

UTILISATION OF LOW DENSITY VACUUM ZONES
BY WHITE RHINOS IN THE UMFOLOZI GAME RESERVE

by

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Abstract

White rhinos in the Umfolozi Game Reserve (UGR) are managed with a 'Sink Management Policy' which utilises natural dispersal patterns of white rhinos from an area of high density (the core), to areas of low density (vacuum zones). This study was initiated to determine how white rhinos utilised the vacuum zones, as the management staff of the UGR felt that white rhinos were not dispersing into them but utilising them only as areas of trophic resources.

Significantly different white rhino densities were established in the Makhamisa and Masinda vacuum zones by removing white rhinos from Masinda. Changes in the density of white rhinos were monitored and the age and sex compositions determined. No significant changes in the density of white rhino groups were recorded during the study, however, the density of individuals in Makhamisa increased significantly in the dry season, while the density in Masinda did not change. The reason for this increase could not be determined, however, the most likely explanation was that rhinos moved toward the Makhamisa study area in search of surface water which was present in the White Umfolozi River. During the dry season the water level in the Umfolozi River was low so the white rhinos were able to cross into the study area. However, owing to the above average rainfall, resources were not limited in either study area, and most likely in most of the reserve. Thus, it could not be determined why white rhinos would need to enter the Makhamisa study area.

Changes in grass height, grass colour, and the availability of water in pans and streams were monitored throughout the study. The grassland community

compositions of the two study areas were found not to be significantly different. The total utilisation of the different grassland communities by white rhinos during the study were determined for both study areas. White rhinos in the two study areas utilised the grassland communities in a similar pattern throughout the study. During the wet and dry seasons, white rhinos primarily foraged in the short grassland community (Panicum coloratum & Themeda-Urachloa), their staple grassland community, and were not observed to switch and start foraging in the tall grassland community (Themeda & Themeda-Panicum), their reserve community. White rhinos in both study areas were able to forage in their stable grassland community throughout the dry season because of the above average rainfall experienced during the study

The results of the study suggest that white rhinos outside the study areas did not utilise the vacuum zones for trophic resources. However, as the study was conducted in a year with above average rainfall, these findings may not represent how white rhinos utilise the vacuum zones in years with average or below average rainfall.

PREFACE

The data described in this dissertation were collected in the Umfolozi Game Reserve from July 1995 to July 1996. Experimental work was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from September 1996 to January 1998, under the supervision of Professor Mike Perrin and Professor Norman Owen-Smith (University of the Witwatersrand).

These studies represent original work by the author and have not otherwise been submitted in any other form for a degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.



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Introduction

I.1 Historical

The management staff of the Umfolozi Game Reserve have been conserving white rhinos for over a hundred years (Rogers 1995). In 1895, the South African government declared the area between the White and Black Umfolozi Rivers a reserve (Penny 1987) making it, along with Hluhluwe and St. Lucia, one of South Africa's first nature reserves (Player 1972). When the reserve was first established the population of white rhinos comprised of only a few remaining individuals located in the valley of the Umfolozi River (Penny 1987).

Presently, the Hluhluwe-Umfolozi Park, which consists of the Hluhluwe Game Reserve to the North, and the Umfolozi Game Reserve to the South, maintains one of the world's largest concentrations of rhinoceroses with large populations of both white (*Ceratotherium simum simum*) and black (*Diceros bicornis*) rhinoceroses. In 1996 the white rhino population was estimated at 1,350 individuals (Balfour & Howison 1996) while the black rhino population approximated 400 individuals.

In the 1960's, as the population of white rhinos increased within the Umfolozi Game Reserve, concern arose over the implications of maintaining a large population in the reserve. To deal with this situation the Natal Parks Board started removing white rhinos from the reserve in 1961 (Owen-Smith 1981, Player 1972) and translocating them to other reserves in southern Africa. This removal policy, called Operation Rhino, was an attempt to not only reduce the number of white rhinos in Umfolozi so as to maintain a healthy population of white rhinos that was less susceptible to 'catastrophes' such as disease and starvation, but also to establish other populations of white rhinos throughout South Africa (Penny 1987, Player 1972).

