent feeding (Owen-Smith and Cooper 1989, Owen-Smith 1994, 1997, Prins 1996), 3) maintaining a constant intake rate by increasing bite size (Spalinger et al. 1988, Laca et al. 1994), or, perhaps 4) buffering nutrient deficiencies by using fat reserves stored during the vegetation growing season (Adamezewski and Hudson 1993, Parker et al. 1993, 1996).

Intake rate of large grazers is dependant on sward structure and the ingestive behaviour of the animal (Distel et al. 1995). Herbage height and bulk density (herbage weight per unit volume) are the most important sward determinants of intake rate within a patch (Black and Kenney 1984, Laca et al. 1992, Shipley et al. 1994). Intake rate, however, is also influenced by bite mass, as larger bites result in higher intake rates (Hodgson 1985, Spalinger et al. 1988, Gross et al. 1993, Laca et al. 1994). Assuming that a herbivore attempts to maximise its intake rate, herbivores may compensate, to some extent, for changes in bite mass by changing bite rates (Black and Kenney 1984, Wickstrom et al. 1984). Studies of mammalian grazers have largely found that as bite size (or bite mass) obtained by herbivores decreases, bite rate increases (Hodgson 1985, Spalinger et al. 1988, Laca et al. 1994). Increases in bite rate, however, cannot fully compensate for declines in bite mass (Hodgson, 1985, Wickstrom et al. 1984), as constraints such as mouth volume and chewing rate make the cropping of new grass directly compete with chewing of grass already within the mouth (Laca and Demment 1991, Spalinger et al. 1988, Spalinger and Hobbs 1992).

For herbivores, maximum bite rate is determined by mouth morphology (tooth size, jaw musculature) and the mechanics of food consumption (cropping and chewing processes; Shipley et al. 1994). Maximum bite rate seems to scale allometrically with body mass. For example, moose (Alces alces) achieve a maximum bite rate of only 25 bites/min, while smaller kudu (Tragelaphus strepsiceros) and mule deer (Odocoileus hemionus) obtain a maximum of 45 bites/min (Owen-Smith 2002). For even smaller impala (Aepyceros melampus; Cooper and Owen-Smith 1986) and sheep (O'Reagain and Owen-Smith 1996), maximum bite rate is about 60 bites/min, while Thompson’s gazelle (Gazella thomsoni) have been found to achieve bite rates as high as 78 bites/min (Bradbury et al. 1996).

Shipley et al. (1994), suggested that maximum bite rate is constrained by pendulum movements of the lower jaw which are dependant on the allometric scaling of jaw length with body mass raised to the power of approximately negative one-sixth ($M^{-0.17}$). Owen-Smith (1973) recorded that white rhinoceroses (Ceratotherium simum) achieved an average bite rate in short grass of about 72 bites/min. It is probable that, as white rhinos use their lips to crop grass (Owen-Smith 1973), constraints on maximum bite rate are likely to be dependent on the shorter pendulum movements of a rhino’s lips and not on the longer pendulum movements of the lower jaw.

The understanding of how a herbivore’s body size, physical features and digestive system influences foraging allows us to hypothesize about how herbivores should respond to seasonal changes in food quality and availability. As the availability of high quality food declines during the dry season, the time required to search for and thus obtain high quality bites increases. As small ruminants require higher quality food than larger ruminants and non-ruminants, small ruminants should focus their feeding on scarce high quality food items (i.e. green leaves) during the dry season. Due to the increase in search time between successive high quality bites, a small ruminant’s intake of dry matter should decline. However, as small ruminants feed on high quality food throughout the dry season, nutritional gain should remain relatively high.

Throughout the seasonal cycle large bodied ruminants and non-ruminants should feed on high quality food when it is available (Bell 1971, Jarman 1974). However, as the availability and thus intake of high quality food declines during the dry season, large herbivores should incorporate previously avoided lower quality food. As non-ruminants are more tolerant of lower quality food than ruminants, non-ruminants are able to incorporate a greater variety of food types. By incorporating lower quality food, large herbivores can maintain a high intake of dry matter during the dry season. Initially, this high intake may compensate for seasonal declines in food quality. However, eventually late in the dry season the high intake of dry matter will not compensate for declines in food quality and thus the nutritional gain of large herbivores will decline (Owen-Smith and Cooper 1989, Owen-Smith 1994, 1997).

To determine how a very large bodied non-ruminant, the white rhino, coped with seasonal declines in food resources, I focused on the trade-offs made between dry matter intake rate (i.e. diet quantity) and nutritional intake rate (i.e. diet quality). The aims of my study were to 1) determine changes in the availability (i.e. sward height) and quality (i.e. greenness and nutritional content as measured by crude protein (CP), P and Na content) of grasses constituting food resources of free ranging white rhinos during the dry season, 2) explain how changes in food quality and availability influence changes in bite mass, bite rate, the resulting intake rate and nutritional intake rate, and 3) determine the degree to which white rhinos compensate for seasonal declines in nutrients by increasing their intake of dry matter.

## METHODS

### *Study area*

The study was conducted in the western section of the 950 km² Hluhluwe-Umfolozi Park (HUP) in KwaZulu-Natal, South Africa (28° 20’ S, 31° 51’ E). Annual rainfall patterns for HUP are characterised by a wet summer period, roughly from September to March, followed by a dry winter period from April to August. Rainfall was measured by the management staff using a permanent rain gauge situated in the western section of HUP at the Mbuzane ranger station. Rainfall data used in my analysis included rainfall from 7 months prior to the study so as to cover the previous wet season (October-February; Fig. 1), which would influence the availability of food resources during the dry season. Rainfall was below average (545 mm) during the first seasonal cycle of the study (October 1998-September 1999), and above average (791 mm) during the second seasonal cycle (October 1999-September 2000), relative to the 690 mm long-term mean (1981-1998) for the western side of HUP (KwaZulu Natal Wildlife, unpublished data). During both years, portions of all the grassland types available in the study area were burnt during July and August. After the rains commenced (in September 1999 and October 2000) these burns provided flushes of green grass.

### *Bite mass, bite rate and intake rate*

Radio telemetry was used so that feeding data could be recorded from specific individuals on a regular basis. MOD-125 radio transmitters from Telonics were inserted into the anterior horns of ten white rhinos (5 subadult males (5-9 years of age), 2 subadult females (6-7 years of age) and 3 adult females (>10 years of age; see Shrader and Beauchamp 2001 (Appendix I) for procedure).

Observations were made through the early (April-May 2000) and late dry season periods (June-August 1999, June-September 2000) into the start of the wet season (September-October 1999; October 2000). This initial portion of the wet season constitutes the transitional period. Rhinos were located using radio telemetry and approached on foot from downwind. Due to the poor eyesight of white rhinos, observations could be made from a distance of 10-40 meters. Data collection was not restricted to rhinos with radio transmitters, but was also gathered from any subadult (2.5-7 years) or adult companions (>7 years) of these rhinos.

During 1999, each of the ten radio-equipped individuals was located approximately every five days, over a three week period each month, and feeding data collected in either the morning or afternoon. During 2000, three pre-selected individuals were observed each month. Two individuals were observed for ten consecutive days, either in the morning or afternoon, while the third was followed throughout the day for five consecutive days during the subsequent week.

Bite rate was recorded using a Psion Organiser II which had been programmed to enable the number of bites taken per step and the number of bites per second to be recorded (Appendix III). Each bite rate observation comprised ten consecutive feeding steps. A feeding step was defined as a step where the rhino took at least one bite before taking another step. Bite rate observations could include non-feeding steps. However, ten feeding steps were required for the observation to be used in the statistical analysis. Bite rate for each observation was calculated as the total number of bites over the total duration of the 10 feeding steps. Median duration of these observations was 48 seconds (range 13 to 376 seconds, N=579). The median value is reported as the data were not symmetrically distributed. Consecutive bite rate observations were not taken from the same individual at less than ten minute intervals, in an attempt to minimise serial autocorrelation of the observations.

Bite mass observations were recorded from the same place where the bite rate data had been recorded. Once the rhino had moved a safe distance away, the bite volumes ($cm^3$) of ten bites (a single observation) were recorded. Bites were readily located along the easily discernible feeding path, measuring approximately 70 cm in width. The length (L) and width (W) of each bite were measured as the furthest distances between the severed ends of grass leaves or stems (typically 20 cm X 10 cm). The height of the grass at the point of severance, above ground level, was then measured in five places within the bite area and averaged ($H_b$). Five height measurements were also taken from unbitten grass of the same species surrounding the bite ($H_{unb}$). The height of grass removed in each bite was then estimated as $H_{unb}$-$H_b$ and the bite volume as $LW(H_{unb}-H_b)$.

In the field, bulk density (dry weight per unit volume; Hodgson 1985, Laca et al. 1992) of the grass in the upper and lower stratum was categorised as either high, medium or low. The lower stratum was defined as the portion of the grass below 20 cm in height above ground level, prior to grazing, while the upper stratum was defined as the portion of the grass above 20 cm. Bites within short grasslands were restricted to the lower stratum, while bites in the taller woodland and Themeda grasslands were partitioned between upper and lower strata.

Bulk density estimates in each grassland type were determined by clipping 820 grass samples, which were representative of the different bulk density categories, from areas where rhinos had previously been seen feeding. Each clipping approximated the volume of a rhino bite (i.e. 20 cm X 10 cm X height of grass removed). All clippings were air dried out of direct sunlight in paper bags for over a month prior to being weighed. The bulk density of each clipping was determined by dividing its dry weight, in grams, by its volume (Hodgson 1985). From these clippings, median bulk density was determined for the different bulk density categories in each stratum in the different grasslands (Table 1). Median values were used as the data were not symmetrically distributed. In two situations (woodland grassland upper stratum and Themeda grassland lower stratum), estimates of bulk density were inconsistent (e.g. the medium estimate was larger than the high estimate). Since the estimates did not differ significantly (woodland t=1.47, df=68, p=0.147; Themeda t=-1.90, df=28, p=0.068), the categories were combined (Table 1).

In the different grassland types, bite mass (grams of dry matter) of each bite was estimated as the product of bite volume and the median bulk density for the stratum in which the bite was taken. As a white rhino feeds, consecutive bites slightly overlap. However, as consecutive bites were not measured in each bite mass observation, the volumes of these bites were over-estimated. Estimates of bite mass for each bite were corrected by being multiplied by one minus the median proportion of overlap of consecutive bites; i.e. 0.2. Overlap of consecutive bites was determined by observing a rhino take 10 consecutive bites. Estimates (N=79 estimates) were recorded in all three grassland types. However, no difference was found between the grassland types, thus the data were combined. The area in which these bites were taken was marked visually in relation to landmarks. Once the rhino had moved a safe distance away, the number of bites discernible within this area was recorded. The proportion of overlap of the bites was then estimated as 1-(bites recorded)/(bites observed), where the observed number was 10.

The corrected bite mass estimates of the individual bites were then used to derive the mean dry matter bite mass for each bite mass observation (10 bites). The dry matter intake rate of each observation was then determined as the product of the mean bite mass of an observation and the corresponding bite rate which had been recorded in the same place.

Other data recorded consisted of the broad grassland type (i.e. short, woodland and Themeda grasslands; Downing 1972, Owen-Smith 1973) in which the bites were taken, along with the percentage greenness of grass available and sward height in which the rhinos fed. Percentage greenness and sward height were estimated subjectively from grass of the same species adjacent to each bite. Grass greenness was determined using Walker's (1976) eight point scale (0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100%), while sward height was measured using a ruler and then classified in one of three height categories ($\leq$10 cm, 11-30 cm, or >30cm).

The mean greenness estimate of bite mass, bite rate and intake rate observations (i.e. total of 10 bites) were derived as

$$G_i = \frac{0.5}{10} * (CL + CU) \sum_{j=1}^{10} bij$$

where $c_L$ and $c_U$ were the lower and upper bounds of each greenness category, respectively; $b_{ij}$ was the $j^{th}$ estimate of bite mass in the $i^{th}$ category (i=0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100%). The same equation was applied to estimate the mean sward height of each observation, except that the number of height categories was limited to three (i.e. <10 cm, 11-30 cm, >30 cm), while the lower and upper category bounds were set at 0-10 cm, 11-30 cm and 31-100 cm, respectively.

Prior to statistical analysis, estimates of grass greenness were combined into four categories; very brown (0-10%), mainly brown (11-50%), mainly green (51-90%) and very green (91-100%). Monthly rainfall was recorded by the management staff in the western section of HUP at the Mbuzane ranger station.

### *Nutrient measures*

During the study, white rhinos foraged primarily in Short, Woodland and Themeda grasslands (see Chapter 3), thus chemical analysis was limited to these grassland types. N, P and Na concentration for each of the four grass greenness categories in the three grassland types were determined through the chemical analysis of 101 grass clippings. Clippings were taken from areas where white rhinos had previously been observed feeding. Similar to bulk density clippings, each clipping approximated the length and width of a rhino bite (i.e. 20 cm X 10 cm), while the height of the grass removed varied. Clippings in each grassland type constituted a mix of species. In total, 48 clippings comprising Panicum coloratum, Sporobolus nitens, and Digitaria argyrograpta were collected in short grasslands, 32 clippings of Panicum maximum plus Enteropogon monostachyus in woodland grasslands, and 21 clippings solely of Themeda triandra in Themeda grasslands. All clippings were air dried, out of direct sunlight, in paper bags for over a month prior to being milled and analysed.

Chemical analysis was conducted at the Institute of Commercial Forestry Research (ICFR) at the University of Natal, Pietermaritzburg, South Africa. Nitrogen content was determined through the sulphuric acid digestion of organic nitrogen to ammonium sulphate. Under alkaline conditions, ammonia was distilled into a hydrochloric acid solution and then back-titrated with a standardised solution of HCl. Nitrogen content was then expressed in terms of the dried grass sample. Crude protein (CP) was then calculated by multiplying % N by 6.25 (Owen-Smith and Cooper 1989).

Ammonium molybdate and antimony potassium tartrate reacted in an acid medium with dilute solutions of phosphorus to form an antimony-phosphomolybdate complex. With the addition of ascorbic acid, this complex then reduced to an intensely blue coloured complex. As the colour of the solution was proportional to the concentration of phosphorus within the solution, phosphorus concentration was determined by measuring the solution at 880 nm. Sodium concentration was determined by flame emission spectroscopy using an air-acetylene flame.

In *Themeda* grasslands, the nutrient concentration (% dry matter of CP, P and Na) of bites taken within each greenness category was estimated as the mean nutrient concentration of the clippings of *T. triandra* (N= 21 clippings) taken within the different greenness categories. In woodland grasslands, no significant differences in % CP (ξ difference=2% dry matter, $F_{3,21}$=1.57, P=0.227), % P (ξ difference=0.1% dry matter, $F_{3,21}$=0.96, P=0.432), or % Na (ξ difference=0.1% dry matter, $F_{3,21}$=2.42, P=0.094) were found between *P. maximum* and *E. monostachyus*. Thus, nutrient concentrations were estimated from the combined clippings of *P. maximum* and *E. monostachyus*. In short grasslands, estimates of % CP (ξ difference=4% dry matter, $F_{5,36}$=2.59, P=0.04), % P (ξ difference=0.1% dry matter, $F_{5,36}$=5.62, P=0.0006), and % Na (ξ difference=0.3% dry matter, $F_{5,36}$=2.43, P=0.05) differed significantly between *P. coloratum*, *S. nitens* and *D.*

argyrograpta in the different greenness categories. It is, however, possible that the heterogeneity recorded between the short grass species may be spurious, as the analysis contained single samples of S. nitens and P. coloratum in the very brown and mainly green categories (Appendix IV). Despite this possibility, nutrient concentrations of individual bites were determined using the estimates of CP, P and Na for the individual grass species. In instances in short grasslands, where bites comprised T. triandra or the woodland grass species P. maximum or E. monostachyus, the nutrient concentrations estimated for Themeda and the woodland grassland type were used respectively. For bites that did not contain one of the grass species chemically analysed, the mean nutrient concentration of the short grassland species for the respective greenness category was assigned.

The intake rate (g/min) of CP, P and Na was estimated by multiplying the nutrient concentrations (% dry matter of CP, P and Na) of the grass clippings (see Appendix IV) by the estimates of bite mass (g) of the bites taken within short, woodland and Themeda grassland types. Mean nutrient concentrations were then determined for each of the 695 feeding observations. The mean concentration per observation was multiplied by the corresponding bite rate (bites/min) to give the nutritional intake rate (g/min) of CP, P and Na.

### *Data Analysis*

A 4-way ANOVA was used to analyse the variation in mean bite mass, bite rate and intake rate among grassland types, months, sward height categories and percentage greenness categories. Categorical fixed effects of the model consisted of month (April, May, June, July, August, September, October), grassland type (short, woodland, Themeda), sward height ($\leq$10 cm, 11-30 cm, >30 cm), and grass greenness (very green, mainly green, mainly brown and very brown). Random variation among individual rhinos did not add any additional variance, thus the effect was dropped from the analysis. Monthly differences in mean bite mass, bite rate and intake rate did not differ significantly between years, thus data from the same month in the two years were combined. Bite rate was normally distributed. However, bite mass and intake rate were log transformed for normality.

A 2-way ANOVA was used to analyse the variation in % CP, % P and % Na among grass species in the different greenness categories. Analysis was conducted for grass species in short and woodland grassland types. Categorical effects for the separate grassland types consisted of the grass species (short: P. coloratum, S. nitens and a combination of D. argyrograpta plus P. coloratum; woodland: P. maximum and E. monostachyus) and grass greenness classes (very brown 0-10%, mainly brown 11-50%, mainly green 51-90% and very green 91-100%). Analysis was performed to determine whether nutrient levels of the different grass species within each grassland type differed significantly. If species were found not to differ, the nutrient concentrations for the different greenness categories were derived using the combined data for each grassland type. In the analysis, estimates of % CP, % P and % Na were log transformed for normality.

To determine whether white rhinos compensated in their intake rate for seasonal declines in nutrients, a linear regression was fitted to determine the relationships between dry matter intake rate and % dry matter of CP, P and Na. The slopes of these regressions, however, were greatly influenced by the high intake rates of CP, P and Na recorded in April 2000 (Fig. 2a-c). As these data were from the early portion of the dry season, when high quality food was still available, they were removed from the analysis. To test the assumption that proportional declines in nutrients were matched by proportional increases in intake rate, both intake rate and percentage dry matter of CP, P and Na were log transformed prior to analysis. If the 95% confidence limits of the slopes of these relationships did not contain the slope of perfect compensation (i.e. slope= 1) white rhinos were considered not to have compensated for changes in % dry matter of CP, P and Na by adjusting their dry matter intake rate. All analyses were performed using the statistical package SAS 8.2 (SAS Institute Inc. 2001).

## RESULTS

### *Seasonal changes in grass greenness and sward height*

Mean grass greenness (Fig. 3a) and mean sward height (Fig. 3b) of grass available in all grassland types declined throughout the dry season. Mean greenness declined from approximately 88% in April to approximately 11% in August (Fig. 3a), while mean sward height declined from approximately 51 cm in April to approximately 37 cm in August (Fig. 3b). With the onset of the rains and the emergence of new growth and green flushes on burns, mean grass greenness increased to approximately 57% in September and approximately 74% in October. Mean sward height, however, remained low at approximately 32 cm in both September and October.

### *Seasonal changes in CP, P and Na concentrations of ingested grass*

The six grass species analysed chemically formed 55% of the grass eaten during the early dry period, 58% during the late dry period and 54% during the transitional period. Projected mean crude protein of the grass ingested by white rhinos was approximately 10-12% of dry matter during the early dry period (April-May; Fig. 4a). By the end of the late dry period in August, projected CP levels had dropped to approximately 6%. When rhinos fed on green flush during the transitional period, mean CP content of the ingested grass had increased to between 9% and 10% of dry matter.

The patterns of monthly change projected for both % P (Fig. 4b) and % Na (Fig. 4c) were similar to that of % CP. During the early dry period, P levels ranged between 0.13% and 0.27% of dry matter, while Na ranged between 0.24% and 0.40%. By August, at the end of the late dry period, P levels had dropped substantially to approximately 0.07% of dry matter, while Na levels had dropped to approximately 0.16%. In the transitional period, both P and Na levels increased, with P ranging between 0.15% and 0.24% of dry matter, and Na levels approximately 0.26% of dry matter.

### *Bite Mass*

White rhinos obtained a geometric mean bite mass of 0.67 g (CL 0.64-0.71 g, range 0.10 g to 3.44 g, N=695 observations) over the period April-October. Most bites (75%) were less than 1 g. As grass greenness declined to below 25% in July and August (Fig. 3a), mean bite mass increased from 0.70 g (CL 0.60-0.82 g) in June to 0.98 g (CL 0.87-1.11 g) in August (Fig 5a). However, with the new growth and green flushes in September, resulting from the onset of the rains, mean bite mass dropped from 0.98 g (CL 0.87-1.11 g) in August to 0.44 g (CI ±0.05 g) in September-October.

Mean bite mass obtained by white rhinos differed among grassland types, sward height, and grass greenness categories. White rhinos obtained a larger mean bite mass in woodland grasslands ($\bar{x}$=0.92g, CL 0.85-1.00 g) than in either <u>Themeda</u> ($\bar{x}$=0.77g, CL 0.71-0.85 g) or short grasslands ($\bar{x}$=0.46 g, CI ±0.04 g; $F_{2,679}$=17.86, p<0.0001). Mean bite mass increased substantially from 0.29 g to 1.55 g as sward height increased from $\leq$10 cm to >30 cm ($F_{2,679}$=455.89, p<0.0001; Fig. 6a). The largest mean bite masses were obtained in mainly brown ($\bar{x}$ =0.77 g, CL 0.70-0.85 g) and very brown grass ($\bar{x}$ =0.82 g, CI ±0.09 g), with smallest bites masses in very green ($\bar{x}$ =0.64 g, CL 0.57-0.73 g) and mainly green grass ($\bar{x}$ =0.55 g, CL 0.51-0.61 g; $F_{3,679}$=4.05, p=0.007).