1.2 Sink Management Policy

A management policy was introduced by the Natal Parks Board in 1986 to deal with the increasing white rhino population in the Umfolozi Game Reserve. This 'sink management policy' was based on recommendations from a study conducted in the late 60's and early 70's (Owen-Smith 1973; 1974; 1981). Owen-Smith (1973) found that white rhinos regulated their density through the dispersal of individuals from areas of high density (sources) into areas of low density (sinks). Dispersal is defined as a one way movement away from an animal's birth or breeding site. The resource-induced dispersal that was observed for white rhinos was prevalent in both sexes of sub-adults and adult males, but never in females with calves (Owen-Smith 1982a).

Historically, white rhinos in Umfolozi regulated their population by dispersing widely throughout the landscape (Owen-Smith 1981). This dispersal was possible as there were no fences along the boundary of the reserve. However, when a fence was constructed in 1965, effectively enclosing Umfolozi on all sides, rhinos were prevented from dispersing across the reserve boundary (Owen-Smith 1981). In an attempt to manage for all aspects of biodiversity, the natural processes that regulated the white rhino population in the Umfolozi Game Reserve were simulated by establishing areas of low white rhino density, called sinks or vacuum zones, and an area of high white rhino density called the core (Maddock 1992). The original sink boundaries were established in 1986, however, in 1992 they were repositioned to the locations during the study (Fig. 1) (Maddock 1992). These vacuum zones were established along the boundaries of the reserve to absorb white rhinos dispersing from the central core. To create these vacuum zones, white rhinos were removed from specific areas and translocated out of the reserve. The density in these zones was then maintained at approximately 1 rhino/km² to create a density gradient between the vacuum zones and the core area (Maddock 1992). The perceived benefits of

managing white rhinos in the Umfolozi Game Reserve with the sink management policy are:

- 1) that the natural processes that regulate white rhino numbers in Umfolozi are maintained; and
- 2) that it establishes habitat heterogeneity similar to what was present prior to the erection of the fence by having different white rhino densities in the core and vacuum zones.

In contemporary literature, sources and sinks are associated with metapopulations, niche quality, natality and mortality (Holt 1996; Howe & Davis 1991; Pulliam 1988; Pulliam & Danielson 1991). This study, however, monitored white rhino movements in high and low density areas, locally termed sources and sinks respectively. To differentiate between the terms used in this study and those in the literature, the source is here referred to as a core and the sinks as vacuum zones.

During the study (1995-1996), the sink management policy utilised fixed-wing aerial counts to determine the number of rhinos that were to be removed from the reserve annually. The number of rhinos counted in the vacuum zones that exceeded the 1 rhino/km² density were removed, sold and translocated out of the reserve to various locations throughout southern Africa and the rest of the world.

Prior to this study, the effectiveness of the sink management policy and the utilisation of the vacuum zones by white rhinos as areas for dispersal, were questioned by the management staff in the Umfolozi Game Reserve (Maddock 1992). Management maintained that the white rhinos were not, as predicted, dispersing into the vacuum zones but only moving into them temporarily to utilise the available trophic resources (i.e. grass and water). If this was the case, then there was a possibility that too many rhinos were being removed from the reserve and thus the white rhino population was being depleted. To address this problem, this study was initiated in order to determine

the movements of white rhinos in relation to the vacuum zones. Changes in the density of two selected vacuum zones were used to indicate the seasonal movements of the white rhinos, while specific grassland habitat utilisation patterns were also monitored.

1.3 The Study Area

The study was conducted from July 1995 until August 1996 in the Umfolozi Game Reserve (UGR) (28° 20' S, 31° 51' E). The UGR covers approximately 628 km² and is located in southern Zululand about 50 km north of Empangeni and 50km west of St. Lucia in KwaZulu-Natal, South Africa.

The UGR, for the purpose of white rhino management, is divided into two broad areas, the core and vacuum zones (Fig. 1). The central core is 287 km² and lies roughly in the centre of the reserve. Surrounding the central core are the vacuum zones (A,B,C,D,E,F) which have a combined area of 341 km². The white rhino density in the core is unmanaged and approximates 2 rhino/km² while the white rhino density in the vacuum zones is maintained at approximately 1 rhino/ km².

Two vacuum zones were selected in the UGR and a study area was established in each (Fig. 2). The first study area, Makhamisa (55.5 km²), was located in vacuum zone F in the southern section of Umfolozi, while the second study area Masinda (51.7 km²), was located in vacuum zone D in the eastern section of the reserve. Both study areas had a variety of grassland habitats and were bordered by approximately equal lengths of one of the Umfolozi rivers. The Makhamisa study area was bounded in the North by the White Umfolozi river while the Masinda study area's South-western boundary was the Black Umfolozi river.

A difference between the two study areas was that the Makhamisa study area was located in the 'Wilderness' portion of the reserve. A wilderness area, is defined as an area that is managed for people to experience untouched wild country (Anderson *et al.* 1995). In a wilderness area, minimum tools are used for all management activities and thus there are no permanent human impacts of any form allowed in the wilderness area (i.e. roads, buildings, etc). Due to these restrictions, Game Capture operations were limited in vacuum zones (including the Makhamisa study area) found in the Wilderness area. The result of these restrictions was that Game Capture were unable to use their game removal trucks to remove rhinos from the wilderness area and thus the rhino density in the wilderness area could not be maintained at 1 rhino/km².

I.4 Aims and Objectives

The purpose of the project was to assist the Natal Parks Board and the management staff of the Umfolozi Game Reserve in assessing the efficacy of the sink management policy. At present the seasonal movement patterns of white rhinos with respect to the vacuum zones are presently not understood. The sink management policy is to be assessed through the determination of these movement patterns and their relationships to population density and resource availability.

I.4.1 Main objective

Determine the effect that different white rhino densities have on the utilisation of the grassland communities available to white rhinos in the low density vacuum zones.

I.4.2 Auxiliary objectives

1. Determine the movements of the white rhinos in each study area.
2. Determine seasonal utilisation of the grassland communities by the white rhinos in the Makhamisa and Masinda study areas.
3. Determine if rhinos utilise different grassland communities at specific times of the year.
4. Predict which grassland communities white rhinos are most likely to occupy at any specific time of the year.

I.4.3 Hypotheses

1. The fluctuations in the density of white rhinos in the vacuum zones are similar for the two study areas throughout the year.
2. White rhinos in both the Makhamisa and Masinda study areas utilise the grassland communities in proportion to their availability.
3. The utilisation of the grassland communities by white rhinos is similar in the two study areas.
4. The rhinos will utilise the vacuum zones more during the dry season than in the rainy season.
5. White rhinos use the vacuum zones only as a source of trophic resources.