*Bite Rate*

White rhinos achieved a mean bite rate of 57 bites/min (CI ±1 bite/min, range 34 to 83 bites/min, N= 483 bite rate observations) and a maximum of 83 bites/min during April-October. When bite rate was regressed on bite mass only a weak inverse, although statistically significant, relationship was recorded, aggregating all three grassland types (slope=-6.8 bites per min/g; SE=0.66; $F_{1,481}$=99.49; P<0.001; $R^2$=0.17). This weak relationship was due to bite rate being highly variable towards low bite mass (Fig. 7).

Seasonally, when bite rate was regressed on bite mass, a weak inverse relationship was recorded in each seasonal period (Fig. 7). In the early dry (slope=-4.8 bites per min/g; SE=1.47; $F_{1,74}$=10.70; P=0.002; $R^2$=0.13) and late dry seasonal periods (slope=-4.2 bites per min/g; SE=0.73; $F_{1,217}$=42.35; P<0.0001; $R^2$=0.16), significant relationships were recorded, while in the transitional period, the relationship was half as great and non-significant (slope=-2.2 bites per min/g; SE=1.48; $F_{1,481}$=2.24; P=0.136; $R^2$=0.01). Bite rates achieved for the same bite mass differed between the three periods. White rhinos obtained faster bite rates relative to bite mass on the new growth available during the transitional period than on the more mature grass available in either the early dry or late dry season periods.

Mean bite rate varied monthly in a pattern similar to that of grass greenness (Fig. 3a) and rainfall (Fig. 5b), but opposite to that of bite mass. As the dry season progressed, bite rate declined from 58 bites/min in April to 50 bites/min in August. After the start of the rains in September, mean bite rate increased to 62 bites/min in

September-October as white rhinos fed on new growth and the green flushes on burns. Mean bite rate differed between months, with the highest bite rates obtained after the start of rains in September-October ($\bar{x}$ =62 bites/min, CI ±1 bite/min; $F_{6,467}$=4.47, p=0.0002).

Among grassland types, lower bite rates were obtained in woodland grasslands ($\bar{x}$ =52 bites/min, CL=51-54 bites/min) than in either Themeda ($\bar{x}$ =59 bites/min, CI ±1 bite/min) or short grasslands ($\bar{x}$ =59 bites/min, CI ±1 bite/min; $F_{2,467}$=8.14, p<0.001). Bite rate increased from 49 bites/min to 63 bites/min as sward height declined from tall (>30 cm) to short (≤10 cm; $F_{2,467}$=63.70, p<0.0001; Fig. 6b), and increased as grass greenness went from very brown to very green (very brown ($\bar{x}$ =51 bites/min, CL 50-53 bites/min), mainly brown ($\bar{x}$ =53 bites/min, CL 52-55 bites/min), mainly green ($\bar{x}$ =60 bites/min, CL 58-61 bites/min) and very green ($\bar{x}$ =64 bites/min, CL 63-66 bites/min); $F_{3,467}$=70.54, p<0.0001).

### *Intake Rate*

The geometric mean intake rate achieved by white rhinos was 34 g/min (CI ±2 g/min, N=482 estimates of intake rate), but estimates ranged widely between 8 and 165 g/min. Intake rate varied in a similar pattern to bite mass (Fig. 5c). Mean intake rate increased from 36 grams/min (CI ±6 g/min) in June to 45 g/min (CL 39-52 g/min) in August as grass greenness dropped to below 25% (Fig. 3a). The lowest monthly intake rate obtained by white rhinos occurred in September ($\bar{x}$ =25 g/min, CI ±3 g/min) and October ($\bar{x}$ =33 g/min, CI ±4 g/min) when white rhinos fed on new growth and green flush (Fig. 5c).

Mean intake rate was larger in woodland ($\bar{x}$ =44 g/min, CL 40-49 g/min) and Themeda grasslands ($\bar{x}$ =41 g/min, CI ±4 g/min) than in short grasslands ($\bar{x}$ =25 g/min, CI ±2 g/min; $F_{2,468}$=16.81, p<0.0001). Mean intake rate increased substantially from 18 g/min to 74 g/min as sward height increased from short ($\leq$10 cm) to tall (>30 cm; $F_{2,462}$=356.71, p<0.0001; Fig. 6c). Unlike bite mass, however, the largest mean intake rates obtained were in very green ($\bar{x}$ =40 g/min, CI ±6 g/min), mainly brown ($\bar{x}$ =37 g/min, CI ±4 g/min) and very brown grass ($\bar{x}$ =38 g/min, CL 34-44 g/min), with the smallest intake rate in mainly green grass ($\bar{x}$ =29 g/min, CI ±3 g/min; $F_{3,468}$=20.20, p<0.0001). These larger intake rates were the result of the large bite mass obtained in mainly brown and very brown grass during the dry season, and the large bite mass and bite rate of very green grass obtained during the early dry period in April and May.

### *CP, P and Na intake rate*

The nutritional intake rates of CP, P and Na all declined as the dry season progressed (Fig. 8 a-c). The intake rate (g/min) of CP declined from approximately 6 g/min (CI ±1 g/min) in April to 2 g/min (CI ±0.3 g/min) in September (Fig. 8a). CP intake then increased during the transitional period from 2 g/min (CI ±0.3 g/min) in September to 4 g/min (CI ±0.5 g/min) in October. Intake rate of P declined from approximately 0.12 g/min (CI ±0.03 g/min) in April to its lowest point 0.03 g/min (CI ±0.01 g/min) in July (Fig. 8b). As with CP, the intake rate of P increased during the transitional period from 0.04 g/min (CI ±0.01 g/min) in September to 0.09 g/min (CI ±0.02 g/min) in October. The intake rate of Na followed a similar pattern to that of CP (Fig. 8c). Na intake declined from 0.19 g/min (CI ±0.04 g/min) in April to 0.06 g/min (CI ±0.01 g/min) in September, but then increased only marginally to 0.08 g/min (CI ±0.02 g/min) in October.

### *Compensation for declines in percentage nutrients*

Changes in intake rate were not found to compensate for changes in nutrient concentrations. The slope of perfect compensation (i.e. slope= 1) was not contained within the 95% confidence limits of the slopes of, 1) intake rate of dry matter and % CP (slope=-0.33, CI ±0.73, $F_{1,6}$=1.212, $R^2$=0.17), 2) intake rate of dry matter and % P (slope=-0.26, CI ±0.54, $F_{1,6}$=1.394, $R^2$=0.19), or 3) intake rate of dry matter and % Na (slope=-0.23, CI ±0.52, $F_{1,6}$=1.289, $R^2$=0.18) over the dry season.

## DISCUSSION

Illius et al. (2002) suggested that the foraging of mammalian herbivores can be seen as a trade-off between diet quality and quantity. As the greenness and nutritional quality of grass declined late in the dry season, white rhinos responded by increasing their bite mass and intake rate. However, despite these adjustments, the white rhinos' intake of nutrients declined throughout the dry season.

Previous studies have indicated that to compensate for declines in food quality and availability large herbivores may adjust their feeding rate, daily feeding duration, or diet (Spalinger et al. 1988, Owen-Smith and Cooper 1989, Owen-Smith 1994, Prins 1996). Owen-Smith (1994, 1997) recorded that, by increasing daily foraging time and the amount of time spent feeding, kudus, a medium-sized ruminant, were able to maintain their nutritional intake above maintenance requirements for most of the year. However, despite these behavioural adjustments, daily energy gain declined progressively as the dry season continued, owing to the ingestion of lower quality food. During the present study, daily activity patterns of the white rhinos were not recorded. However, observations suggest that, unlike what was observed by Owen-Smith (1973, 1988), white rhinos did not spend 50% of the daylight hours feeding. In the early morning, white rhinos generally started foraging around sunrise and then fed for approximately 3 to 4 hours before lying down and resting for the greater part of the day. On many occasions, white rhinos only resumed feeding around sunset. Whether, white rhinos increased their night time feeding, however, is uncertain.

Owen-Smith and Cooper (1989) recorded that kudus (Tragelaphus strepsiceros) widened their diet breadth to include previously avoided plant species as the dry season progressed. During the present study, however, white rhinos did not expand their diet, but fed primarily on eight grass species (P. maximum, E. monostachyus, T. triandra, H. contortus, D. argyrograpta, P. coloratum, S. nitens and U. mosambicensis) throughout the dry season (see Chapter 2). Spalinger et al. (1988) recorded that, as bite size declined, Sitka black-tailed deer (Odocoileus hemionus sitkensis) compensated by increasing bite rate. During the present study, the availability of food resources did not seem to be a limiting factor. However, white rhinos seemed to respond to declines in grass greenness by increasing bite mass and intake rate.

### *Bite mass, bite rate relationship*

Results indicate that, for white rhinos, changes in bite rate were to some degree affected by changes in bite mass. Higher bite rates relative to bite mass were achieved on new growth and green flush in the transitional period than on the more mature grass in the dry season periods. Differences in the plant structural features (i.e. fibre content, stem:leaf ratio, cell wall thickness and tensile strength of stems and leaves) of grass may influence bite rate by increasing handling time (Spalinger et al. 1986, Spalinger et al. 1988, Dougherty et al. 1989 (cited in Laca et al. 1994), Bergman et al. 2000). As grass matures, cellulose crystallises and bonds with lignin. These changes increase plant strength but also increases the plant’s resistance to chewing and digestion by large herbivores (Spalinger et al. 1988, Dougherty et al. 1989 (cited in Laca et al. 1994), Dove 1996). New growth, however, has a lower fibre content than mature plants (Dove 1996).

Spalinger et al. (1988) suggested that when plant availability is limiting, intake rate will be a function of the rate at which herbivores can chew and swallow food. Under experimental conditions, Spalinger et al. (1988) found that the chewing (processing) time of Stika black-tailed deer increased as plant fibre increased. Dougherty et al. (1989; as cited in Laca et al. (1994)) found that cattle chewed longer per unit dry matter in swards of alfalfa which had a higher proportion of fibrous material (i.e. stem). Bergman et al. (2000) indicated through experimental manipulation of sward complexity that wood bison (Bison bison athabascae) reduced their bite depth in tall swards to avoid ingesting high fibre stem. In short swards, however, bison did not adjust their bite depth in response to increased stem proportions, and thus obtained lower intake rates than on higher fibre swards. Thus, I suggest that the seasonal differences in bite rate relative to bite mass were the result of varying handling times which increased as fibre content of grass swards increased.

### *Intake Rate*

Shipley et al. (1994) determined that maximum intake rate of mammalian herbivores scales allometrically at body mass raised to the power of approximately three-fourths ($M^{0.71}$). Using their formula, a 40 kg impala (Aepyceros melampus) is predicted to have a maximum intake rate of approximately 9 g/min, while a 650 kg bison (Bison bison) is predicted to have a maximum intake rate of approximately 63 g/min. Feeding data were recorded from both subadult and adult female white rhinos, which weighed between approximately 1000 kg and 1600 kg (estimated weights of subadult and adult female white rhinos respectively; Hillman-Smith et al. 1986). Using Shipley et al.'s (1994) formula, the maximum intake rate predicted for these animals falls between 85 and 119 g/min.

During my study, 10 of the 483 samples of intake rate, (ranging between 120 and 165 g/min), were above the predicted maximum intake rate of 119 g/min, while 98% of intake rate estimates were within a range between 8-120 g/min (N=475). The eight estimates which were higher than 120 g/min gave values of 127, 132, 134, 136, 139, 143, 159 and 165 g/min. It may be possible that white rhinos were able to achieve intake rates greater than the 119 g/min predicted by Shipley et al. (1994), as maximum bite rate for white rhinos is not restricted by the longer pendulum movements of the lower jaw, but by the shorter movements of the lips. However, the 8 estimates that were above 120 g/min could have been the result of compounded measurement error (i.e. estimates of grass height and bulk density). Nevertheless, the possibility remains that maximum intake rate for white rhinos could exceed 120 g/min.

Due to their large size one would expect that white rhinos would have a maximum bite rate somewhat closer to the 25 bites/min recorded for a 350 kg moose (Owen-Smith 2002) and not higher than the 78 bites/min recorded for a 17-20 kg Thomson's Gazelle (Bradbury et al. 1996).

### *Metabolic requirements*

Foose (1982) estimated that the daily energy requirements of adult female white rhinos (approximately 1600 kg) would be met by a daily food intake of 1.5% of body mass from grass hay, with approximately 50% overall digestibility, while the higher metabolic requirements of subadults (approximately 1000 kg) would require a daily food intake of 1.7% of body mass. These estimates of daily food intake would result in subadult and adult female white rhinos having to ingest between 17 and 24 kg of dry matter/day. To achieve this, assuming Foose's (1982) 1.5% and 1.7% estimate of daily food intake, white rhinos feeding at the recorded mean intake rate of 34 g/min would need to feed between 8.5-11.8 hours a day. These estimates of daily feeding time are less than the observations made by Owen-Smith (1988), who reported that, as a year round average, white rhinos foraged for approximately 50% of the 24 hour cycle.

By using Foose's estimates of digestibility I may have underestimated the daily feeding time required for the white rhinos to achieve their daily energy requirements. However, I may have also estimated that white rhinos would be able to achieve their daily energy requirements in less time, as food resources may have been more readily available and possibly of higher quality during my study than during the drought conditions recorded during Owen-Smith's (1974, 1988) study (see Chapter 2).

Bell (1971) indicated that, due to their lower metabolic rate, large herbivores lose condition more slowly on a sub-maintenance diet than smaller herbivores. Selous (1899; as cited in Owen-Smith 1988) and Cave and Allbrook (1958) reported that white rhinos build up relatively large deposits of subcutaneous fat during the wet season. At the extreme end of the body size scale, blue (*Balaenoptera musculus*; Sinclair 1983), humpback (*Megaptera novaeangliae*; Perry et al. 1999) and grey whales (*Eschrichtius robustus*; Taber 1984) survive for several months while in their calving/breeding areas by primarily utilising fat reserves stored while they are in their winter feeding areas. The findings of the study suggest the possibility that white rhinos may not fully compensate for seasonal declines in grass nutrients through the adjustment of dry matter intake, but that they may rely on the mobilisation of stored fat reserves to help maintain nutritional gain.

# REFERENCES

Adamezewski, J.Z. and R.J. Hudson. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest territories: the relative importance of foraging and body reserves. Canadian Journal of Zoology **71**:1221-1229.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American **225**:86-93.

Bergman, C.M., J.M. Fryxell and C.C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of Wood Bison. Functional Ecology **14**:61-69.

Black, J.L. and P.A. Kenney. 1984. Factors affecting diet selection by sheep. II height and density of pasture. Australian Journal of Agricultural Research **35**:565-578.

Bradbury, J.W., S.L. Vehrencamp, K.E. Clifton, and L.M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. Ecology **77**:2237-2255.

Cave, A.J.E. and D.B. Allbrook 1958. Epidermal structures in a rhinoceros Cerototherium simum. Nature **182**:196-197.

Cooper, S.M. and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. Oecologia **68**:446-455.

Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist **125**:641-672.

Distel, R.A.,E.A. Laca, T.C. Griggs, and M.W. Demment. 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. Applied Animal Behaviour Science **45**:11-21.

Dougherty, C.T., N.W. Bradley, P.L. Cornelius and L.M. Lauriault. 1989. Ingestive behaviour of beef cattle offered different forms of lucerene (Medicago sativa L.). Grassland Forge Science **44**:335-342.

Dove, H. 1996. The ruminant, the rumen and the pasture resource: nutrient interactions in the grazing animal. *in* J. Hodgson and A.W. Illius, editors. The ecology and management of grazing systems. CAB international, Oxon, UK.

Downing, B.H. 1972. A plant ecological survey of the Umfolozi Game Reserve, Zululand, Unpublished PhD thesis. University of Natal, Pietermaritzburg, South Africa.

Duncan, P., T.J. Foose, I.J. Gordon, C.G. Gakahu and M. Lloyd. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia **84**:411-418.

Foose, T.J. 1982. Trophic strategies of ruminant vs nonruminant ungulates. Unpublished PhD thesis. University of Chicago, USA.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. American Zoology **14**:205-220.

Gross, J.E., N.T. Hobbs, and B.A. Wunder. 1993. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? OIKOS **68**:75-81.

Hillman-Smith, A.K.K., N. Owen-Smith, J.L. Anderson, A.J. Hall-Martin, and J.P. Selaladi. 1986. Age estimation of the white rhinoceros (Ceratotherium simum). Journal of Zoology, London **210**:355-379.

Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. Proceedings of the Nutrition Society **44**:339-346.

Illius, A. W. and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia **89**:428-434.

Illius, A.W. and I.J. Gordon. 1993. Diet selection in mammalian herbivores: constraints and tactics. Pages 157-181 *in* R.N. Hughes, editor. Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell Scientific Publications, Oxford, UK.

Illius, A.W., P. Duncan, C. Richard and P. Mesochina. 2002. Mechanisms of functional response and resource exploitation in browsing roe deer. Journal of Animal Ecology **71**:723-734.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and cecal digestion. Evolution **30**:757-774.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behavior **48**:215-267.

Laca, E.A., and M.W. Demment. 1991. Herbivory: the delemma of foraging in a spatially heterogeneous food environment. Pages 30-44 *in* R.T. Palo & C.T. Robbins, editors. Plant defences against mammalian herbivory . CRC Press, Boca Raton, Louisiana, USA.

Laca, E.A., E.D. Ungar, N. Seligman, and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science **47**:91-102.

Laca, E.A., E.D. Ungar, and M.W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. Applied Animal Behaviour Science **39**:3-19.

O'Reagain, P.J. and N. Owen-Smith. 1996. Effect of species composition and sward structure on dietary quality in cattle and sheep grazing South African sourveld. Journal of Agricultural Science, Cambridge **127**:261-270.

Owen-Smith, N. 1973. The behavioural ecology of the white rhinoceros. Unpublished PhD thesis, University of Wisconsin, Madison, USA.

Owen-Smith, N. 1988. Megaherbivores. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. 1994. Foraging responces of kudus to seasonal changes in food resources: elasticity in constraints. Ecology **75**:1050-1062.

Owen-Smith, N. 1997. Control of energy balance by a wild ungulate, the kudu (*Tragelaphus strepsiceros*) through adaptive foraging behaviour. Proceedings of the Nutritional Society. **56**:15-24.

Owen-Smith, N. 2002. Adaptive herbivore ecology. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. and P. Novellie. 1982. What should a clever ungulate eat? The American Naturalist **119**:151-178.

Owen-Smith, N. and S. M. Cooper. 1989. Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. Journal of Zoology, London **219**:29-43.

Parker, K.L., M.P. Gillingham, T.A. Hanley and C.T. Robbins. 1993. Seasonal patterns of body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. Canadian Journal of Ecology **71**:1397-1404.

Parker, K.L., M.P. Gillingham, T.A. Hanley and C.T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Ecology **74**:442-450.

Perry, S.L., D.P. DeMaster, and G.K. Silber. 1999. The humpback whale. Marine Fisheries Review **61**:24-74.

Prins, H.H.T. 1996. Ecology and behaviour of the African Buffalo: social inequality and decision making. Chapman Hall, London, UK.

Selous, F.C. 1899. The white or square-lipped rhinoceros. *in* H.A. Bryden, editor. Great and small game of Africa. Rowland Ward, London, UK.

Senft, R.L. 1989. Hierarchical foraging models: effects of stocking and landscape composition on simulated resource use by cattle. Ecological Modelling **46**:283-303.

Shipley, L.A., J.E. Gross, D.E. Spalinger, N.T. Hobbs and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. American Naturalist **143**:1055-1082.

Shrader, A.M. and B. Beauchamp. 2001. A new method for the implantation of radio transmitters into the horns of white and black rhinoceroses. Pachyderm **30**:81-86.

Sinclair, A.R.E. 1983. The function of distance movements in vertebrates. Pages 240-258 *in* I.R. Swingland and P.J. Greenwood, editors. The ecology of animal movement. Oxford Press, Clarendon, UK.

Spalinger, D.E., C.T. Robbins and T.A. Hanley. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. Canadian Journal of Zoology **64**:312-321.

Spalinger, D.E., T.A. Hanley, and C.T. Robbins. 1988. Analysis of the functional response in foraging in the sitka blacked-tailed deer. Ecology **69**:1166-1175.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Stephens, D.W. and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Taber, A.B. 1984. Grey Whale. Pages 216-221 *in* D. Macdonald, editor. The encyclopaedia of mammals:1. George Allen and Unwin, London, UK.

Walker, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegitation. South African Journal of Wildlife Resources **6**:1-32.

Wickstrom, M.L, C.T. Robbins, T.A. Hanley, D.E. Spalinger, and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management **48**:1285-1301.

# FIGURE CAPTIONS

Fig. 1. Monthly rainfall for the western section of the Hluhluwe-Umfolozi Park, measured at the Mubuzane ranger station from October 1998 to October 2000.

Fig. 2. Variation in dry matter intake rate (g/min) relative to percentage dry matter a) CP, b) P, and c) Na contents. Asterisk (*) indicates April 2000 data. (Note that statistical analysis was performed on log transformed data.)

Fig. 3. Monthly changes in a) mean grass greenness and b) mean sward height in relation to mean monthly rainfall.

Fig. 4. Mean monthly variation (±95% CI) of estimated percentage of dry matter a) CP, b) P, and c) Na contents of grass ingested by white rhinos, data for 1999 and 2000 combined in relation to mean monthly rainfall.

Fig. 5. Monthly changes in a) geometric mean bite mass (±95% CI), b) mean bite rate (±95% CI) and c) geometric mean intake rate (±95% CI) obtained by white rhinos in relation to mean monthly rainfall.

Fig. 6. Changes in a) bite mass, b) bite rate and c) intake rate, in relation to sward height categories.

Fig. 7. Regression of bite rate on bite mass obtained by white rhinos in the early and late dry and transitional periods.

Fig. 8. Mean monthly variation (±95% CI) of nutritional intake rate (g/min) of a) CP, b) P, and c) Na relative to dry matter intake.

Table 1. Median bulk density estimates (g/100 $cm^3$) for the upper and lower strata in short, woodland, and Themeda grasslands. Estimates are given as g/100 $cm^3$ to approximate a white rhino's bite dimension. Estimates were derived from grass clippings taken from within areas where rhinos had fed.

| Bulk Density Category | N= | Median (g/100 $cm^3$) | Lower quartile | Upper quartile |
|---|---|---|---|---|
| Short Low | 50 | 0.10 | 0.06 | 0.18 |
| Short Medium | 50 | 0.11 | 0.09 | 0.16 |
| Short High | 30 | 0.15 | 0.11 | 0.20 |
| Wood Low | 50 | 0.06 | 0.05 | 0.10 |
| Wood Medium | 50 | 0.11 | 0.09 | 0.15 |
| Wood High | 40 | 0.15 | 0.12 | 0.21 |
| Wood Upper Low | 40 | 0.06 | 0.03 | 0.09 |
| Wood Upper Medium/High | 70 | 0.11 | 0.08 | 0.14 |
| Themeda Low | 40 | 0.09 | 0.06 | 0.11 |
| Themeda Medium/High | 50 | 0.14 | 0.11 | 0.19 |
| Themeda Upper Low | 20 | 0.04 | 0.03 | 0.05 |
| Themeda Upper Medium | 20 | 0.12 | 0.10 | 0.16 |
| Themeda Upper High | 10 | 0.16 | 0.11 | 0.19 |

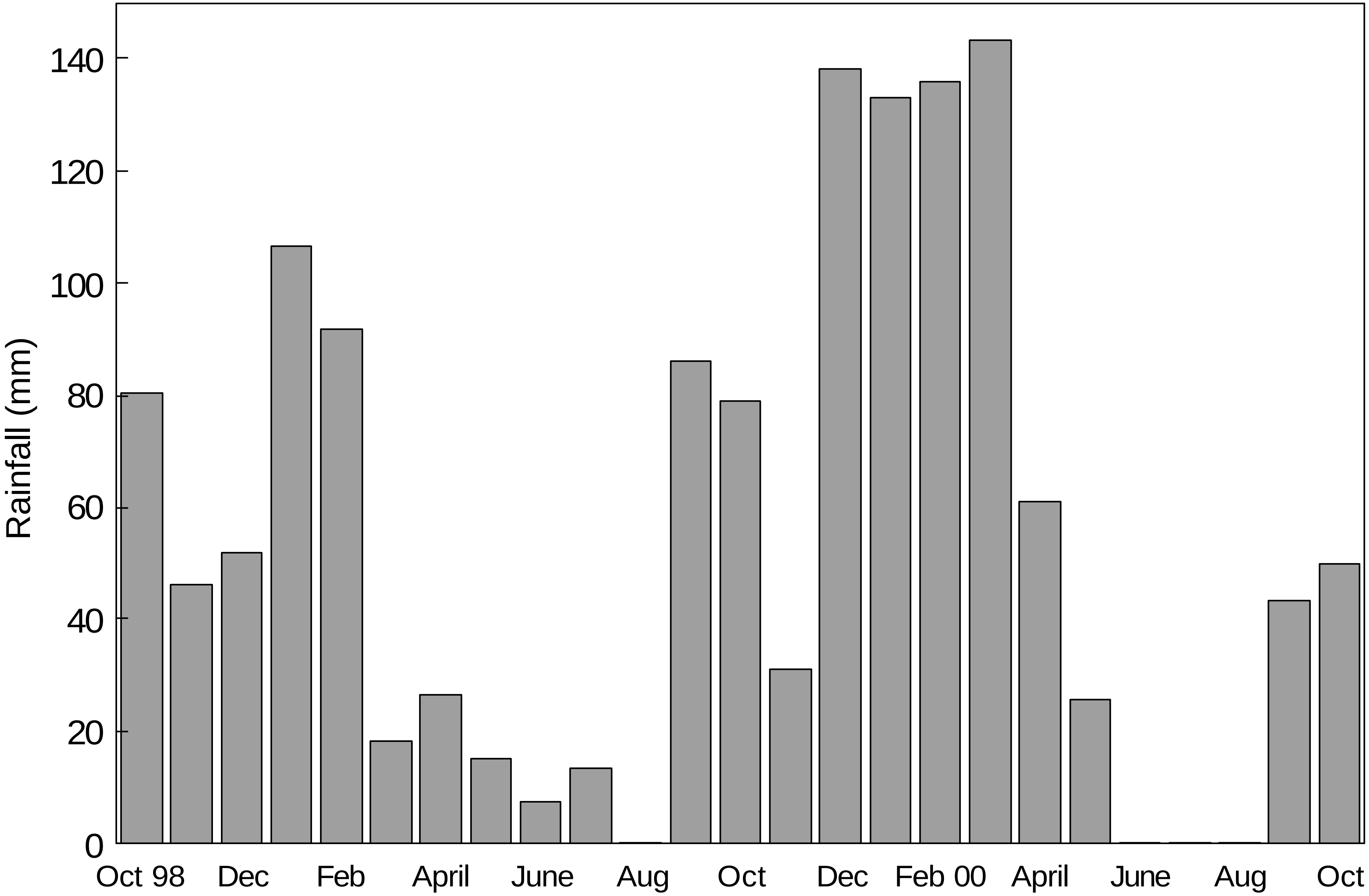
Rainfall (mm)
0
20
40
60
80
100
120
140
Oct 98
Dec
Feb
April
June
Aug
Oct
Dec
Feb 00
April
June
Aug
Oct

Fig. 1.

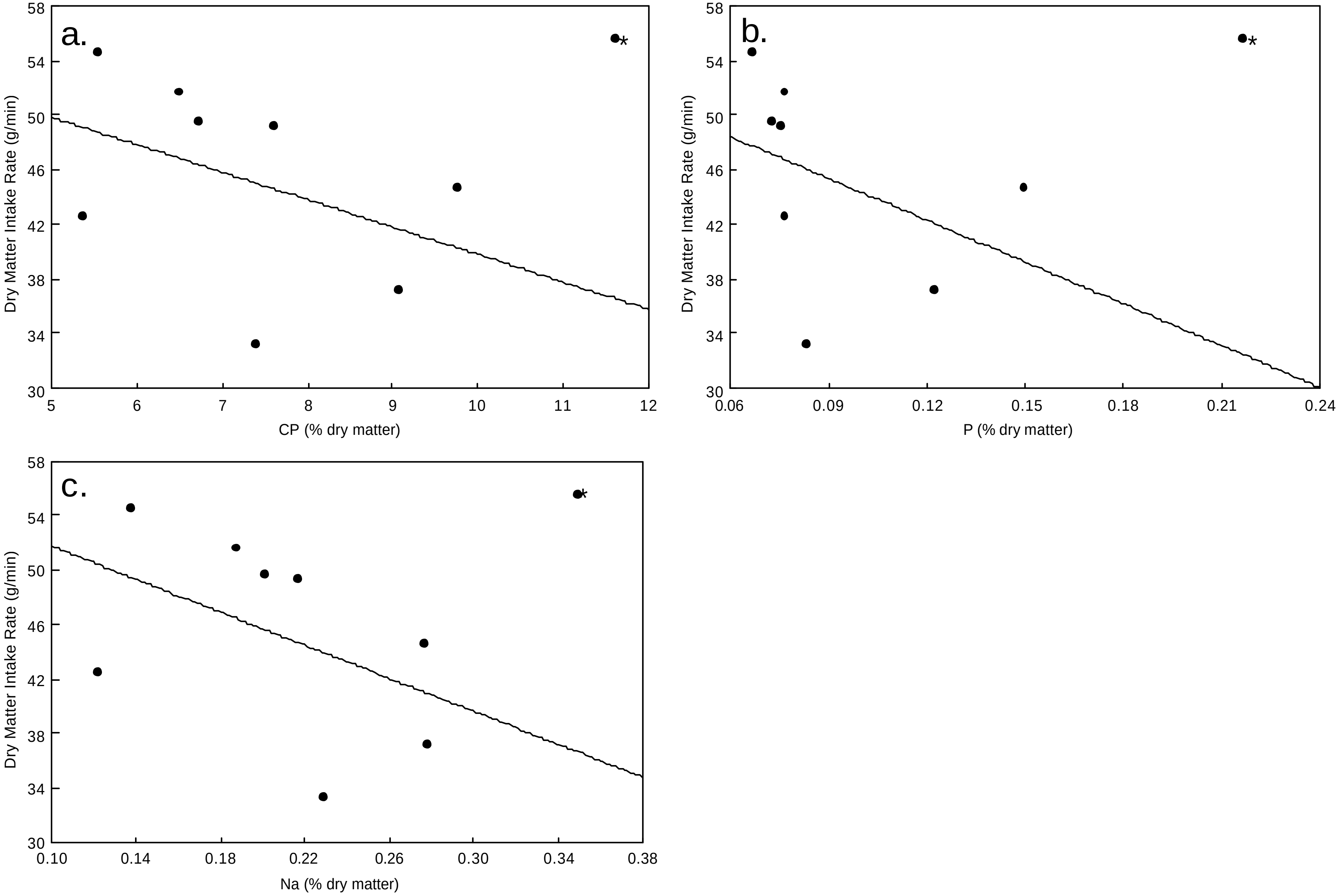
a.
b.
c.
*
Dry Matter Intake Rate (g/min)
58
54
50
46
42
38
34
30
5
6
7
8
9
10
11
12
CP (% dry matter)
0.06
0.09
0.12
0.15
0.18
0.21
0.24
P (% dry matter)
0.10
0.14
0.18
0.22
0.26
0.30
0.34
0.38
Na (% dry matter)

Fig. 2. (a-c).

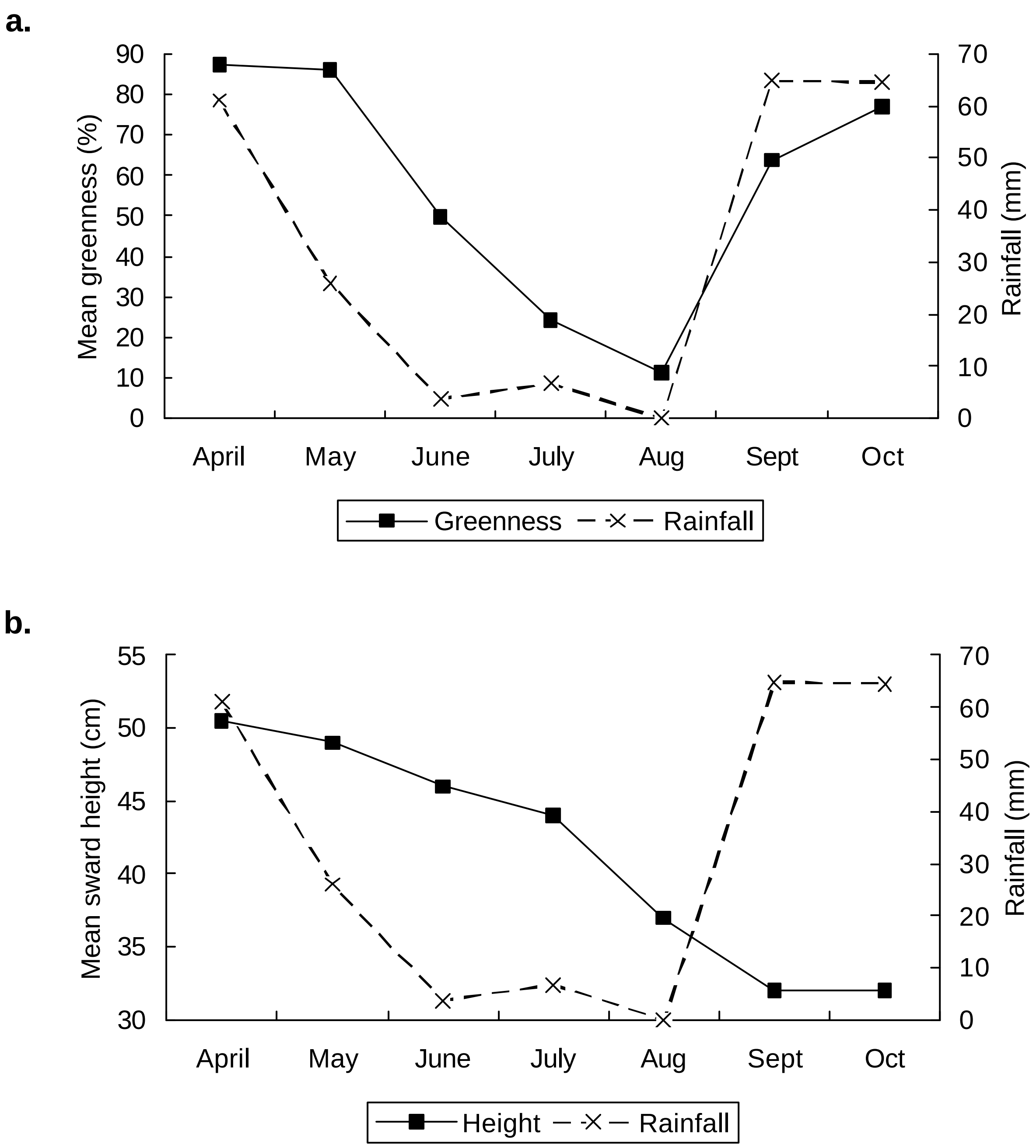
a.
Mean greenness (%)
90
80
70
60
50
40
30
20
10
0
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Greenness
Rainfall
b.
Mean sward height (cm)
55
50
45
40
35
30
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Height
Rainfall

Fig. 3 (a and b).

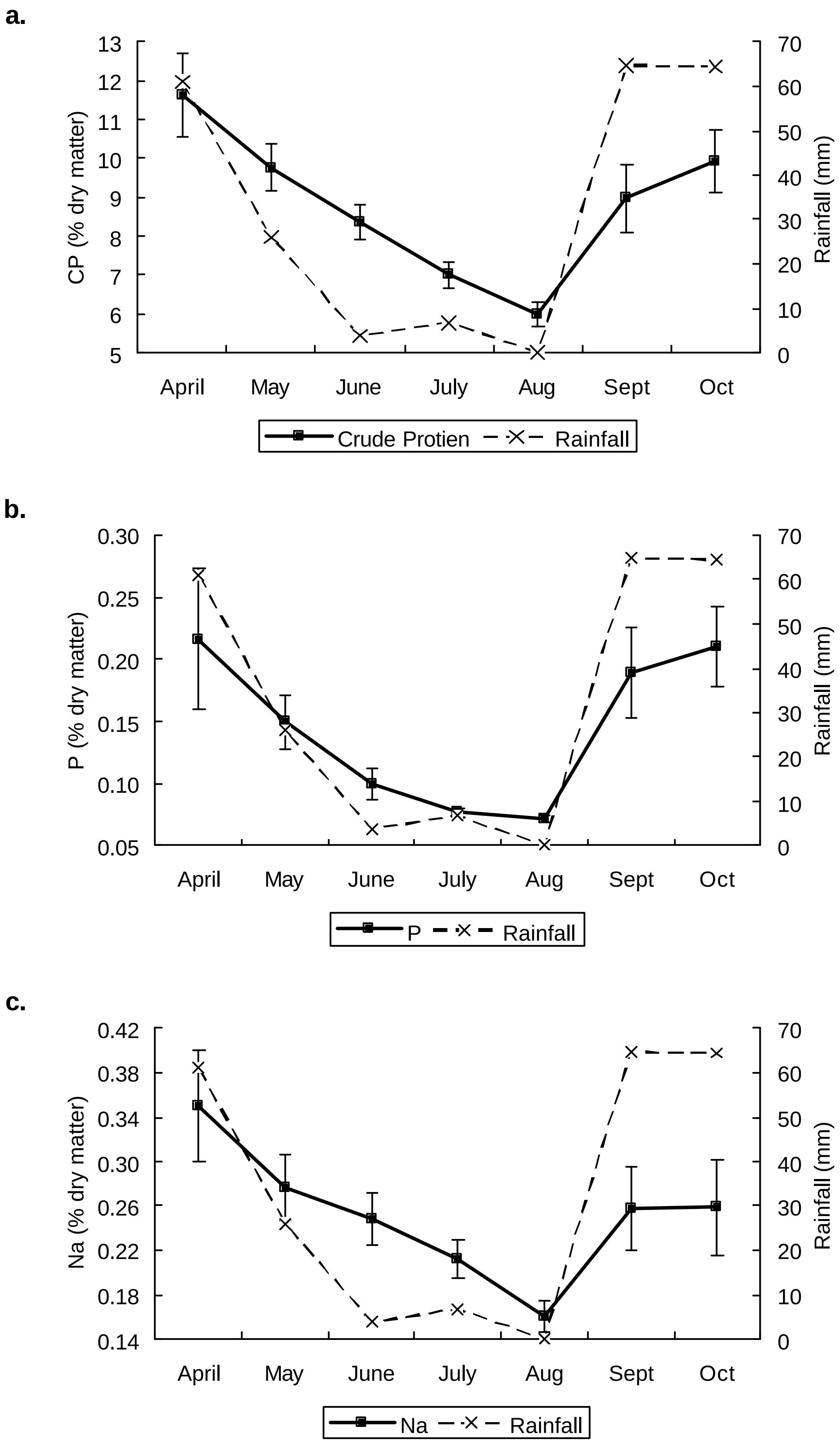
a.
CP (% dry matter)
13
12
11
10
9
8
7
6
5
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Crude Protien
Rainfall
b.
P (% dry matter)
0.30
0.25
0.20
0.15
0.10
0.05
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
P
Rainfall
c.
Na (% dry matter)
0.42
0.38
0.34
0.30
0.26
0.22
0.18
0.14
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Na
Rainfall

Fig. 4 (a-c).

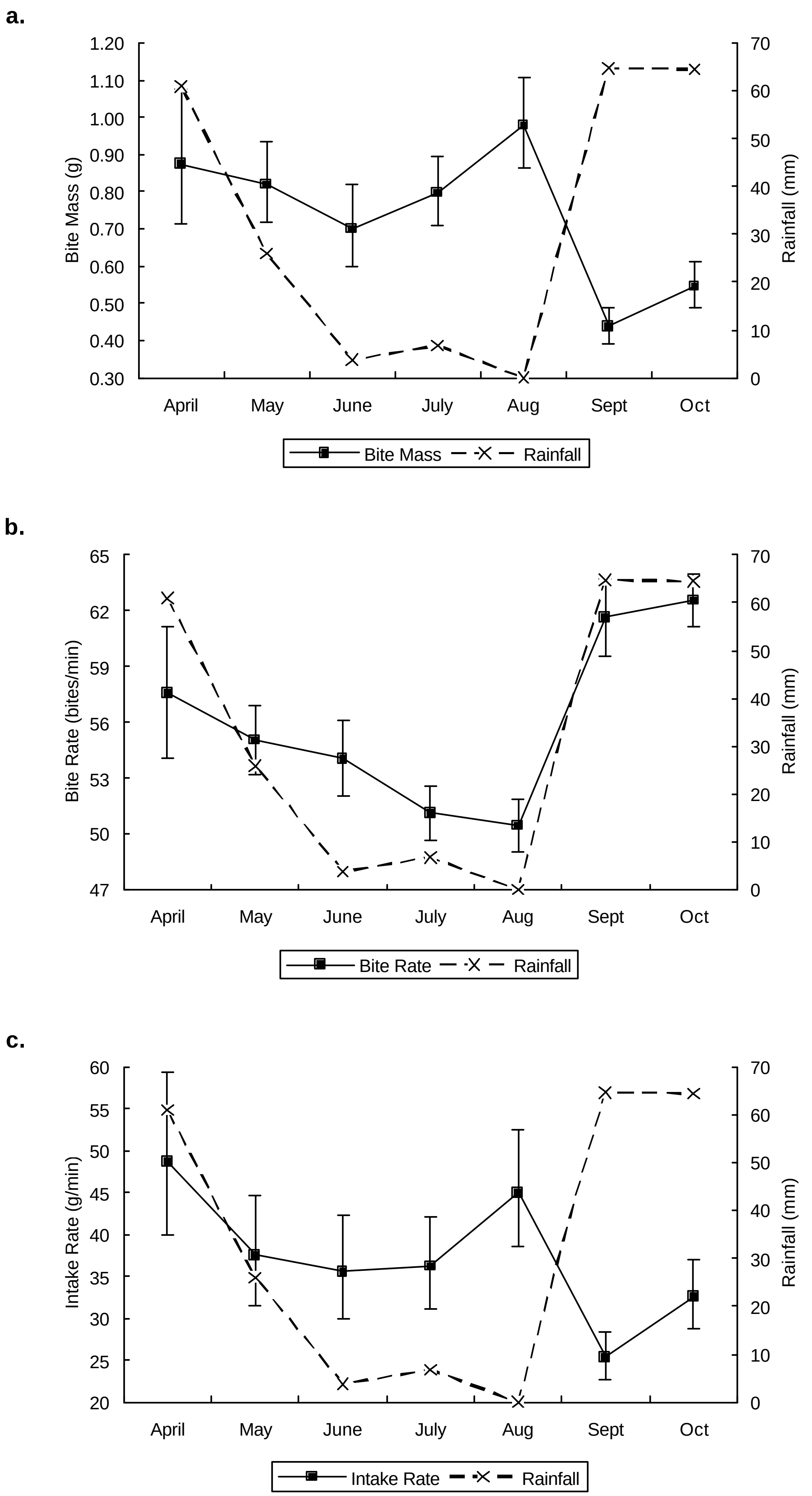
a.
Bite Mass (g)
1.20
1.10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Bite Mass
Rainfall
b.
Bite Rate (bites/min)
65
62
59
56
53
50
47
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Bite Rate
Rainfall
c.
Intake Rate (g/min)
60
55
50
45
40
35
30
25
20
Rainfall (mm)
70
60
50
40
30
20
10
0
April
May
June
July
Aug
Sept
Oct
Intake Rate
Rainfall

Fig. 5 (a-c).