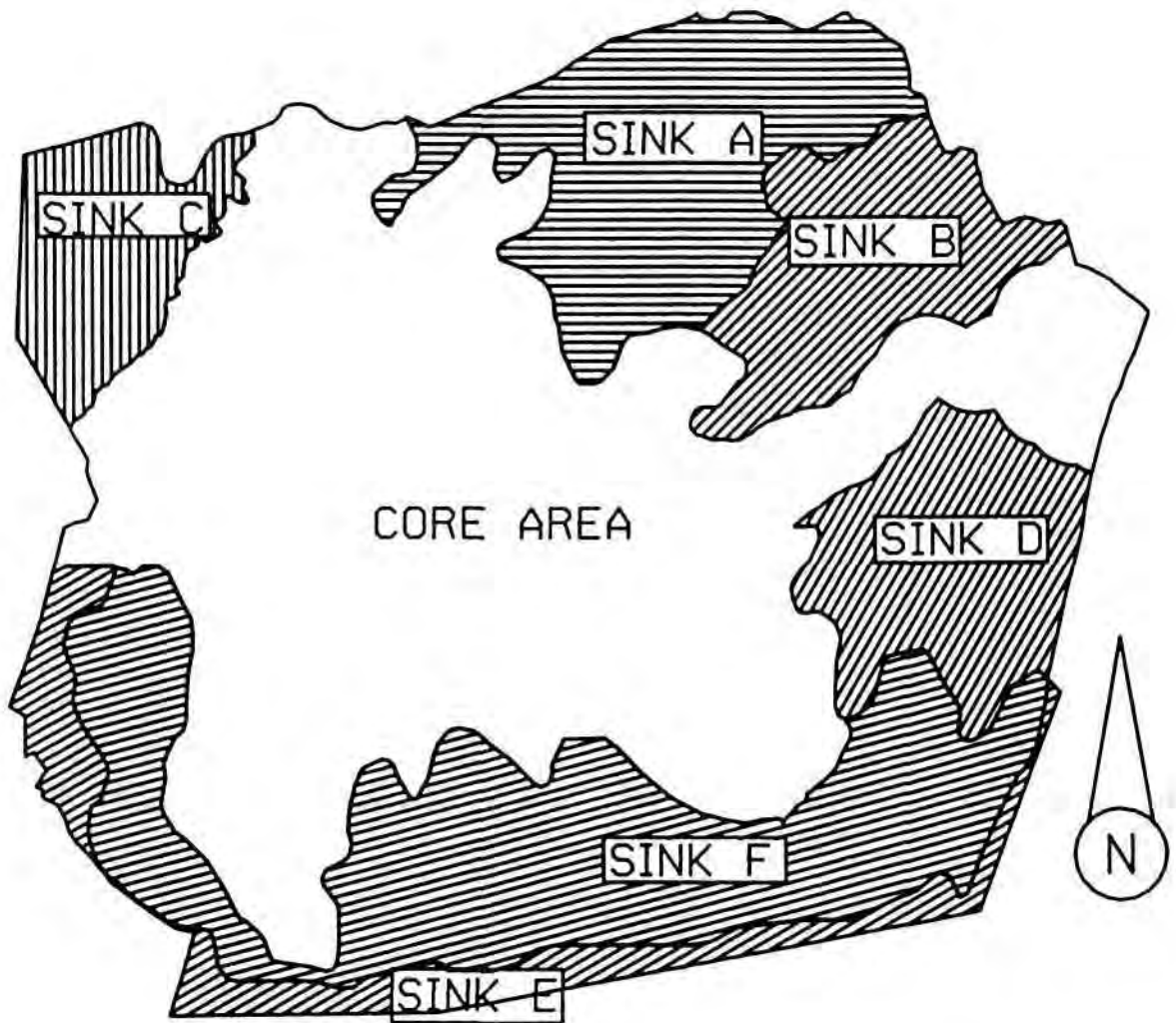


Fig. 1. Position of the white rhino vacuum zones in the Umfolozi Game Reserve in 1995-1996. (Scale 1: 200,000)