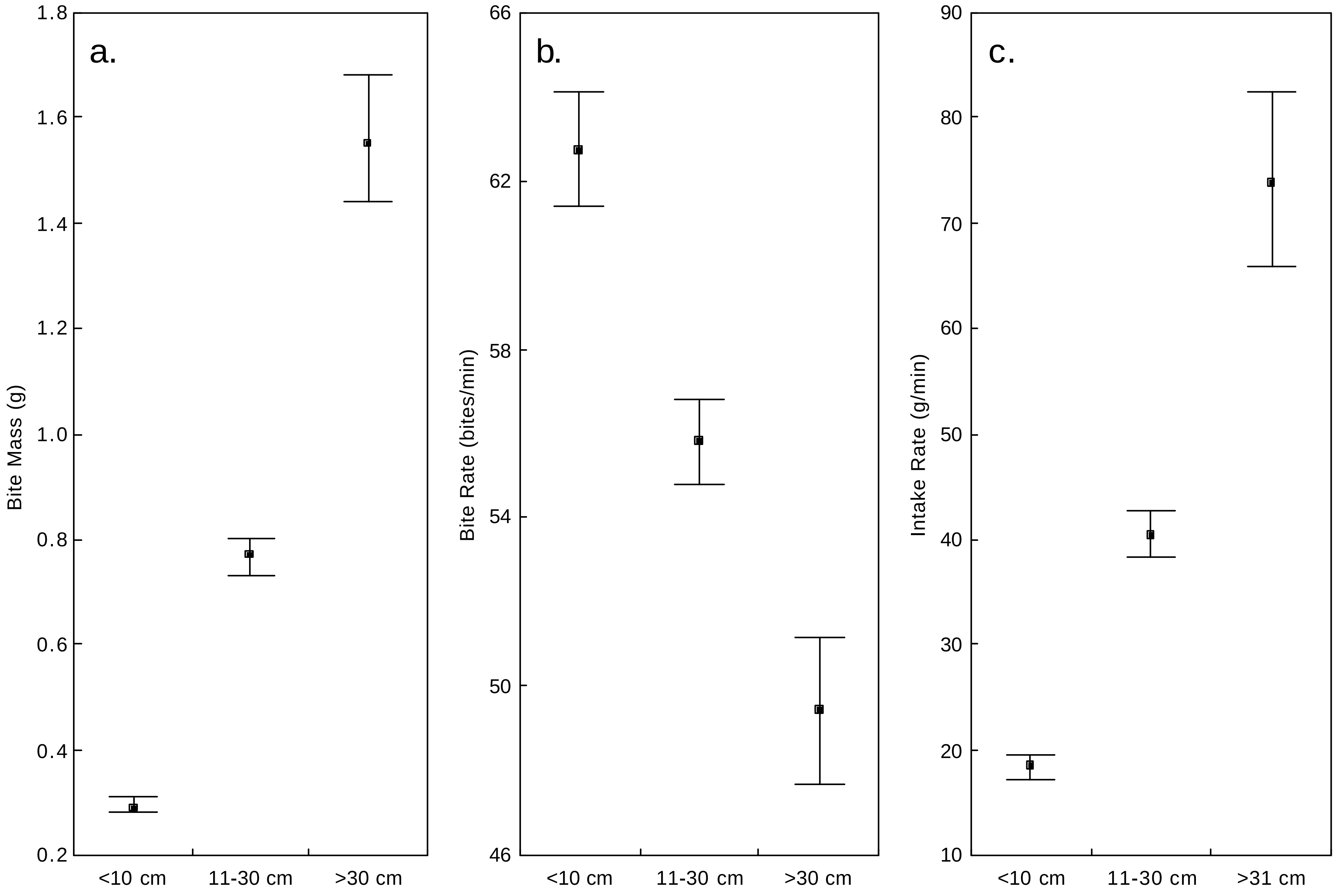
a.
Bite Mass (g)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
<10 cm
11-30 cm
>30 cm
b.
Bite Rate (bites/min)
66
62
58
54
50
46
<10 cm
11-30 cm
>30 cm
c.
Intake Rate (g/min)
90
80
70
60
50
40
30
20
10
<10 cm
11-30 cm
>31 cm

Fig. 6 (a-c).

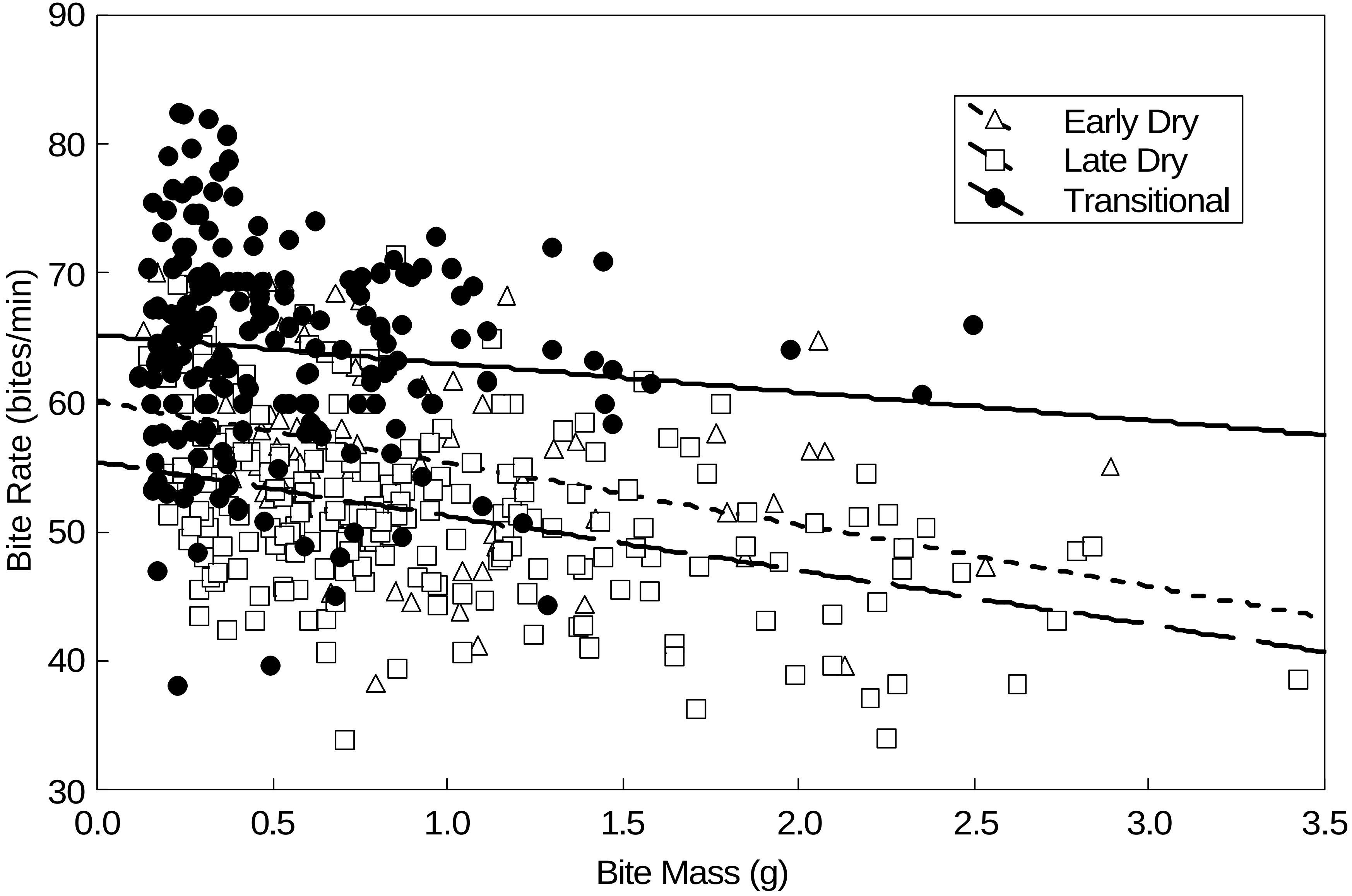
90
80
70
60
50
40
30
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Bite Rate (bites/min)
Bite Mass (g)
Early Dry
Late Dry
Transitional

Fig. 7.

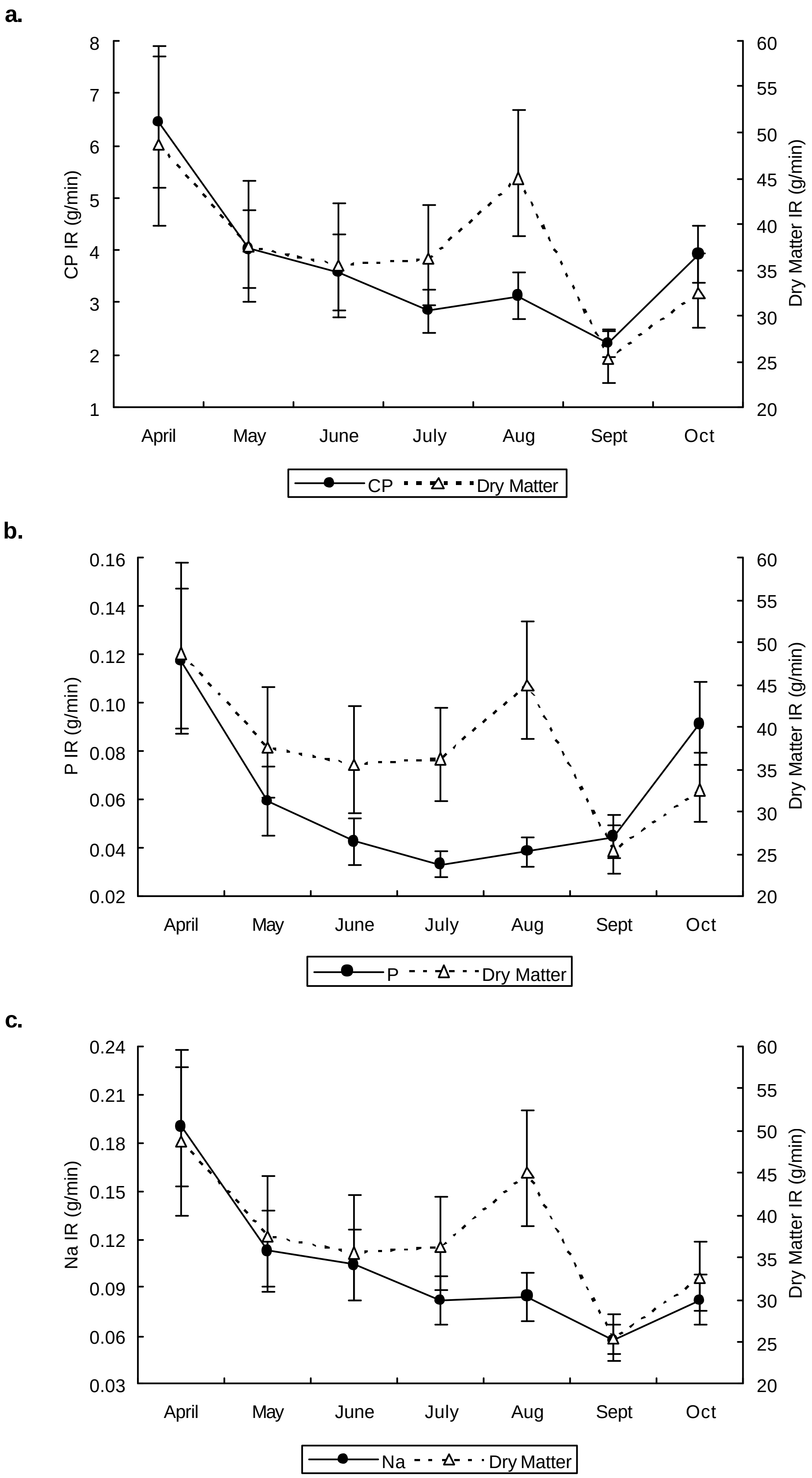
a.
CP IR (g/min)
Dry Matter IR (g/min)
1
2
3
4
5
6
7
8
20
25
30
35
40
45
50
55
60
April
May
June
July
Aug
Sept
Oct
CP
Dry Matter
b.
P IR (g/min)
Dry Matter IR (g/min)
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
20
25
30
35
40
45
50
55
60
April
May
June
July
Aug
Sept
Oct
P
Dry Matter
c.
Na IR (g/min)
Dry Matter IR (g/min)
0.03
0.06
0.09
0.12
0.15
0.18
0.21
0.24
20
25
30
35
40
45
50
55
60
April
May
June
July
Aug
Sept
Oct
Na
Dry Matter

Fig. 8 (a-c).

# CHAPTER 4

# Shrader, A.M. and N. Owen-Smith. 2002. The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). Behavioral Ecology and Sociobiology 52:255-261

(see attached pdf)

Behav Ecol Sociobiol (2002) 52:255–261
DOI 10.1007/s00265-002-0506-y

ORIGINAL ARTICLE

**Adrian M. Shrader · Norman Owen-Smith**

# The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*)

Received: 25 April 2002 / Revised: 27 May 2002 / Accepted: 28 May 2002 / Published online: 28 June 2002

**Abstract** Dispersal is a risky process, both through social pressures and the uncertainty in finding resources. The white rhinoceros is unusual among rhinoceros species in its incipient sociality, manifested through the formation of temporary or more persistent groups involving subadults of both sexes plus adult females without small calves. We describe the probing excursions made by subadult white rhinos out of their established home ranges which were invariably made with a companion. We suggest additional benefits of companionship in such dispersal movements, besides diluting predation risk, via (1) reducing the likelihood of being attacked by territorial males and (2) familiarization with a wider region of the environment, guided by the companion. This "buddy system" may be important in reducing the high costs potentially associated with dispersal.

**Keywords** Associations · Buddy system · Dispersal · Exploratory excursions · White rhinoceros

## Introduction

Dispersal is an important life history trait for most species of mammals and birds (Greenwood 1980; Dobson 1982). For many species, dispersal is conducted through the one-way movement of lone individuals away from natal areas (Holekamp 1986; Woollard and Harris 1990; Beaudette and Keppie 1992). In a few species, however, individuals disperse with conspecifics in groups rather than singularly. Dispersal by groups of individuals has been recorded for some primate species (Enomoto 1974; Cheney and Seyfarth 1977, 1983), lions (*Panthera leo*; Schaller 1972; Hanby and Bygott 1987; Pusey and Packer 1987), bighorn sheep (*Ovis canadensis*; Geist 1967) and suggested for voles (*Microtus*; Hilborn 1975).

Dispersal is potentially a risky process. Animals move from familiar places where forage and water have been available, even if under exploitative pressure, to novel areas where resource locations must be learnt, or where habitat conditions may even be unsuitable for settlement. Many dispersal movements lead only into population sinks, where reproductive performance would be inadequate to sustain a population in the absence of immigration (Pulliam 1988; Pulliam and Danielson 1991; Dias 1996). Conspecifics can play a role in the dispersal of individuals by acting as cues for where dispersers should ultimately settle (Stamps 1987, 1988, 1991, 2001; Smith and Peacock 1990; Reed and Dobson 1993; Dobson and Poole 1998). Through the presence of conspecifics, dispersing individuals can gain evidence that the local habitat is suitable (Stamps 1987).

The white rhinoceros (*Ceratotherium simum*) differs from other species of rhinoceros in its degree of sociality (Owen-Smith 1975, 1988). This is expressed through the occurrence of cohesive pairs or larger groups involving subadults, in addition to adult female-calf pairs. Subadult white rhinos form persistent associations with one or more subadults, of the same or opposite sex, or with an adult female without a small calf (Owen-Smith 1975). While groupings of 2–3 individuals are most common, long-lasting associations among up to six animals have been recorded. Groups including an adult female adopt the home range of this adult female (9–15 km$^2$), but dissolve when this female gives birth and no longer tolerates additional companions. Subadult groups seem to establish temporary home ranges (2–7 km$^2$), being observed in a particular region for a period then disappearing elsewhere. Overall, the subadult period extends from when a calf is chased away by its mother at the time of birth of a new offspring, at an age of 2–3 years, until socio-sexual maturity is attained. For females this occurs at first parturition around 7 years of age, while males be-

Communicated by C. Nunn

A.M. Shrader (✉) · N. Owen-Smith
Centre for African Ecology, School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand,
Private Bag 3, WITS 2050, South Africa
e-mail: adrian@gecko.biol.wits.ac.za
Tel.: +27-11-7176458, Fax: +27-11-4031429

come solitary and settle within a territory (1–2.5 km$^2$), either as a dominant or subordinate, between 10 and 12 years of age.

Rates of dispersal by subadult white rhinos, outwards from the population core towards peripheral regions where conditions were less crowded, were estimated to be 7–10% per subadult per year, during a period when the population was at high density and rainfall generally below-average (Owen-Smith 1981, 1983, 1988). Because subadults of both sexes were involved, such movements seemed to be primarily a response to resource inadequacy, rather than to social pressures (Owen-Smith 1973, 1974). During his study, Owen-Smith (1973) documented only two instances of dispersal. The first involved a 6-year-old female, which made a short movement of 5.5 km before eventually dispersing a further 20 km. The second case involved another 6-year-old female which dispersed approximately 15 km.

Subadult males are potentially subject to territorial aggression from dominant adult males, and even subadult females may sometimes be attacked (Owen-Smith 1975). Adult females occupy extensively overlapping home ranges, with little animosity. Subadult males benefit from being associated in pairs, through diluting or deflecting challenges by the dominant adult males whose territories they occupy or traverse. Solitary subadult males seem more likely to be attacked, and sometimes even killed, than subadults in groups (Owen-Smith 1973).

Current management of the white rhino population in the Hluhluwe-Umfolozi Park in South Africa is based on the source-sink concept, with animals being captured and removed from designated sink areas around the periphery of the fenced protected area (see Owen-Smith 1983, 1988).

In this paper, we present evidence suggesting the benefits of companionship in facilitating dispersal, through familiarizing animals with novel areas beyond the bounds of their established home ranges, prior to eventual emigration. The operation of such a “buddy system” in white rhinos may underlie the widespread success of conservation actions to re-establish this species in areas of its former occurrence through southern and eastern Africa (Owen-Smith 1988), in contrast to the problems experienced with the more solitary black rhinoceros (*Diceros bicornis*; Brett 1998).

## Methods

The study was conducted over 2 years (1999–2000) in the southern Umfolozi section of the 896 km$^2$ Hluhluwe-Umfolozi Park in KwaZulu-Natal, South Africa (28°20′S, 31°51′E). Rainfall was below average during the first year of the study (614 mm), and above average (893 mm) during the second year, relative to the long-term mean of 690 mm. The total white rhino population was approximately 1,600, mostly concentrated in the Umfolozi section.

To enable individuals to be contacted regularly, MOD-125 radio transmitters from Telonics were inserted into the anterior horns of five males and two females (see Shrader and Beauchamp 2001 for procedure). Subadults over 5 years of age, with horns sufficient to accommodate the telemetry equipment, were selected. One individual without a radio observed regularly was also included in the analysis. Observations were restricted to the dry season months (March–October). During 1999, each of the seven radio-equipped individuals were located approximately every 5 days. During 2000, three pre-selected individuals were monitored each month. Two of them were observed over 10 consecutive days, one in the morning and one in the afternoon, while the third was followed throughout the day for 5 consecutive days during the subsequent week. Information routinely recorded on accompanying individuals included sex, age (following Hillman-Smith et al. 1986) and identifying marks, as well as location using a Global Positioning System (GPS) device.

The two radio-equipped females (D and E) both gave birth in early 2000, and so were socially subadult only during 1999. One of the subadult males (B) became mostly solitary and appeared to settle within a home range during 2000.

### Data analysis

Associations were recorded as cohesive if individuals moved together for several hours or longer. Those enduring more than a month were regarded as stable (following Owen-Smith 1975). The minimum duration of each association was estimated from the period between the first and last sightings of the same individuals seen together.

Home ranges were plotted by entering GPS positions from both years into the home range analysis program Calhome (Kie et al. 1996). Data from both years were used as areas utilized by the rhinos remained consistent between years. A maximum of two points per day were plotted, provided these locations were recorded more than 6 h apart. Home range limits were identified from the 85% utilization contour, using the adaptive kernel method with the least squares cross-validation for the smoothing parameter (Worton 1995; Seaman and Powell 1996). This procedure seemed most reliable for establishing the area regularly used, allowing for fairly frequent excursions by subadults. Home ranges delineated using the Adaptive Kernel, Minimum Convex Polygon and Harmonic Mean procedures gave similar estimates of home range extent for the 85% contour, but not when a higher proportion of sightings was included. This was because excursions that lasted longer than a day generated autocorrelated position records, hence exaggerating the home range delineated by the estimation procedure (Swihart and Slade 1985). Where necessary, the home range boundaries indicated by Calhome were adjusted to coincide with a physical barrier (e.g., a major river). GPS locations were plotted using ArcView (Anon 1996). Rhinos located less than 1 km beyond the 85% contour were considered to be using the periphery of their home ranges, while locations greater or equal to 1 km from this contour were interpreted as exploratory excursions.

To test whether subadults were more often accompanied by companions when making excursions, than when within their home range, we used a one tailed Fisher exact test (Zar 1996) to compare the relative frequency of associations (as defined above) with records where animals were seen alone, between these situations.