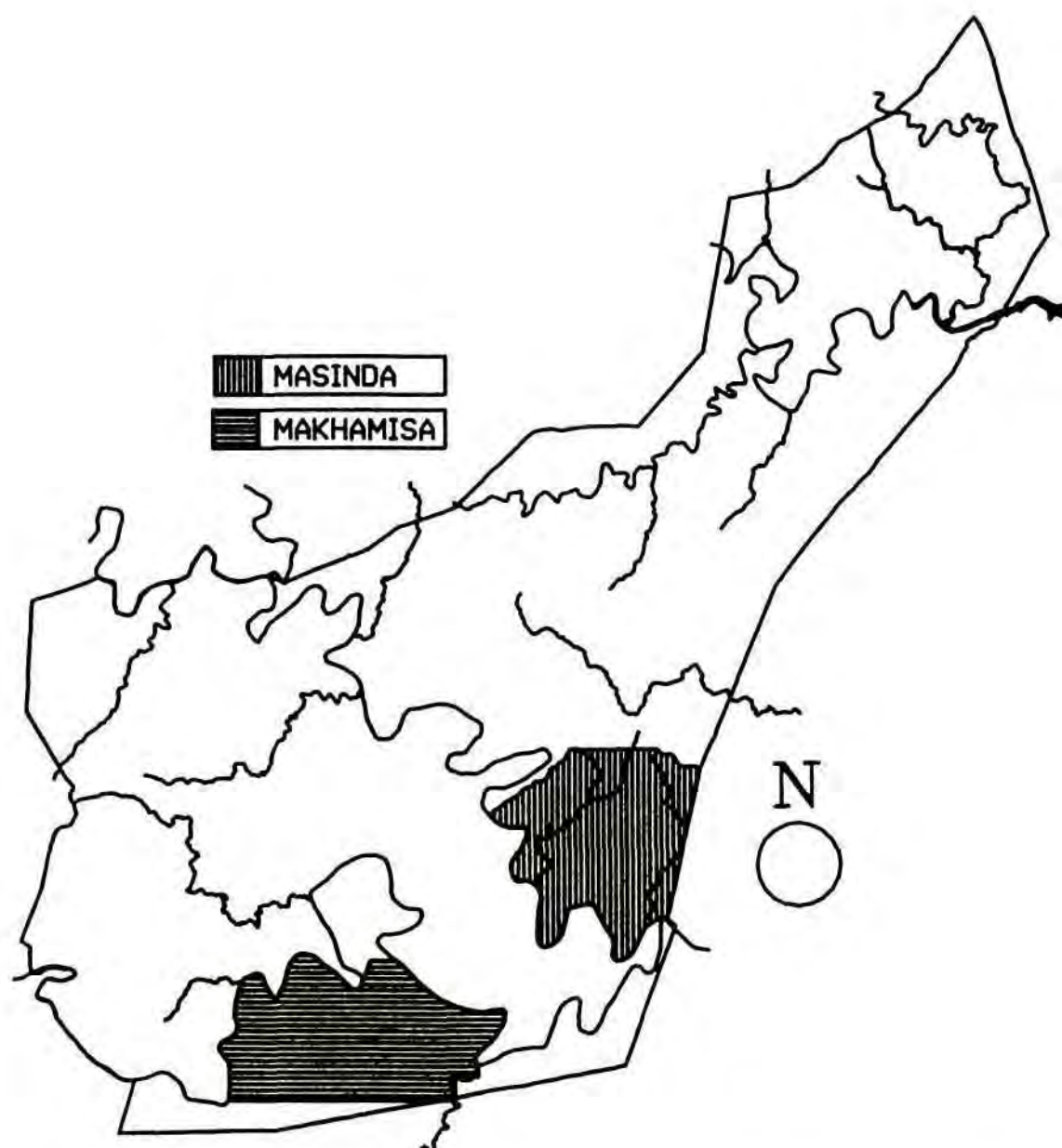


Fig. 2. Position of the Makhamisa (high density) and Masinda (low density) study areas in the Umfolozi Game Reserve in 1995-1996. (Scale 1: 300,000)

Chapter 1

Seasonal changes in the density of white rhinos in the low density vacuum zones

1.1 Introduction

In the late sixties and early seventies, the large white rhino population in the Umfolozi Game Reserve caused a large scale deterioration in the quality of the grassland habitats (Owen-Smith 1981). This, along with the fact that the white rhino population was still increasing in size, led to the recommendation by Owen-Smith (1981), for the creation of vacuum zones in the reserve to absorb excess animals. This removal policy, presently called the Sink Management Policy, created an opportunity for the natural dispersal process of white rhinos to operate (Owen-Smith 1981). However, the management staff in Umfolozi expressed concerns that white rhinos were not dispersing into the vacuum zones, but only moving in temporarily to utilise trophic resources. Management staff speculated that the possibility existed that the annual white rhino removals were being conducted during a time when large numbers of transient rhinos were in the vacuum zones. This implied that the removals were not be removing "excess" rhinos that may have dispersed into the vacuum zones, but may be depleting the population by removing too many rhinos from the reserve. To help answer the question as to how white rhinos utilise the vacuum zones, the seasonal changes in the density of two vacuum zones were monitored.