## Results

Subadult white rhinos were observed in many different associations, most of which were temporary, i.e. lasting less than a month (93%, $n$=180 associations). Grouping patterns closely matched those previously recorded by Owen-Smith (1975). However, each of the two female subadults was mainly associated with an adult female rather than another subadult.

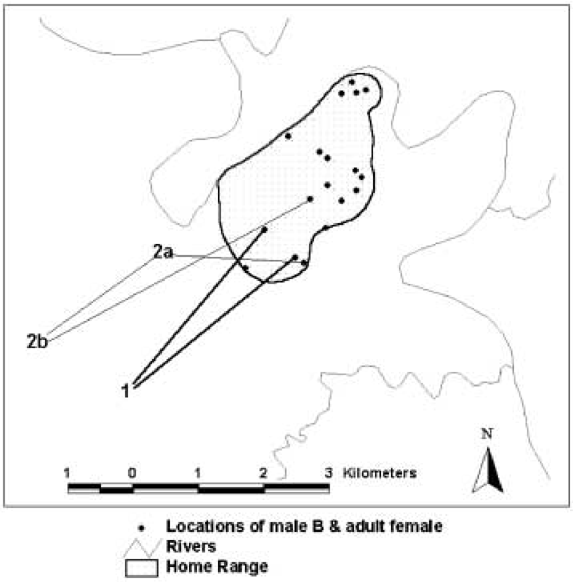

**Fig. 1** Locations of subadult male B, when he had formed a stable association with an adult female. During the association subadult B's movements were restricted to the adult female's home range, except when he followed her as she made two excursions (*1* and *2a–2b*), possibly in search of water. Excursions lasted less than a day and covered approximately 5 km (*1*) and 6 km (*2*) outside of the female's home range

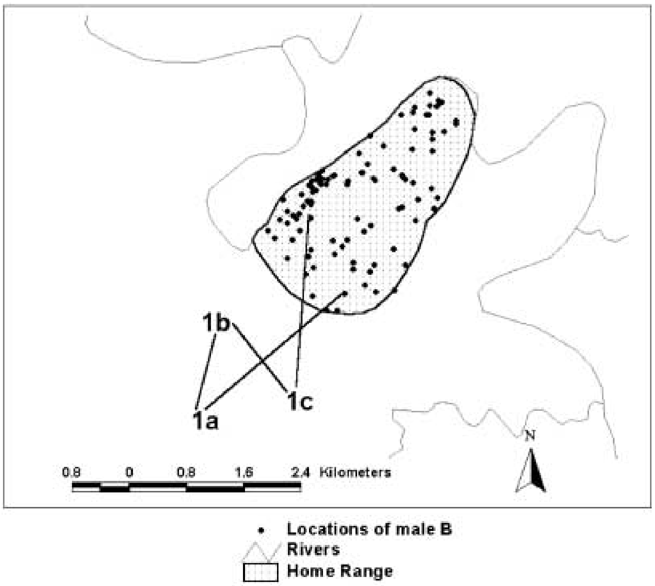

**Fig. 3** Exploratory excursion of subadult male B outside of his home range. Excursion was made with an adult female and her calf with which the subadult had formed a temporary association. The excursion lasted 2 days, covered approximately 7.5 km outside of the subadult B's home range and was into an area familiar to the adult female

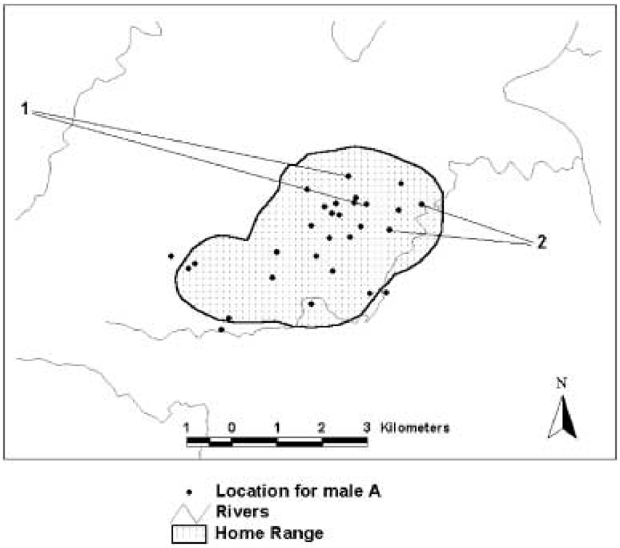

**Fig. 2** Two exploratory excursions of subadult male G out of his home range. Both excursions were made with the same stable subadult companion. Each excursion lasted 1 day and covered approximately 10 km (*1*) and 4 km (*2*) outside of subadult G's home range

Twenty excursions beyond home range limits were recorded (Tables 1, 2 and 3). All eight of the monitored subadults made such excursions. About one-quarter of the excursions were made together with a subadult that had been a stable companion (Table 1), and another quarter with a long-term adult female companion (Table 2). The remaining half of the excursions were made with animals that had been companions for less than a month, in a few cases just briefly for the duration of the excursion (Table 3). Specific examples of some excursions are described below, illustrated by maps.

1. Subadult male B attached himself to an adult female and restricted his movements to her home range. During the 3 months they were associated subadult B accompanied this female on two excursions (1 and 2), each lasting a day and extending about 3 km beyond their shared home range limits (Fig. 1). The first (1) was 2.5 km beyond her home range and occurred 12 days after he had joined this female, and the second (2a–2b) was 50 days later and extended 3 km beyond her home range. During this second excursion, a territorial male accompanied the pair for 2 h, but was not aggressive towards either individual.
2. Subadult male G accompanied another subadult male, which he had been associated with for 12 days, on a single day excursion 5 km beyond his home range (Fig. 2, point 1). These same two subadults then made another 1-day excursion 2 km beyond G's home range, in a different direction, 69 days later (Fig. 2, point 2). No other rhinos were encountered.
3. Subadult male B, previously solitary, joined an adult female with a calf that occupied an overlapping home range. The first day they were associated, he followed this adult female on a 2-day excursion that took him 2.5 km beyond his home range limits (Fig. 3, points 1a–1c). On the second day, a territorial male joined them. On the third day, this trio moved back within

the home range boundary of the subadult, who remained associated with this adult female until the afternoon of the following day.

4. Male subadult C accompanied an older subadult male A, who had been his companion for 33 days, on an excursion taking him 4.5 km beyond his own home range limits (Fig. 4, points 1a–1b). The next day, male C had separated from subadult A and had joined a resident adult female plus calf (Fig. 4, point 1c). That afternoon he was found alone, (Fig. 4, point 1d), and was followed while he moved alone back into his home range.

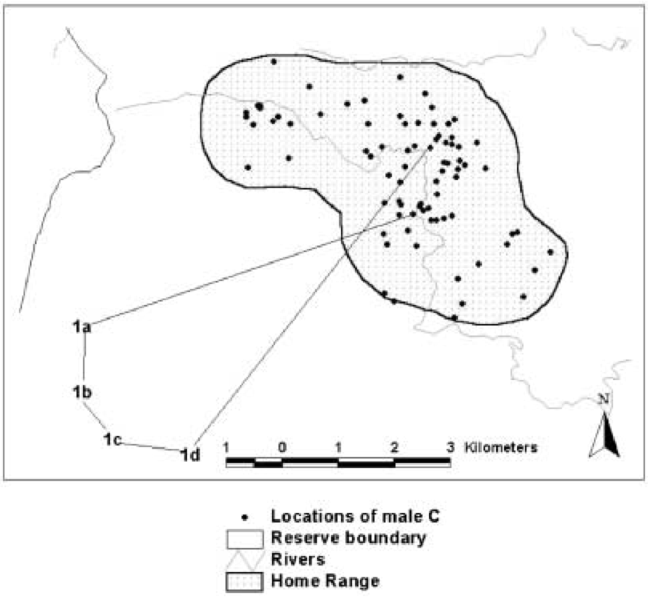

**Fig. 4** Exploratory excursion of subadult male C outside of his home range. Excursion was made with a stable subadult companion. However, subadult C split from the male during the excursion and temporarily joined with an adult cow before returning to his home range. The excursion lasted 2 days and covered 12 km outside of subadult C's home range

Subadults were significantly more likely to be associated with a companion while making an excursion than was found when they were seen within their home range (20 out of 20 cases, compared with 92% of 143 records, $P$=0.013, $n$=163 associations).

Generally, subadults seemed to form associations with individuals inhabiting an overlapping home range. In two instances, two different subadults transferred their attachment from the companion during the initial excursion to another individual while they were out of their home range. When subadults were associated with adult females, they restricted their movements to the adult female's home range. On six occasions, subadults accompanied these adult females while they made long distance excursions, possibly in search of water. On two of these excursions, the adult females moved into areas where they had been observed prior to the excursions. On four occasions, excursions made by subadults out of their home ranges were restricted to the companion's home range or within an area familiar to the companion. However, little information was known about many of the different companions, so we are unsure to what extent the remaining 14 excursions were into areas previously known by the companion.

In some cases, multiple excursions were made by subadults together with a single stable companion. Subadult G made two excursions with the same subadult male (Table 1; Fig. 4), while subadult D made three excur-

**Table 1** Excursions of subadults made with stable subadult companions

| ID | Rhino age (years) | Sex | Companion Age (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max. distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| G | 5–6 | ♂ | 7 ♂ | 12 | 1 | 5.0 | 10.5 |
| G | 5–6 | ♂ | 7 ♂ | 81 | 1 | 2.0 | 4.0 |
| G and H | 5–6 | ♂ | 5–6 ♂ | 17 | 1 | 2.5 | 4.5 |
| C | 7–8 | ♂ | 10 ♂ | 13 | 1 | 1.5 | 2.0 |
| C | 7–8 | ♂ | 9 ♂ | 32 | 2 | 4.5 | 12.0 |

**Table 2** Excursions of subadults made with adult females with which they had formed stable associations

| ID | Rhino age (years) | Sex | Companion Age (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max. distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| D | 6–7 | ♀ | Adult ♀ | 51+ | 2 | 7.0 | 14.0 |
| D | 6–7 | ♀ | Adult ♀ | 114+ | 1 | 2.5 | 4.5 |
| D | 6–7 | ♀ | Adult ♀ | 160+ | 1 | 1.0 | 2.0 |
| B | 7–8 | ♂ | Adult ♀ | 12 | 1 | 2.5 | 5.0 |
| B | 7–8 | ♂ | Adult ♀ | 62 | 1 | 3.0 | 6.0 |
| E | 6–7 | ♀ | Adult ♀ | 69 | 1 | 1.5 | 3.5 |

**Table 3** Excursions of subadults made with adult females plus companions with which they had formed temporary associations

| ID | Rhino age (years) | Sex | Companion Ages (years) and sex | Duration of association prior to excursion (days) | Duration of excursion (days) | Max distance from home range (km) | Total distance of excursion (km) |
|---|---|---|---|---|---|---|---|
| F | 6–7 | ♂ | Adult ♀, 3 ♀, 6 ♂, 6 ♂, 3 ♂ | 4 | 2 | 1.5 | 3.0 |
| F | 6–7 | ♂ | Adult ♀, 6 ♂ | 2 | 3 | 1.5 | 5.0 |
| B | 7–8 | ♂ | Adult ♀, 1? | 2 | 1 | 1.5 | 3.0 |
| B | 7–8 | ♂ | Adult ♀, 1 ♀ | ? | 3 | 6.0 | 14.0 |
| B | 7–8 | ♂ | Adult ♀ / <1 ♀ | 0 | 2 | 2.5 | 7.5 |
| B | 7–8 | ♂ | 3 ♀ | ? | 1 | 2.0 | 4.0 |
| C | 7–8 | ♂ | Adult ♀, 3 ♂ | 0 | 1 | 4.0 | 7.5 |
| C | 7–8 | ♂ | 10 ♂ | 21 | 1 | 2.0 | 4.0 |
| C | 7–8 | ♂ | 4 ♀ | ? | 1 | 4.0 | 8.0 |

sions with an adult female (Table 2) and subadult 20 made two excursions with the same adult female (Table 2).

All subadults observed eventually returned to their own home ranges following excursions, either together with the companion or alone. No subadults were observed making solo excursions, and no long-term shifts in home range were documented during the study period.

## Discussion

The basic benefit of group formation by ungulates is generally recognized to be a reduction in the risk of predation (Jarman 1974; Bertram 1978). While predation on white rhinos by lions and other carnivores appeared to be negligible in the study area, this fundamental benefit of companionship cannot be excluded. Owen-Smith (1988) noted how groups of subadults commonly adopted a rump-against-rump defensive formation when disturbed, which, although maladaptive against humans, could offer some protection in the event of a predator attack. White rhinos are probably big enough to be able to ward off attacks by lions alone when they approach full adult size.

A second potential benefit of companionship is to reduce the chance of being attacked, and hence injured, by territory holders. Territorial males have been recorded violently attacking, chasing and in even a few instances killing subadults that were intruding into their territories (Owen-Smith 1975). Owen-Smith (1974) reports an instance where a solitary subadult male (aged 11–12 years) was challenged tensely for 32 min by a territorial male. However, another territorial male had confronted this same subadult only briefly 5 months earlier, when the latter had a subadult male companion. This social security from group formation would apply primarily to males, although subadult females are occasionally attacked (Owen-Smith 1975).

During the present study, groups of subadults were challenged only briefly, or ignored completely, by territory holders, except in two cases. In the first case, two subadult males were chased from where they were sleeping by a territorial male. The male chased the two subadults for a few minutes, then left them and lay down. The following day the subadults were found outside of the adult male's territory. In the second case, a territorial male was courting an adult female when two subadult males approached. The subadults were accosted and chased by the territorial male for about 50 m. Solitary subadults were rarely encountered, and never observed interacting with territory holders.

A third potential advantage is familiarization with new areas (Owen-Smith 1973). Through joining other conspecifics, animals may be led through novel regions of the environment, and more specifically towards the locations of the food and water resources that these areas contain (Stamps 1987; Johnson 1989). This "public information" (Valone 1989) may enable less experienced animals to evade temporary resource shortfalls, and ultimately guide them towards less crowded habitat into which they may disperse. Geist (1967) suggested that a similar process operates among bighorn sheep (*Ovis canadensis*), whereby young males are led towards wintering areas, salt licks, rutting grounds, summer ranges and migratory routes by following older males. Exploratory trips prior to dispersal have been recorded for other species of mammals (Lidicker 1976; Holekamp and Sherman 1989; Johnson 1989; Woollard and Harris 1990; Lidicker and Stenseth 1992; Larsen and Boutin 1994; Künkele and von Holst 1996). However, in all of these cases individuals moved alone.

The benefit of experience, passed on from older to younger animals, has been widely recognized for elephants (Laws 1969; Geist 1971; McKay 1973). However, elephants move in enduring family groups based on mother-daughter associations (Owen-Smith 1988). Dispersal involving shifts in home ranges by such groups is evident from the history of elephant recolonization of South Africa's Kruger National Park (Owen-Smith 1983). White rhinos, although comparably long-lived, lack persistent mother-daughter bonds. Nevertheless, through forming transient bonds with various other individuals, young white rhinos may gain some benefit from the wider experience of older individuals. This was evident as in approximately a quarter of the excursions subadults moved with rhinos that were familiar with the new area. In particular, subadult white rhinos seemed to form attachments preferentially with adult females, although such opportunities are restricted by the intolerance of adult females with young calves for additional companions (Owen-Smith 1973).

In contrast to white rhinos, black rhinoceroses are typically solitary, with social groups rarely extending beyond adult female-calf pairs (Goddard 1967). Subadults do occasionally form temporary associations with adult females and other subadults (Hamilton and King 1969; Adcock et al. 1998), but such opportunities are limited by the much lower densities attained by black rhino populations, relative to white rhinos. High rates of mortality among black rhinos translocated into new reserves have posed a conservation problem (Hitchins 1984; Adcock et al. 1998; Brett 1998). Deaths have been ascribed largely to fighting, but include females as well as males. The additional role potentially played by nutritional stress among animals introduced into unfamiliar areas has perhaps not received adequate recognition.

We suggest that the “buddy system”, exemplified by shifting temporary associations among subadult white rhinos, and between subadults and some adult females, could be of great importance in ameliorating the costs of dispersal into unfamiliar habitat. Although we did not observe actual dispersal, in terms of settlement within a new home range, we were able to document some of the probing excursions beyond established home ranges, in detail. In all observed cases, these movements were conducted together with one or more companions, either a long-standing subadult or adult female associate or an adult female sharing an overlapping home range. Thereby young white rhinos are able to explore an area much larger than the home range they usually occupy, under the guidance of another individual which potentially is familiar with the locations of resources in the novel area. This experience may guide them when ultimately they embark on the large scale dispersal movements documented by Owen-Smith (1988).

**Acknowledgements** We thank Kwa-Zulu Natal Wildlife for permission to undertake the study. Mark Cooke and the Game Capture Unit team undertook and covered the costs of the rhino capture operation. Peter Hartley (Conservator Umfolozi), Paul Havemann (Section Ranger Mbuzane) and Dave Balfour (Regional Ecologist Northern Zululand) provided much appreciated logistical support. Charlie Nunn and the three anonymous reviewers provided constructive comments on this paper. Experimental procedure was consistent with the University of the Witwatersrand and South African animal ethic protocols and was given clearance certificate number 99 32 5.

## References

Adcock K, Hansen HB, Lindemann H (1998) Lessons from the introduced black rhino population in Pilanesberg National Park. Pachyderm 26:40–51

Anon (1996) Using ArcView GIS. Environmental Systems Research Institute, Redlands, Calif.

Beaudette PD, Keppie DM (1992) Survival of dispersing spruce grouse. Can J Zool 70:693–697

Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 1st edn. Blackwell, Oxford, pp 122–147

Brett R (1998) Mortality factors and breeding performance of translocated black rhinos in Kenya: 1984–1995. Pachyderm 26:69–82

Cheney DL, Seyfarth RM (1977) Behaviour of adult and immature male baboons during inter-group encounters. Nature 269:404–406

Cheney DL, Seyfarth RM (1983) Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. Am Nat 122:392–412

Dias PC (1996) Sources and sinks in population biology. Trends Evol Ecol 11:326–330

Dobson A, Poole J (1998) Conspecific aggregation and conservation biology. In: Caro T (ed) Behavioral ecology and conservation biology Oxford University Press, Oxford, pp 193–208

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Enomoto T (1974) The sexual behavior of Japanese monkeys. J Hum Evol 3:351–372

Geist V (1967) A consequence of togetherness. Nat Hist 76:24–30

Geist V (1971) Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago

Goddard J (1967) Home range, behaviour, and recruitment rates of two black rhinoceros populations. E Afr Wildl J 5:133–150

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hamilton PH, King JM (1969) The fate of black rhinoceroses released in Nairobi National Park. E Afr Wildl J 7:73–83

Hanby JP, Bygott JD (1987) Emigration of subadult lions. Anim Behav 35:161–169

Hilborn R (1975) Similarities in dispersal tendency among siblings in four species of voles (Microtus). Ecology 56:1221–1225

Hillman-Smith AKK, Owen-Smith N, Anderson JL, Hall-Martin AJ, Selaladi JP (1986) Age estimation of the white rhinoceros (*Ceratotherium simum*). J Zool 210:355–379

Hitchins PM (1984) Translocation of black rhinoceros (*Diceros bicornis minor*) from the Natal game reserves 1962–1983. Lammergeyer 33:45–48

Holekamp KE (1986) Proximal causes of natal dispersal in Belding’s ground squirrels (*Spermophilus beldingi*). Ecol Monogr 56:365–391

Holekamp KE, Sherman PW (1989) Why male ground squirrels disperse. Am Sci 77:232–239

Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48:215–267

Johnson ML (1989) Exploratory behavior and dispersal: a graphical model. Can J Zool 67:2325–2328

Kie JG, Baldwin JA, Evans CJ (1996) CALHOME: a home range analysis program. Wildl Soc Bull 24:342–344

Künkele J, von Holst D (1996) Natal dispersal in the European wild rabbit. Anim Behav 51:1047–1059

Larsen KW, Boutin S (1994) Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:214–223

Laws RM (1969) The Tsavo research project. J Reprod Fert Suppl 6:495–531

Lidicker WZ (1976) Social behaviour and density regulation in house mice living in large enclosures. J Anim Ecol 45:677–697

Lidicker WZ, Stenseth NC (1992) To disperse or not to disperse: who does it and why? In: Stenseth NC, Lidicker WZ (eds) Animal dispersal: small mammals as a model. Chapman and Hall, London, pp 21–36

McKay GM (1973) Behavior and ecology of the Asiatic elephant in southeastern Ceylon. Smithsonian Contrib Zool 125

Owen-Smith N (1973) The behavioural ecology of the white rhinoceros. PhD dissertation, University of Wisconsin, Madison

Owen-Smith N (1974) The social system of the white rhinoceros. In: Geist V, Walther FR (eds) The behaviour of ungulates and its relation to management. IUCN, Morges, pp 341–351

Owen-Smith N (1975) The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). Z Tierpsychol 38:337–384

Owen-Smith N (1981) The white rhino overpopulation problem and a proposed solution. In: Jewell PA, Holt S, Hart D (eds) Problems in management of locally abundant wild mammals. Academic Press, New York, pp 129–150

Owen-Smith N (1983) Dispersal and the dynamics of large herbivores in enclosed areas: implications for management. In: Owen-Smith N (ed) Management of large mammals in African conservation areas. Haum Educational, Pretoria, pp 127–143

Owen-Smith N (1988) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Pulliam HR, Danielson BJ (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am Nat 137:S50-S66

Pusey AE, Packer C (1987) The evolution of sex-biased dispersal in lions. Behaviour 101:275–310

Reed JM, Dobson AP (1993) Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends Evol Ecol 8:253–256

Schaller GB (1972) The Serengeti lion. University of Chicago Press, Chicago

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085

Shrader AM, Beauchamp B, (2001) A new method for the implantation of radio transmitters into the horns of white and black rhinoceroses. Pachyderm 30:81–86

Smith AT, Peacock MM (1990) Conspecific attraction and the determination of metapopulation colonization rates. Conserv Biol 4:320–323

Stamps JA (1987) Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. Am Nat 129:629–642

Stamps JA (1988) Conspecific attraction and aggregation in territorial species. Am Nat 131:329–347

Stamps JA (1991) The effect of conspecifics on habitat selection in territorial species. Behav Ecol Sociobiol 28:29–36

Stamps JA (2001) Habitat selection by dispersers: integrating proximate and ultimate approaches. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal. Oxford University Press, Oxford, pp 230–242

Swihart RK, Slade NA (1985) Influence of sampling interval on estimates of home-range size. J Wildl Manage 49:1019–1025

Valone TJ (1989) Group foraging, public information, and patch estimation. Oikos 56:357–363

Woollard T, Harris S (1990) A behavioural comparison of dispersing and non-dispersing foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypotheses. J Anim Ecol 59:709–722

Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. J Wildl Manage 59:794–800

Zar JH (1996) Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.

## CHAPTER 5

# Conclusion and recommendations

The broad aim, established at the beginning of the study, was to determine how food resources influenced the movements of white rhinos and hence potentially their dispersal. The objectives that I set out to achieve were to determine; 1) how declines in the quality and availability of food over the dry season influenced the use of different grassland types by white rhinos, 2) how the selection of grass swards within the different grassland types influenced the intake rate and nutritional gain of white rhinos, and 3) how resource conditions influenced large scale movements of white rhinos and possibly dispersal.

Due to the relatively high availability of food resources throughout the study period, I was unable to determine how food resources influenced the movements of white rhinos between grassland types. During Owen-Smith's (1973) study, when rainfall was generally low and population density high, white rhinos transferred their feeding among short, woodland, accessible Themeda and Themeda grasslands on hillslopes as the availability of food resources declined over the seasonal cycle. In the present study, however, with a higher relative availability of food resources, white rhinos did not shift between the different grassland types to the same extent as recorded by Owen-Smith (1973, 1988), but continued to utilise short, woodland and Themeda grasslands throughout the study period. Results from these two studies thus suggest that white rhinos adapt to seasonal variation in food availability through changes in the utilisation of different grassland types. Results from the present study suggest that during periods of high food availability white rhinos primarily utilise preferred grassland types (i.e. short, woodland and Themeda grasslands). However, during periods of low food availability, like during Owen-Smith's study, white rhinos adjust their utilisation of grassland types so as to include less preferred grassland types (i.e. Themeda grasslands on hillslopes), which may help sustain them through the dry season or possibly help prevent starvation during critical periods.

In response to a reduction in the availability of food resources during the dry season, large herbivores may 1) widen their diet breadth (Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Owen-Smith and Cooper 1989, Owen-Smith 1994), 2) increase their daily foraging time, and possibly the proportion of foraging time spent feeding (Owen-Smith and Cooper 1989, Owen-Smith 1997, Prins 1996), or perhaps 3) maintain their intake rate by increasing bite size (Spalinger et al 1988, Laca et al. 1994). Despite the reduction in the quality and availability of food during the dry season, it is possible that white rhinos could have made these adjustments to help compensate for nutritional declines, but results suggest that they did not. However, as daily activity patterns of the white rhinos were not recorded during the study period, the extent to which white rhinos compensated for declines in nutritional intake, by increasing daily foraging time, is unknown.

The selection of food resources is influenced by a herbivore’s body size and digestive system. In chapter 2, the main objective was to determine how the diet selection of white rhinos, a relatively unselective mega-grazer (i.e. body mass exceeding 1000 kg), would change during a period of resource limitation. Based on foraging theory, the predictions of body size theory (Bell 1971, Jarman 1974), and the results of a previous study (Melton 1987), I hypothesised that 1) white rhinos would select for grassland types and very little for specific grass species within grassland types, 2) as the dry season progressed, white rhinos would increase their utilisation of Themeda grasslands, while decreasing their use of short grasslands, and 3) early in the dry season, white rhinos would select for intermediate height swards of green grass, but that, as the dry season progressed white rhinos would shift and utilise taller swards of brown grass.

Results indicated that white rhinos preferred certain grassland types throughout the study period. However, white rhinos utilised the grassland types in a pattern that differed from the pattern observed previously by Owen-Smith (1973, 1988). The findings of chapter 2 make two original contributions to science.

1. Results of the study established that, despite their large body size and thus ability to utilise a wide range of vegetation components and grassland types, white rhinos were relatively selective feeders at the grassland type spatial scale. However, the suggestion that white rhinos were relatively unselective with regard to grass species was not entirely convincing. Some findings suggested that white rhinos also selected for grass species within the different grassland types throughout the study period. However, the extent to which these findings reflected the selection of specific grass species or possibly the selection of the different grassland types is unknown.

2. The white rhinos' selection of grass swards was some what at odds with Fryxell's (1991) suggestion that the effects of sward maturation (i.e. height, greenness, fibre content and biomass) will have a greater effect on the food selection of ruminants than non-ruminants. Fryxell (1991) suggested that ruminants should show a greater selection of swards of intermediate height and greenness than non-ruminants, as daily intake is often more constrained by the digestion and passage of fibrous food through the rumen than through the hind-gut of non-ruminants (Bell 1971, Janis 1976, Foose 1982). Despite being non-ruminants of very large body size, and thus having a higher tolerance of lower quality forage (Bell 1971, Jarman 1974),

white rhinos where similar to smaller ruminants in that they generally favoured short to intermediate height swards of green grass throughout the study period.

Few studies have investigated foraging of large herbivores under free-ranging field conditions (Owen-Smith and Cooper 1989, Wallis de Vries and Daleboudt 1994, Fortin et al. 2002). In chapter 3, to determine how a very large bodied non-ruminant, the white rhino, coped with seasonal declines in food resources, I focused on the trade-offs made between dry matter intake rate (i.e. diet quantity) and the intake rate of specific nutrients (i.e. diet quality). The findings of chapter 3 make three original contributions to science.

1. Under field conditions, results indicated that bite rates achieved for the same bite mass differed between the three seasonal periods. Spalinger and Hobbs (1992) suggested that large bites retard bite rate through mechanical constraints, as larger bites require longer chewing times than smaller ones. Results, however, suggest that seasonal factors may have a greater influence on bite rate than bite mass. White rhinos obtained faster bite rates relative to bite mass on the new growth available during the transitional period than on the more mature grass available in either the early dry or late dry season periods. Seasonal differences in bite rate may have been due to differences in fibre content of grass. Data collection, however, did not extend to measuring fibre content, thus I was unable to determine the extent to which differences in fibre content influenced seasonal differences in bite rate.

2. Results indicate that the maximum intake rate of white rhinos (i.e. 120 g/min) was at the upper end of the theoretical maximum for 1000kg to 1600 kg white rhinos (85 g/min to 119 g/min) using Shipley et al.’s (1994) formula. As white rhinos use their lips to crop grass (Owen-Smith 1975), it is likely that a faster bite rate may be achieved, as constraints on maximum intake rate will be dependent on the shorter

pendulum movements of a rhino’s lips and not the longer pendulum movements of the lower jaw, as predicted by Shipley et al. (1994).

3. Results suggest that, despite increasing bite mass and dry matter intake rate at the end of the dry season, white rhinos did not compensate for declines in nutrient intake rates. It is possible that, as white rhinos build up relatively large deposits of subcutaneous fat during the wet season (Selous 1899), they may have mobilised these fat reserves to sustain them through the dry season. This raises the possibility that white rhinos may follow a strategy similar to large marine mammals, which survive for several months in their calving/breeding areas by utilising fat reserves stored from when they were in their winter feeding areas (Sinclair 1983, Taber 1984, Perry et al. 1999). The utilisation of fat reserves is also prevalent in northern hemisphere ungulates, which mobilise fat reserves for survival during winter when they have to contend with extreme reductions in food resources and possibly snow (Parker et al. 1993, 1996).

A novel discovery of the study in chapter 4 was that the large-scale movements, and possibly dispersal of white rhinos, may be facilitated by subadults following companions (or ‘buddies’) into new areas. For white rhinos, dispersal does not happen on an annual basis, or at specific times of the year (Owen-Smith 1973). Unfortunately, during the study period, none of the subadults monitored dispersed. However, by focusing on a few individuals and monitoring them frequently, I was able to determine that social interactions, and not changes in food resources, seem to be the main factor that may facilitate the dispersal of white rhinos. Through moving with conspecifics, subadults may be able to reduce the high costs potentially associated with large-scale movements, and possibly dispersal. By moving with companions (or ‘buddies’) white rhinos may benefit by 1) reducing the likelihood of being attacked by territorial males, and 2) familiarisation with a wider region of the environment, guided by a companion.

## FUTURE RESEARCH

### *Buddy system dispersal*

Findings of the present study indicate that subadults, through the formation of associations with conspecifics, make exploratory excursions that may lead to dispersal. However, I suggest the possibility that this ‘buddy system’ may not only be limited to exploratory excursions from temporary home ranges by older subadults, but may also be the mechanism by which younger subadults move from their mother’s home range to where they establish temporary home ranges. Based on observations made during the present study, I propose the following conceptual model for the dispersal process.

For white rhinos, dispersal seems to start at about 2-3 years of age, when calves are chased away from their mothers. After being chased away, calves are considered to be subadults (Owen-Smith 1975). New subadults will move alone within their mother’s home range until they form a temporary association with one or more individuals (i.e. either subadults of both sexes or an adult female lacking a young calf), living in an over-lapping home range (Owen-Smith 1975). Both Owen-Smith (1975) and Shrader and Owen-Smith (2002), found that during associations with adult females, subadults adopted the home range of the adult female, and thus restricted their movements to within her home range. It is possible, however, that subadults may adopt the home ranges of all companions with which they form associations (i.e. adult females and other subadults). As a companion’s home range may extend beyond the boundaries of a subadult’s mother’s home range, it is possible that, by moving with and following companions similar to older subadults making exploratory excursions (Shrader and Owen-Smith 2002), young subadults may be led into novel areas outside their mother’s home range.

Associations between subadults and companions (or ‘buddies’) may last anywhere from half a day to over a year (Owen-Smith 1973, Shrader and Owen-Smith 2002). While white rhinos are subadults, they may move with, and transfer between, a large number of different companions (Owen-Smith 1975, Shrader and Owen-Smith 2002). I suggest that, by transferring between companions, subadults have the potential to explore and move over a large portion of the Hluhluwe-Umfolozi Park (HUP) prior to establishing temporary home ranges when they are about 4 years of age (Fig. 1).

Shrader and Owen-Smith (2002), suggested that, from these temporary home ranges, subadults may then make exploratory excursions with ‘buddies’, which may lead them into areas where they may ultimately disperse. As white rhinos consistently form associations during the time that they are subadults (Owen-Smith 1975), and as subadults may move with and transfer between multiple ‘buddies’, it is possible that dispersal may be a process which lasts the entire time that white rhinos are subadults (i.e. 1-2 years for females and up to 10 years for males). Thus, for white rhinos, the ‘buddy system’ may be the mechanism by which subadults disperse from their mother’s home range to where they ultimately settle as adults.

## RECOMENDATIONS

### *Implications of the ‘buddy system’ for the sink management policy*

When the vacuum zones (or ‘dispersal sinks’) were established within the Hluhluwe-Umfolozi Park (HUP) in 1986, physical features such as major rivers, roads, streams and ridge crests were used to delineate the boundaries separating the vacuum zones from the central core area. These boundaries, however, are features that do not restrict the movement of white rhinos between the two management areas. As the location of the boundaries was ‘man-made’ it is likely that the home ranges of some individuals were bisected by these boundaries, and thus portions of their home ranges were located in both the core and vacuum zones. With regard to the sink management policy, it is these individuals which are likely to play an important role in guiding subadults towards the low density vacuum zones into which they may disperse.

Owen-Smith (1973, 1988) recorded that, as the dry season progresses, and the quality and availability of food resources decline, white rhinos use a greater extent of their home range. For white rhinos with home ranges spanning both the core and vacuum zones, this increase in utilisation will result in white rhinos spending a proportion of the annual cycle within the vacuum zones. Through forming companionships with these individuals while they are in the core, and then following them as they utilise a greater proportion of their home range, it is possible for subadult white rhinos to be lead from the core into the vacuum zones (Fig. 2). Thus, individuals with home ranges spanning both the core and vacuum zones are important to the sink management policy, as these individuals may ultimately guide subadults into the vacuum zones where they may disperse.

The importance of these individuals may be evident in the low white rhino density in the Okhukho section of HUP. In the late 80’s and early 90’s rhino poaching was a major problem along the fence line in Okhukho. In an attempt to reduce poaching, a majority of the white rhinos within Okhukho were removed. At the time of the present study, despite a very low removal of white rhinos from the area, white rhino numbers in the Okhukho section had not reached previous levels. It is possible that, due to the heavy removals in the 80’s and 90’s, there are very few individuals remaining with home ranges spanning both Okhukho and the central core. If this is the case, then the low white rhino density in the Okhukho section could be the result of a lack of individuals to guide subadult white rhinos from the core into this section.

It is thus important, with regard to the continued management of white rhinos using the sink management policy, that a proportion of the individuals with home ranges spanning both the core and vacuum zones be left and not removed for the annual game auctions. As adult females have more established home ranges than subadults, and as groups of subadults (2-6 individuals) have been known to form associations with adult females (Owen-Smith 1973, 1975), it is likely that adults females are the main class guiding dispersing subadults from the core into the vacuum zones. Thus, to limit the removal of these individuals, it is recommended that adult females found within 1 km of the vacuum zone boundaries not be removed, as their home ranges may span into the core and thus be the main catalyst helping subadults find and disperse into the vacuum zones.

# REFERENCES

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American **225**: 86-93.

Foose, T.J. 1982. Trophic strategies of ruminant vs nonruminant ungulates. Unpublished PhD thesis. University of Chicago, USA.

Fortin, D., J.M. Fryxell and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Ecology **80**:970-982.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and cecal digestion. Evolution **30**:757-774.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behavior **48**:215-267.

Laca, E.A., E.D. Ungar, and M.W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. Applied Animal Behaviour Science **39**:3-19.

Melton, D. A. 1987. Habitat selection and resource scarcity. South African Journal of Science **83**:646-651.

Owen-Smith, N. 1973. The behavioural ecology of the white rhinoceros. Unpublished PhD. Thesis, University of Wisconsin, Madison, USA.

Owen-Smith, N. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). Zeitschrift für Tierpsychologie **38**:337-384.

Owen-Smith, N. 1988. Megaherbivores. Cambridge University Press, Cambridge, UK.

Owen-Smith, N. 1994. Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. Ecology **75**:1050-1062.

Owen-Smith, N. 1997. Control of energy balance by a wild ungulate, the kudu (*Tragelaphus strepsiceros*) through adaptive foraging behaviour. Proceedings of the Nutritional Society. **56**:15-24.

Owen-Smith, N. and P. Novellie. 1982. What should a clever ungulate eat? The American Naturalist **119**:151-178.

Owen-Smith, N. and S. M. Cooper. 1989. Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. Journal of Zoology, London **219**:29-43.

Parker, K.L., M.P. Gillingham, T.A. Hanley and C.T. Robbins. 1993. Seasonal patterns of body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. Canadian Journal of Ecology **71**:1397-1404.

Parker, K.L., M.P. Gillingham, T.A. Hanley and C.T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Ecology **74**:442-450.

Perry, S.L., D.P. DeMaster, and G.K. Silber. 1999. The humpback whale. Marine Fisheries Review **61**:24-74.

Prins, H.H.T. 1996. Ecology and behaviour of the African Buffalo: social inequality and decision making. Chapman Hall, London, UK.

Selous, F.C. 1899. The white or square-lipped rhinoceros. *in* H.A. Bryden, editor. Great and small game of Africa. Rowland Ward, London, UK.

Shipley, L.A., J.E. Gross, D.E. Spalinger, N.T. Hobbs and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. American Naturalist **143**:1055-1082.

Shrader, A.M. and N. Owen-Smith. 2002. The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). Behavioral Ecology and Sociobiology **52**:255-261

Sinclair, A.R.E. 1983. The function of distance movements in vertebrates. Pages 240-258 *in* I.R. Swingland and P.J. Greenwood, editors. The ecology of animal movement. Oxford Press, Clarendon, UK.

Spalinger, D.E., T.A. Hanley, and C.T. Robbins. 1988. Analysis of the functional response in foraging in the sitka blacked-tailed deer. Ecology **69**:1166-1175.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Stephens, D.W. and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Taber, A.B. 1984. Grey Whale. Pages 216-221 *in* D. Macdonald, editor. The encyclopaedia of mammals:1. George Allen and Unwin, London, UK.

Wallis de Vries, M.F. and C. Daleboudt. 1994. Foraging strategy of cattle in a patchy grassland. Oecologia **100**:98-106.

# FIGURE CAPTIONS

Fig. 1. Possible pattern of dispersal for a subadult white rhino as it moves from its mother's home range at about 2-3 years of age (1), with buddies through their home ranges (2-5), to where it establishes a temporary home range at about 4 years of age (6).

Fig. 2. Dispersal of subadult white rhinos from an established home range within the core, to the surrounding vacuum zones in the Hluhluwe-Umfolozi Park, by way of forming a companionship with an individual who's home range spans the boundary of both management areas.

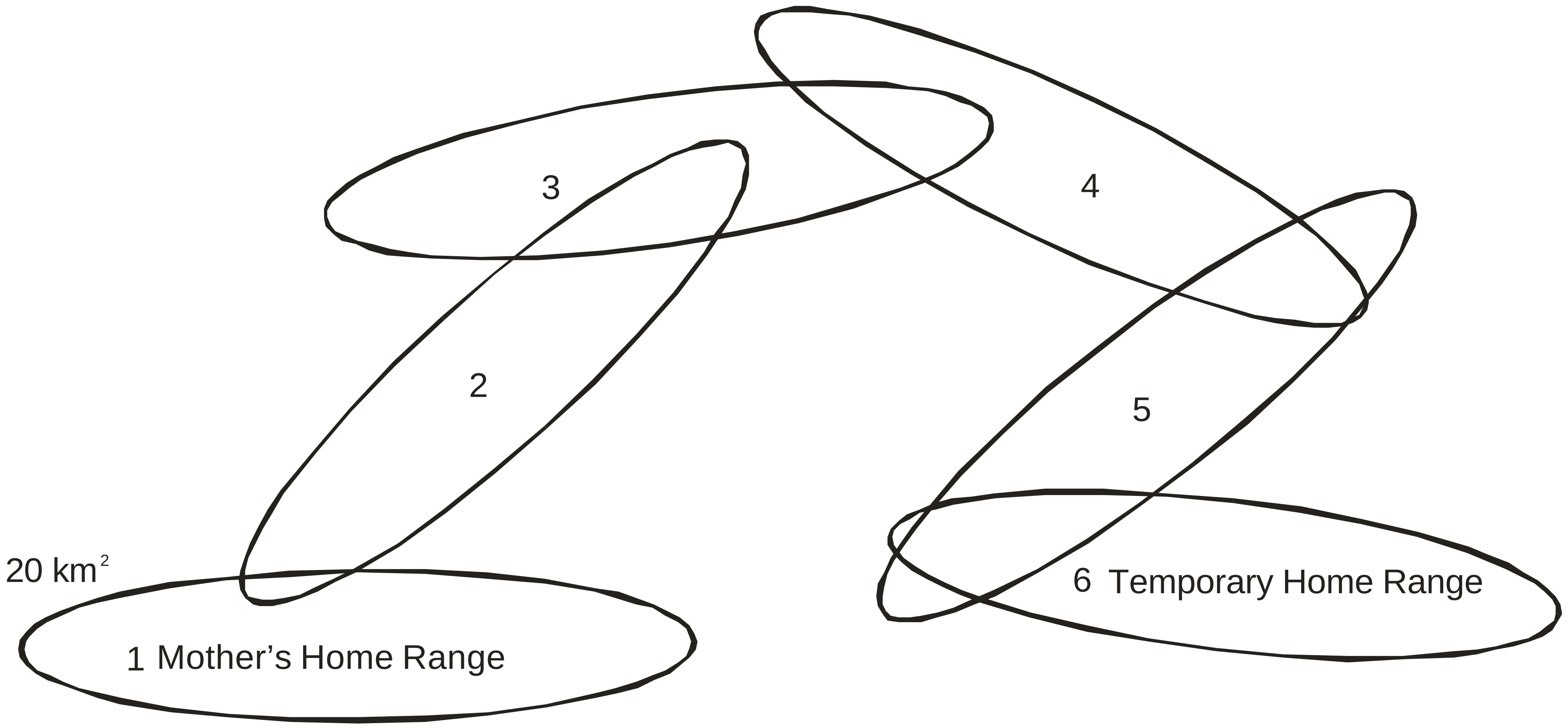

Fig. 1.

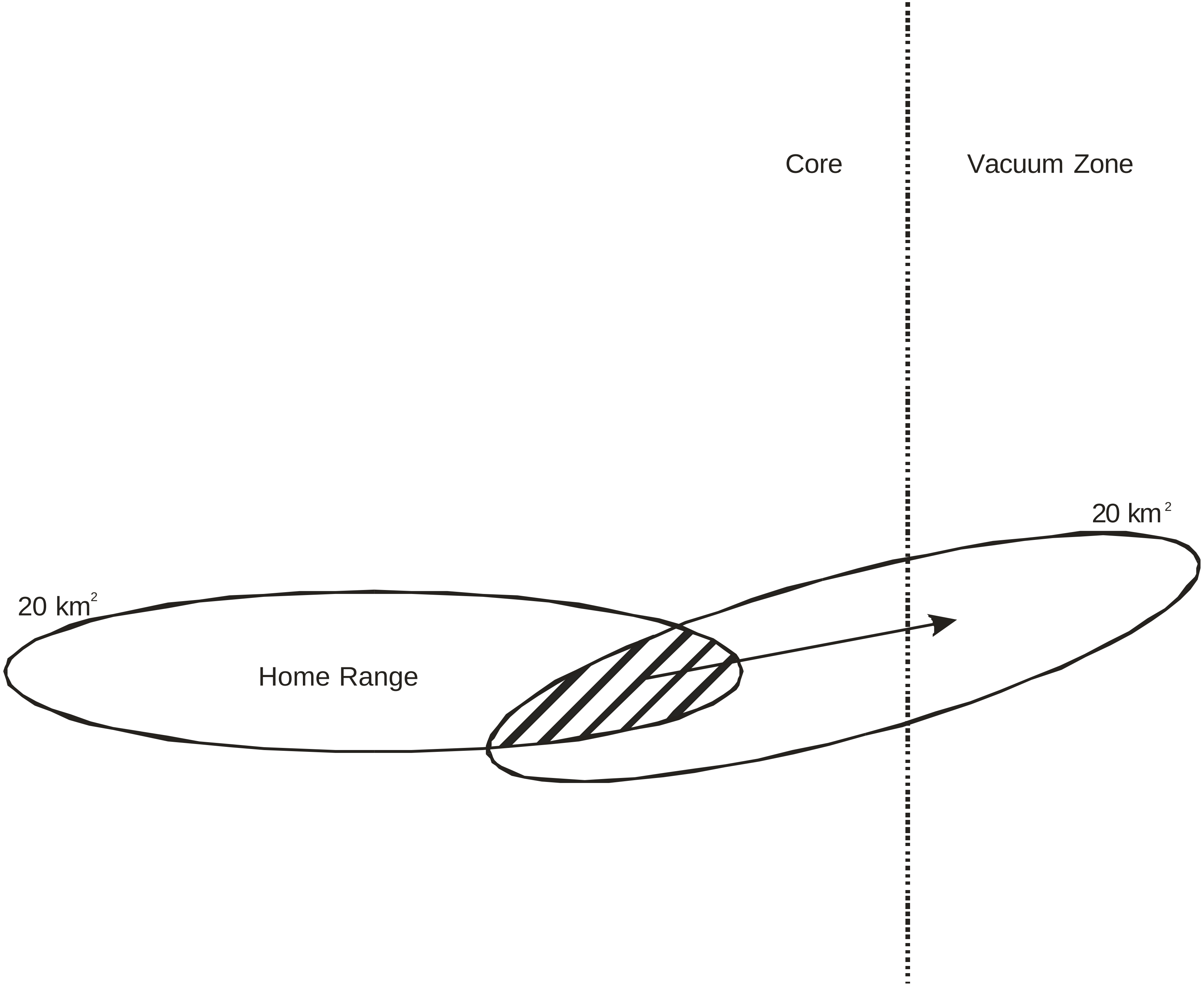

Fig. 2.

## APPENDIX I

# Shrader, A.M. and B.A. Beauchamp 2001. A new method for implanting radio transmitters into the horns of black and white rhinoceroses. Pachyderm 30:81-86

(See Pages – in attached Pachyderm)

**APPENDIX II**

# Home Ranges

The home ranges of the ten white rhinos with radio transmitters, along with two frequently seen rhinos (adult female ’L’ and male subadult ‘A’), were estimated by entering GPS positions into the home range analysis program Calhome (Kie et al. 1996). Home range limits were identified from the 85% utilization contour, using the adaptive kernel method with the least squares cross validation for the smoothing parameter (Worton 1995; Seaman and Powell 1996). This procedure seemed most reliable for establishing the area regularly used, allowing for fairly frequent excursions by subadults and occasional excursions by adult females. Home ranges delineated using the Adaptive Kernel, Minimum Convex Polygon and Harmonic Mean procedures gave similar estimates of home range extent for the 85% contour, but not when a higher proportion of sightings was included. Excursions lasting longer than a day generated autocorrelated position records, and hence could exaggerate the home range delineated by the estimation procedures (Swihart and Slade 1985). Where necessary, the home range boundaries indicated by Calhome were adjusted to coincide with a physical barrier (e.g., a major river). GPS locations were plotted using ArcView (Anon 1996). Locations of each individual located outside the 85% contour identifying the home range boundary were interpreted as exploratory excursions.

# REFERENCES

Anon. 1996. Using ArcView GIS. Redlands: Environmental Systems Research Institute.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085

Swihart, R. K. and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Worton, B. J. 1995. Using monte carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794-800.

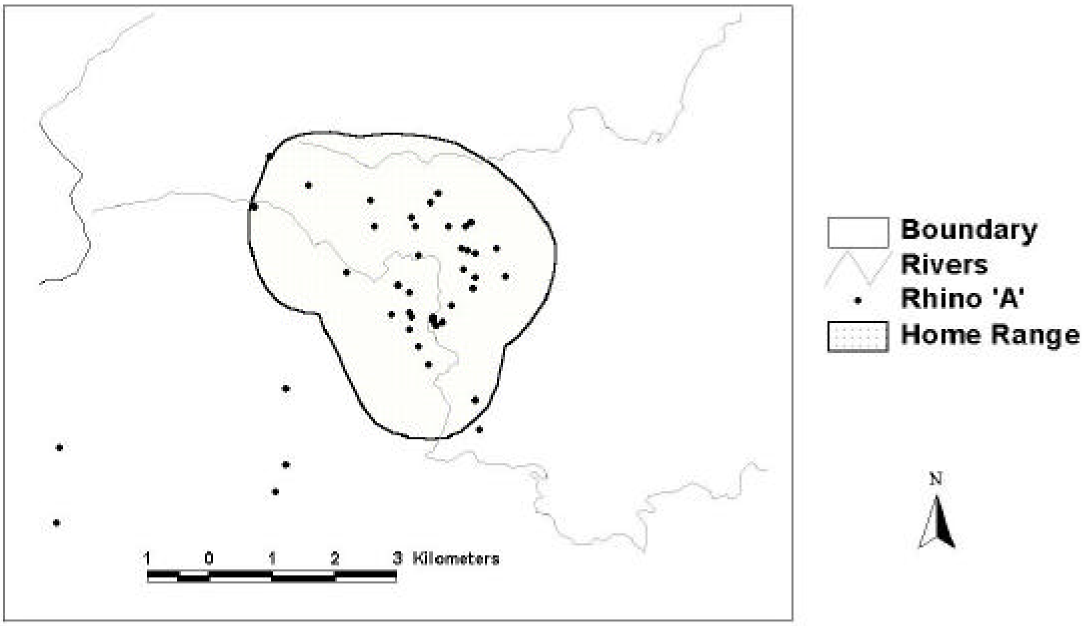

Fig 1. Home range (16.7 km$^2$) of the 9-10 year old subadult male ‘A’.

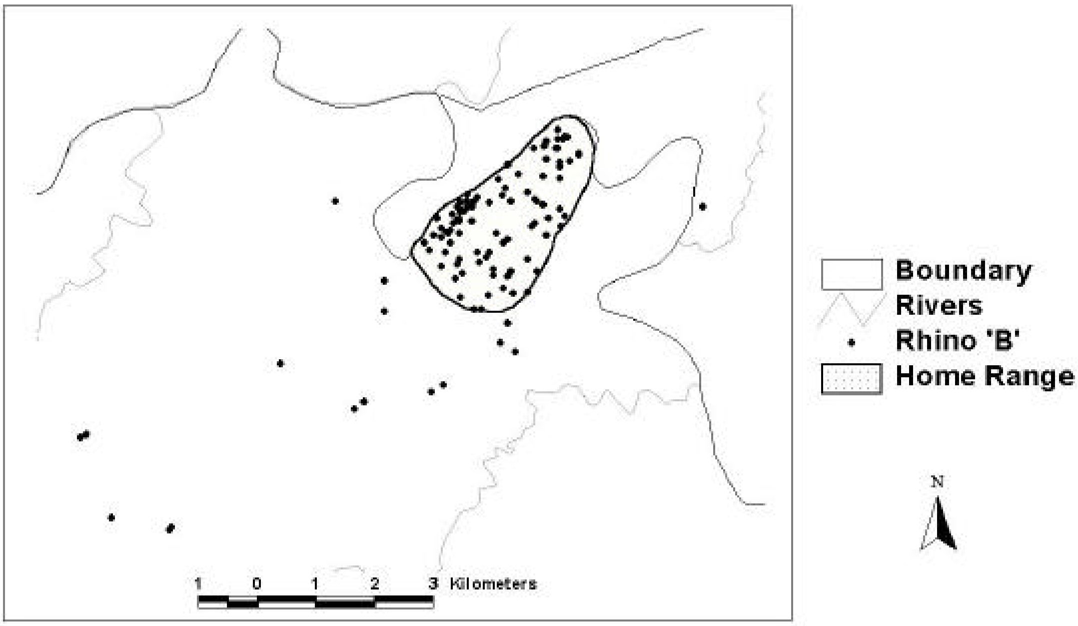

Fig 2. Home range (5.54 km$^2$) of the 8-9 year old subadult male ‘B’.

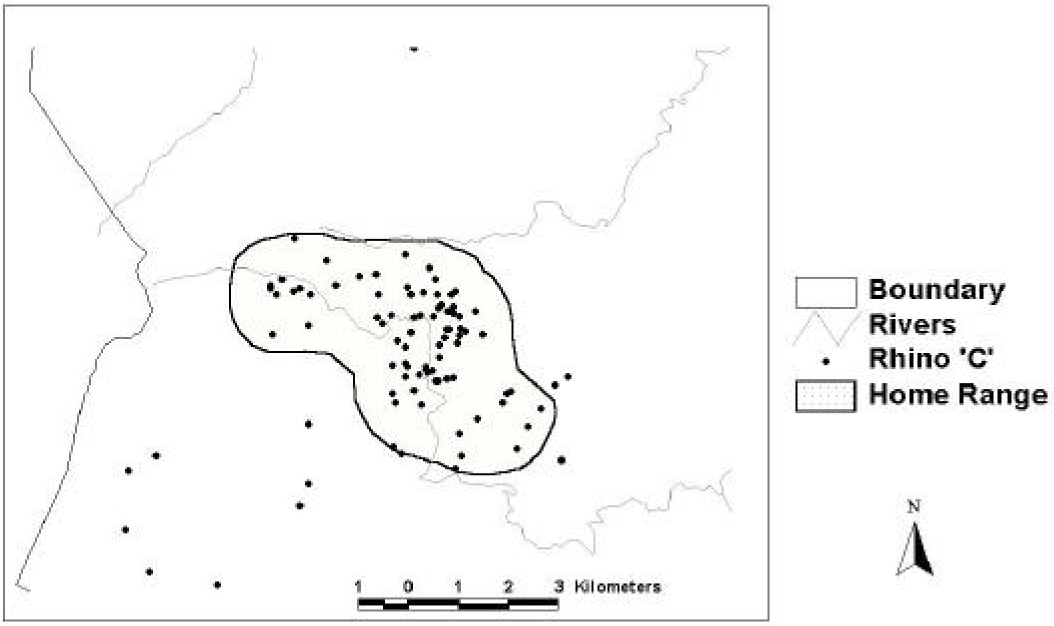

Fig 3. Home range (19.7 km$^2$) of the 7-8 year old subadult male ‘C’.

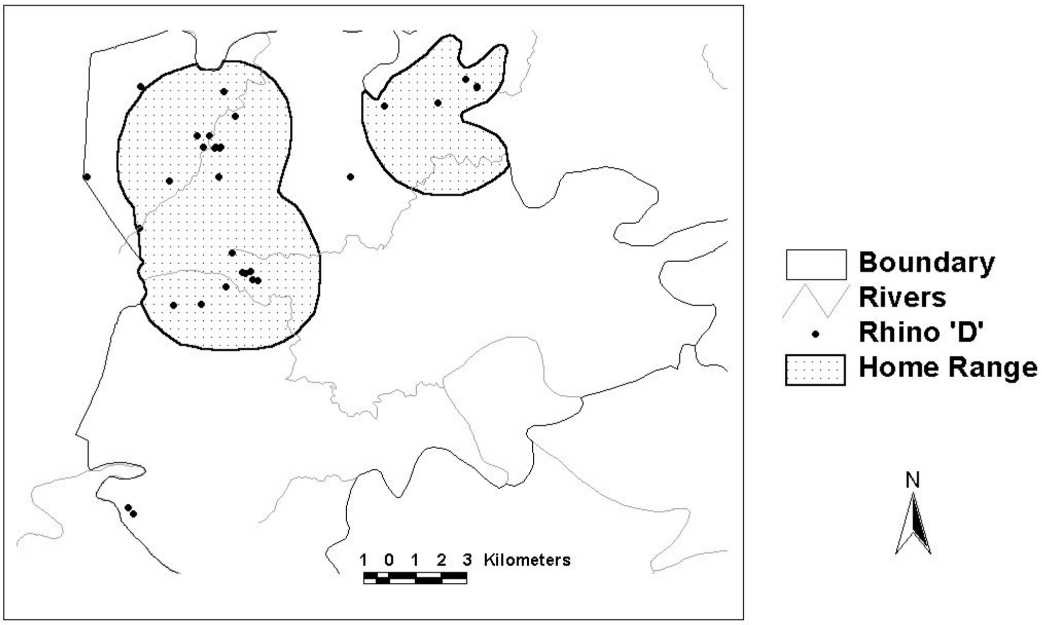

Fig 4. Home ranges of the adult female ‘D’. First home range (left) was estimated to be 66.4 km$^2$. Following a fight, where she was wounded by another white rhino, she moved and settled in a new area (right; 23.4 km$^2$).

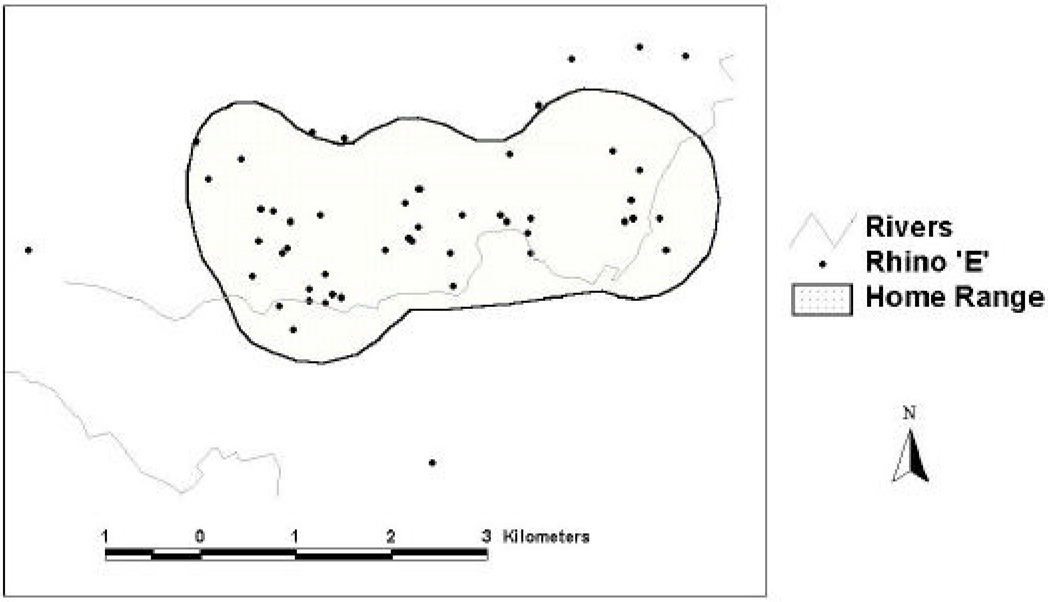

Fig 5. Home range (11.1 km$^2$) of the 6-7 year old subadult female ‘E’.

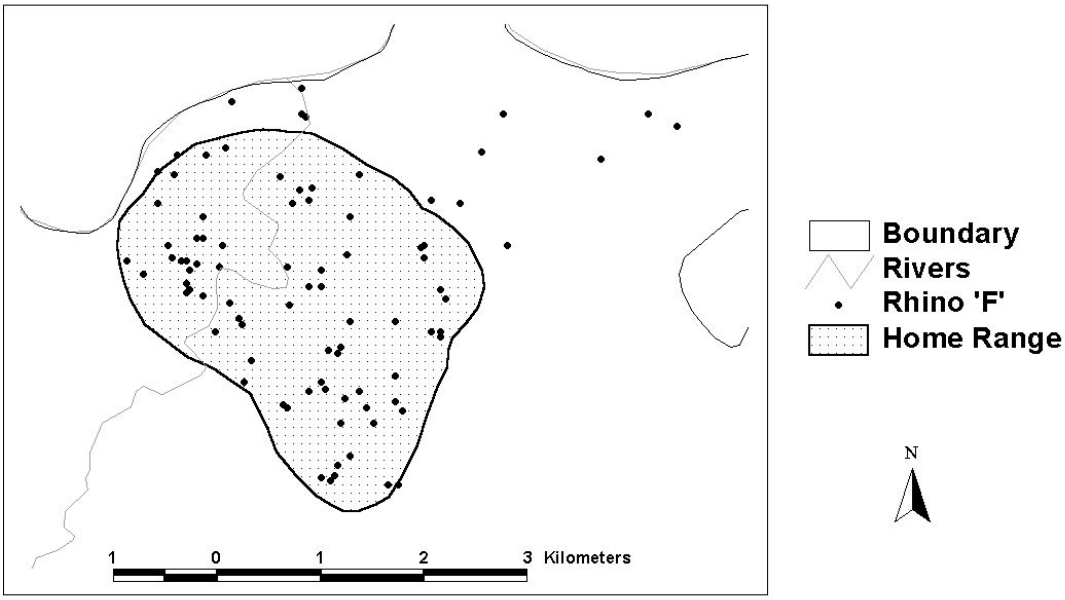

Fig 6. Home range (8.2 $km^2$) of the 6-7 year old subadult male ‘F’.

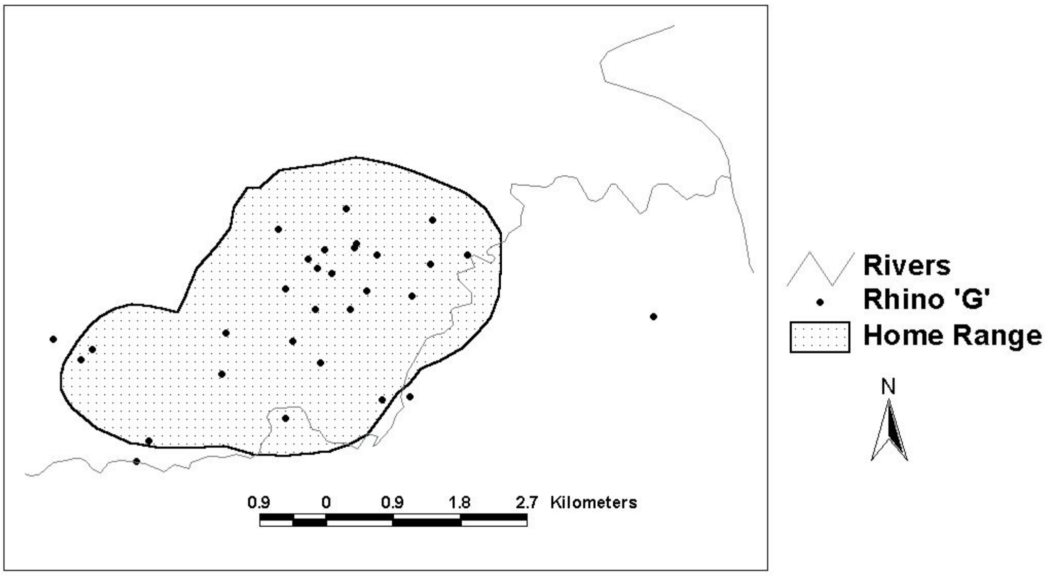

Fig 7. Home range (15.4 km$^2$) of the 5-6 year old subadult male ‘G’. Observations were made between April and October 1999.

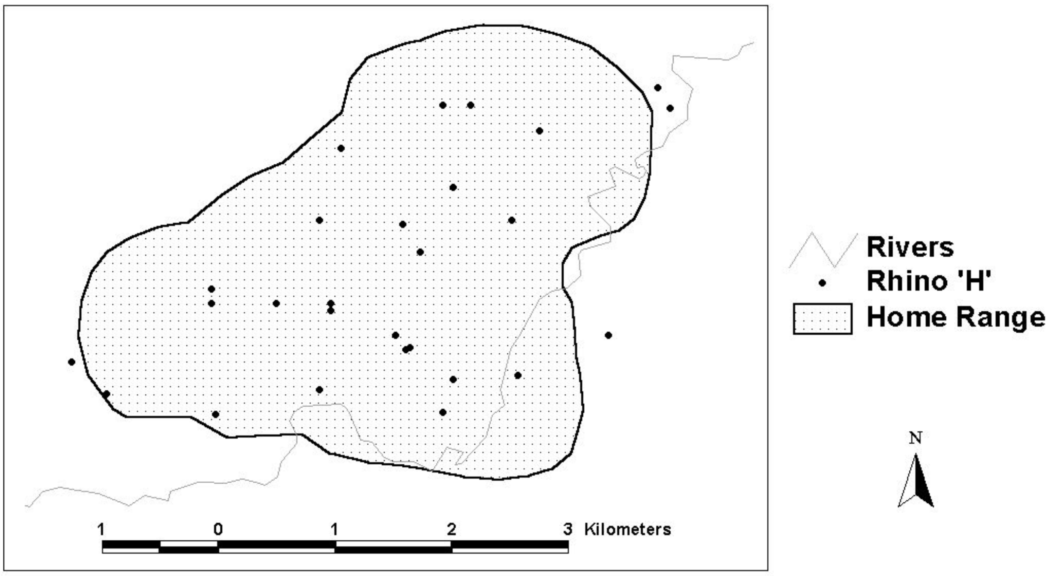

Fig 8. Home range (13.6 km$^2$) of the 5-6 year old subadult male ‘H’. Observations were made between April and October 1999.

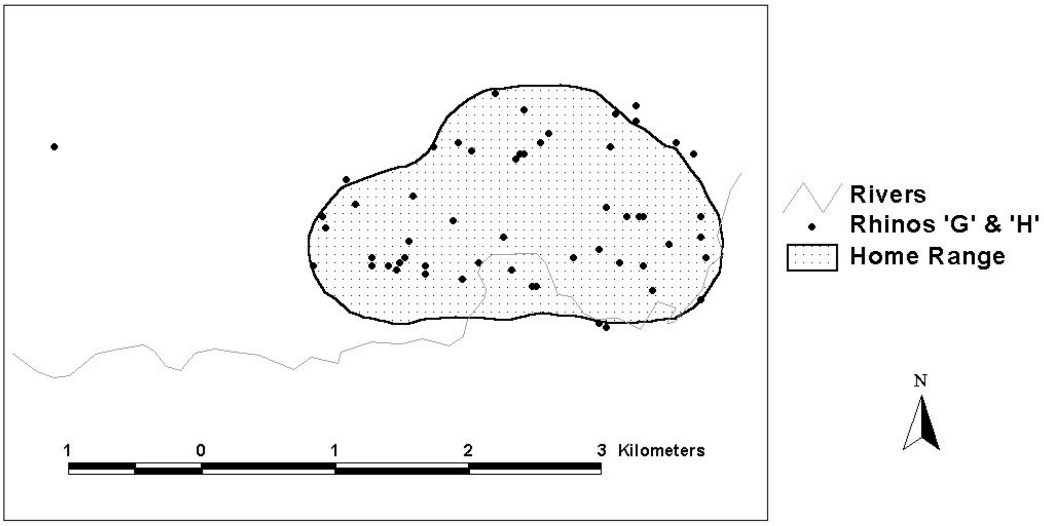

Fig 9. Home range (4.1 km$^2$) of the subadult males ‘G’ and ‘H’ after they paired up.. Observations were made between October 1999 and October 2000.

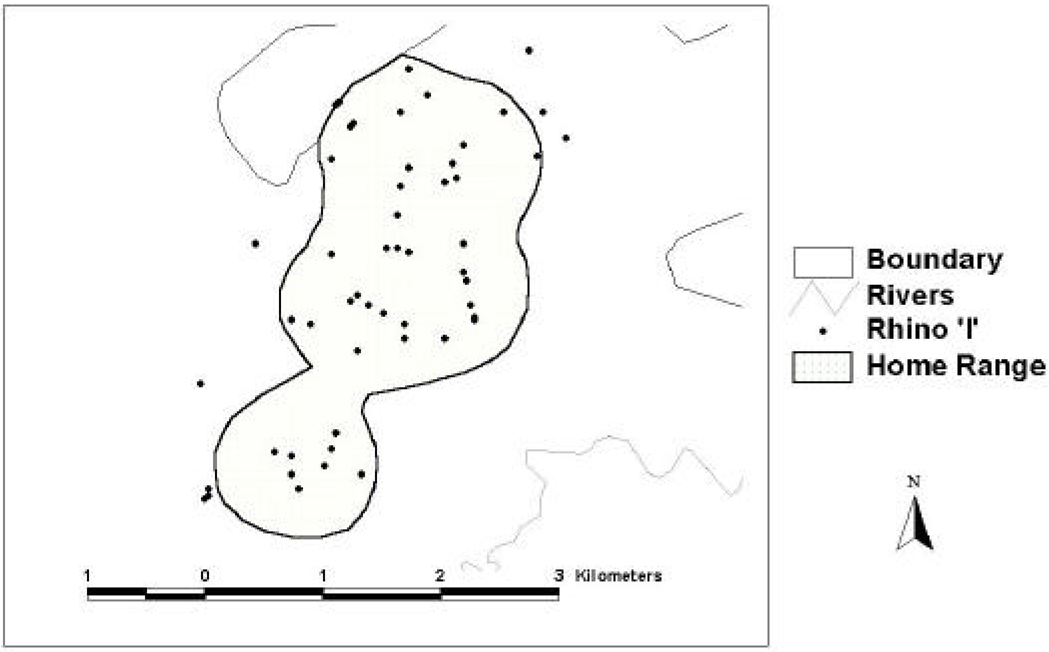

Fig 10. Home range (6.2 km$^2$) of the adult female ‘I’.

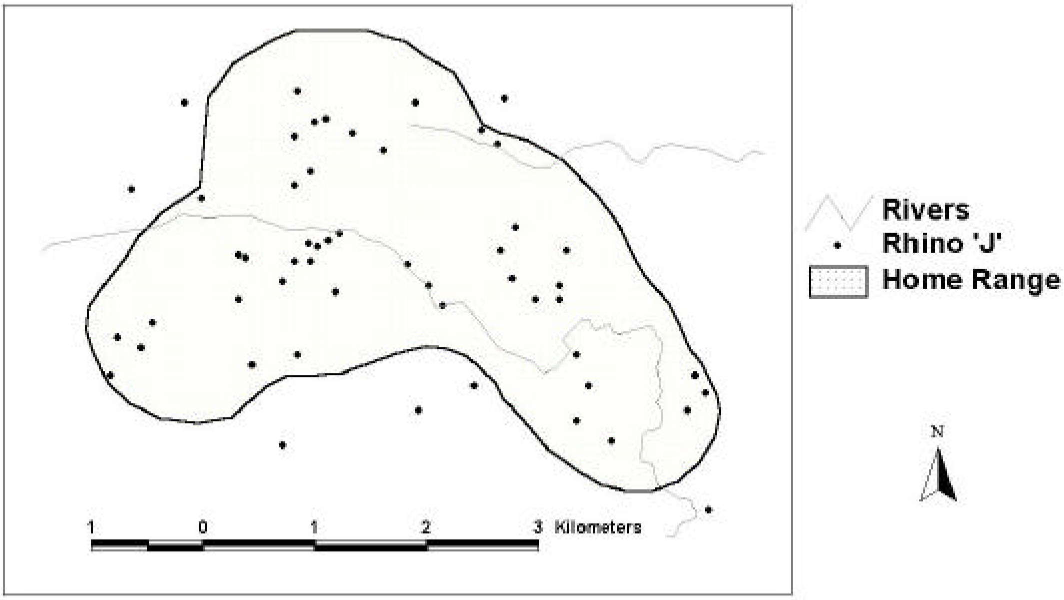

Fig 11. Home range (13.1 $km^2$) of the adult female ‘J’.

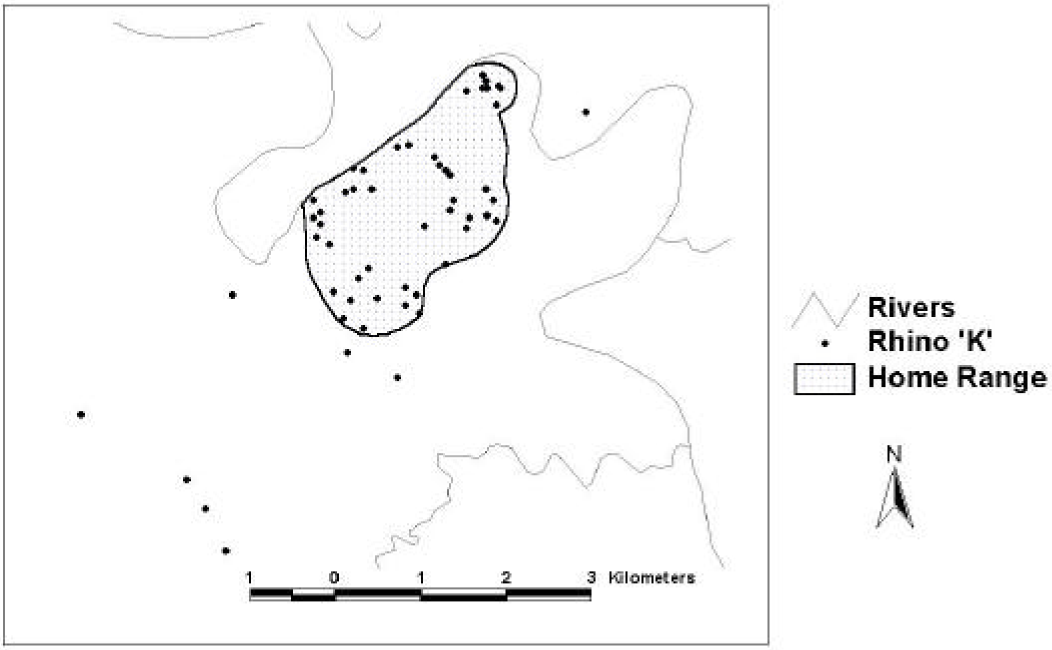

Fig 12. Home range (4.7 km$^2$) of the adult female ‘K’.

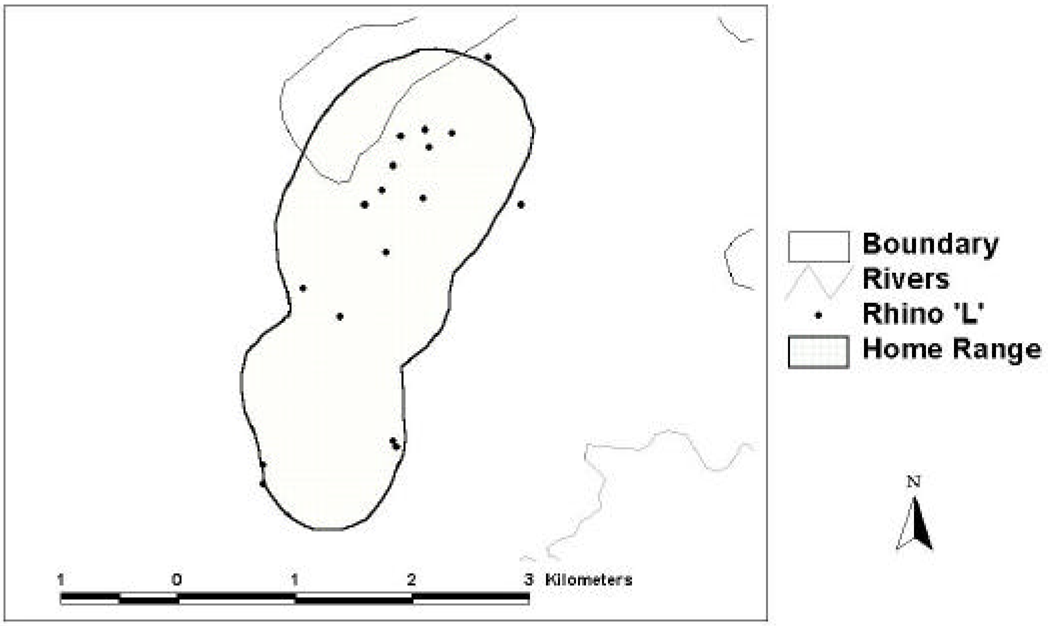

Fig 13. Home range (5.9 km$^2$) of the adult female ‘L’.

## APPENDIX III

### Psion program

The computer program ‘Rhino’ was used to record the number of bites that an individual rhino took per step (i.e. bites per feeding station). The program was written for a Psion Organiser II by James Murry at Psion, South Africa.

Keys and their functions:

Y- Initiated the program and printed the date (day/month/year) and ‘Start’ followed by the time (hour/minute/second).

Z- Terminated the program and printed ‘Stop’ followed by the time (hour/minute/second).

S- Recorded a single bite.

T- Recorded a step, printed the time (hour/minute/second) and reset the bite counter for the next step.

M- Paused the program and printed the time (hour/minute/second) when the program was paused.

Once started, the program requested the ID number of the animal that was being observed. In the study, the last three digits of the rhino’s transmitter frequency (i.e. 110 for 148.110) or a two letter code (i.e. FF for adult (F), female) was entered for animals without radio transmitters. Once the ID number had been entered, the program was ready for input. To initiate the program the ‘Y’ key was pressed when the rhino took what was the first step of the feeding observation. When ‘Y’ was pressed, the date and start time of the initial step were printed. The number of bites taken by the rhino in a feeding station were recorded by pressing the ‘S’ key each time the animal took a bite.

The ‘T’ key was pressed when the rhino took a step, and thus moved to another feeding station. Each time that the ‘T’ key was pressed, the time of the step was printed and the bite counter reset for the new feeding station.

To insure that a complete feeding observation (ten feeding steps) was recorded, the program was designed to count the number of feeding steps recorded. Once ten feeding steps had been recorded, the Organiser II beeped three times. Once the Organiser II had beeped, the ‘Z’ key was pressed to terminate the program and print the stop time.

When an animal forages, it divides its time between looking for and ingesting food. While feeding an animal may decide to stop ingesting food and chew (or process) what is in its mouth. As the study focused on feeding time and not foraging time, a ‘pause’ function was put into the program. If a rhino stopped feeding and started chewing the grass in its mouth, the ‘M’ button was pushed on the Psion. When ‘M’ was pushed, the time and the word ‘Pause’ was printed. If the rhino resumed feeding without taking a step, the ‘S’ button was pushed to record the additional bites within the feeding station. When the ‘S’ button was pushed while the program was paused, the time that the bite was taken along with the word ‘Resume’ was printed. If, however, the rhino took a step and moved to a new feeding station before resuming to feed the ‘T’ button was pushed. Pushing ‘T’ while the program was paused completed the feeding step and printed the time and reset the bite counter for the next step.

The only problem (or ‘bug’) with the ‘rhino’ program was that if the pause button (‘M’) was pushed during a feeding step, the program would not recorded the step as a feeding step. This resulted in more than ten ‘true’ feeding steps being recorded in the sample before the Psion would beep. This was not considered to be a serious problem as more than the required ten steps were recorded.

Bite rate of each feeding observation was derived by summing the total number of bites in the observation and then dividing that number by the total time spent feeding during the observation.

The Psion computer code for the ‘Rhino’ program is listed below.

```
rhino:

local kp%,rhino$(10),b$(250),cnt%,pse%

if exist("a:bites")
 open "a:bites",a,a$
else
 create "a:bites",a,a$
endif

cls
print "Rhino:"
edit rhino$
if rhino$=""
 return
endif
a.a$=rhino$
append
a.a$=mid$(datim$,5,11)
append

do
 kstat 1
 kp%=get
 if kp%=%Y
  if len(b$)
   a.a$=b$
   append
   b$=""
  endif
  cnt%=0
  pse%=0
  print "Start "+right$(datim$,9)
  a.a$="Start"+right$(datim$,9)
  append
 elseif kp%=%Z
  if len(b$)
   a.a$=b$
   append
   b$=""
```

```
  endif
  cnt%=0
  print "Stop "+right$(datim$,9)
  a.a$="Stop"+right$(datim$,9)
  append
  break
 elseif kp%=%S
  if pse%=1
   print "Resume "+right$(datim$,9)
   a.a$="Resume"+right$(datim$,9)
   append
   pse%=0
  endif
  b$=b$+"S "
 elseif kp%=%T
  pse%=0
  if len(b$)
   cnt%=cnt%+1
   print b$
   a.a$=b$
   append
   b$=""
  endif
  print "Step "+right$(datim$,9)
  a.a$="Time"+right$(datim$,9)
  append
 elseif kp%=%M
  pse%=1
  if len(b$)
   cnt%=cnt%+1
   print b$
   a.a$=b$
   append
   b$=""
  endif
  print "Pause "+right$(datim$,9)
  a.a$="Pause"+right$(datim$,9)
  append
 else
  beep 200,200
 endif
 if cnt%=10
  beep 250,200
  beep 280,230
  beep 250,200
  print "10 steps with bites"
  cnt%=0
 endif
until 0
return
```

The Psion used in the study was unable to delete the data files generated by the above Rhino program. Once the data had been transferred from the Psion to a PC, the following program was run to delete the bites/step data stored on the ‘A’ drive in the Psion.

```
Delfile:

if  exist(“a:bites”)
 kstat 1
if view (2, “Delete Bites File (Y/N)” + chr$(63))=%Y
 delete “a:bites”
endif
endif
```

**APPENDIX IV**

# Grass nutrients

Table 1. Mean % crude protein for whole plant samples of the different grass greenness categories in the short, woodland and Themeda grasslands. Greenness codes are very brown (VB), mainly brown (MB), mainly green (MG) and very green (VG). Grass species in the short grasslands are Panicum coloratum (P), Sporobolus nitens (S), Digitaria argyrograpta (D) and the combination of P. coloratum and D. argyrograpta (DP).

| Habitat/ Species | Greenness | N= | Mean %CP | -95% CL | +95% CL |
|---|---|---|---|---|---|
| Short | | | | | |
| P | VB | 3 | 5.24 | 3.73 | 7.36 |
| P | MB | 3 | 8.07 | 5.36 | 12.16 |
| P | MG | 1 | 17.06 | - | - |
| P | VG | 2 | 20.17 | 1.65 | 246.61 |
| S | VB | 1 | 11.81 | - | - |
| S | MB | 5 | 9.06 | 6.55 | 12.51 |
| S | MG | 1 | 9.81 | - | - |
| S | VG | 7 | 21.43 | 17.56 | 26.16 |
| DP | VB | 4 | 6.04 | 4.93 | 7.41 |
| DP | MB | 11 | 8.34 | 7.44 | 9.35 |
| DP | MG | 6 | 8.71 | 5.94 | 12.78 |
| D | MG | 4 | 9.34 | 5.41 | 16.13 |
| Woodland | | | | | |
| | VB | 3 | 5.98 | 3.16 | 8.80 |
| | MB | 8 | 7.94 | 6.63 | 9.24 |
| | MG | 12 | 8.95 | 7.40 | 10.50 |
| | VG | 9 | 11.47 | 8.41 | 14.52 |

Table 1 (cont.)

| Themeda | Greenness | N= | Mean %CP | -95% CL | +95% CL |
|---|---|---|---|---|---|
| | VB | 3 | 3.22 | 0.92 | 11.23 |
| | MB | 6 | 4.41 | 3.71 | 5.23 |
| | MG | 6 | 5.36 | 4.16 | 6.91 |
| | VG | 6 | 8.28 | 4.88 | 14.04 |

Table 2. Mean phosphorus levels of whole plant samples in the different grass greenness categories in the short, woodland, and Themeda grasslands. Greenness and grass species codes same as Table 1.

| Habitat/ Species | Greenness | N= | Mean %P | -95% CL | +95% CL |
|---|---|---|---|---|---|
| Short | | | | | |
| P | VB | 3 | 0.05 | 0.03 | 0.09 |
| P | MB | 3 | 0.10 | 0.09 | 0.12 |
| P | MG | 1 | 0.13 | - | - |
| P | VG | 2 | 0.45 | 0.0002 | 1174.63 |
| S | VB | 1 | 0.01 | - | - |
| S | MB | 5 | 0.01 | 0.003 | 0.02 |
| S | MG | 1 | 0.1 | - | - |
| S | VG | 7 | 0.74 | 0.43 | 1.31 |
| DP | VB | 4 | 0.06 | 0.04 | 0.05 |
| DP | MB | 11 | 0.11 | 0.14 | 0.08 |
| DP | MG | 6 | 0.13 | 0.10 | 0.16 |
| D | MG | 4 | 0.05 | 0.003 | 0.66 |
| Woodland | | | | | |
| | VB | 3 | 0.06 | 0.04 | 0.11 |
| | MB | 8 | 0.09 | 0.08 | 0.11 |
| | MG | 12 | 0.10 | 0.07 | 0.14 |
| | VG | 9 | 0.143 | 0.09 | 0.22 |
| Themeda | | | | | |
| | VB | 3 | 0.06 | 0.01 | 0.39 |
| | MB | 6 | 0.06 | 0.04 | 0.08 |
| | MG | 6 | 0.07 | 0.04 | 0.10 |
| | VG | 6 | 0.14 | 0.05 | 0.39 |

Table 3. Mean sodium levels of whole plant samples in the different grass greenness categories in the short, woodland, and Themeda grasslands. Greenness and grass species codes same as Table 1.

| Habitat/ Species | Greenness | N= | Mean %Na | -95% CL | +95% CL |
|---|---|---|---|---|---|
| Short | | | | | |
| P | VB | 3 | 0.17 | 0.07 | 0.40 |
| P | MB | 3 | 0.28 | 0.10 | 0.84 |
| P | MG | 1 | 0.85 | - | - |
| P | VG | 2 | 0.81 | 0.61 | 1.08 |
| S | VB | 1 | 0.20 | - | - |
| S | MB | 5 | 0.15 | 0.11 | 0.21 |
| S | MG | 1 | 0.22 | - | - |
| S | VG | 7 | 0.60 | 0.35 | 1.01 |
| DP | VB | 4 | 0.17 | 0.11 | 0.29 |
| DP | MB | 11 | 0.41 | 0.34 | 0.48 |
| DP | MG | 6 | 0.36 | 0.25 | 0.52 |
| D | MG | 4 | 0.33 | 0.13 | 0.88 |
| Woodland | | | | | |
| | VB | 3 | 0.11 | 0.04 | 0.28 |
| | MB | 8 | 0.29 | 0.23 | 0.38 |
| | MG | 12 | 0.19 | 0.14 | 0.27 |
| | VG | 9 | 0.24 | 0.13 | 0.44 |
| Themeda | | | | | |
| | VB | 3 | 0.05 | 0.01 | 0.31 |
| | MB | 6 | 0.07 | 0.04 | 0.12 |
| | MG | 6 | 0.07 | 0.04 | 0.14 |
| | VG | 6 | 0.05 | 0.02 | 0.13 |