1.2 Materials and Methods

To determine the effect that density had on white rhino movement patterns, the white rhino density in one of the two study areas, Masinda, was manipulated. In Masinda, Game Capture removed 32 rhinos prior to the start of the study. While the density was manipulated in order to effect the study, the exact details concerning the number of rhinos that had to be removed to generate the manipulation were not planned by the study. The removals reduced the density of white rhinos in the Masinda study area to below 1 rhino/km². The white rhino population in the Makhamisa study area, however, was left unchanged with an estimated density of around 3 rhino/km².

To monitor the changes in rhino density, eight transects of five kilometres in length were established in each study area. Two transects were walked per day during the times when the white rhinos were the most active. The first transect was walked in the early morning, about 10-20 minutes after sunrise, and the second one in late afternoon, approximately three hours before sunset. Data were collected in seven sampling sessions of 32 days each, over a fourteen month period starting in July-August 1995. A total of sixteen days were spent in each study area per sampling session, during which, each transect was walked four times.

During each sampling session, the number of rhino groups seen per day was recorded for Makhamisa, the high density area, and Masinda, the low density area. To determine if this ratio was a reliable representation of the changes in rhino density, the seasonal visibility profiles for the two areas were compared. To generate the seasonal profiles, the sampling sessions were divided into wet (October 1995- March 1996) and dry (July 1995- September 1995 & April 1996- August 1996) seasons. These

seasons were differentiated by a minimum of a three fold increase or decrease in the amount of rainfall between consecutive months.

The visibility profiles of the two areas were determined by using the perpendicular distances of the rhino groups from the centrelines of the transects in each season. As the data were not normally distributed, they were tested for significance by using the non-parametric Mann-Whitney U test. The visibility profiles for each study area were compared between seasons, while in each season, the visibility profiles of the two study areas were compared. If the seasonal profiles were found not to differ then:

- 1) a combined visibility profile derived with the data from both study areas and seasons could be applied to the two study areas; and
- 2) it was assumed that the changes in the mean number of rhino groups seen/day between each sampling session, was not a factor of varying visibility between seasons or study areas, but due to actual changes in the number of rhino groups present.

Data on the number of white rhino groups were recorded using the line-transect method (Bothma *et al.* 1990; Brooks & Emslie 1995; Buckland *et al.* 1993; Krebs 1989). The perpendicular distance from the transect (y_i) was determined by multiplying the sighting distance (r_i) and the sine of the sighting angle (Θ_i) (Krebs 1989).

$$y = r \sin\Theta$$

Data were gathered on groups of white rhinos that were within a 500m strip on either side of the transect. Transects were truncated to 500m to reduce the chance that a rhino would be sampled on more than one transect in a single day and thus reduce

errors in the density estimation associated with double counting (Buckland *et al.* 1993). A full description of how the line transect method techniques and assumptions were applied is located in Appendix I. For each group, the number of rhinos found in the group (1-n individuals), the age and sex of the rhinos (Hillman-Smith *et al.* 1986; Owen-Smith 1973), the date and time they were seen, the grassland community they were in (Downing 1972; Owen-Smith 1973) and the observer's GPS position were recorded.

To determine the density of white rhino groups found in the two study areas, line transect data were analysed using the computer program Distance 2.1 (Laake *et al.* 1994). To generate large enough sample sizes to analyse with Distance 2.1, data from the seven sampling sessions, in each study area, were combined into the wet and dry seasonal categories.

Distance sampling techniques require 60-80 samples per sampling session to determine accurate density estimates. When the data were combined to form the wet and dry seasonal categories, a sufficient number of white rhino groups was found in each category (N=94 wet & N=213 dry) in the Makhamsa study area. In the Masinda study area, however, there were fewer than the 60 rhino groups per season (N= 36 wet & N=54 dry). Despite there being fewer than the recommended number of samples in Masinda, the data from the two study areas were analysed using Distance 2.1 (Laake *et al.* 1994) to estimate the density of rhino groups/ km².

Once the visibility profiles of the two study areas were determined not to differ significantly between the seasons or study areas (see results), a combined visibility

profile for the study was derived. This combined profile was derived by combining the wet and dry seasonal data from both Makhamisa and Masinda and analysing it with Distance 2.1 (Laake *et al.* 1994). The combined profile was then applied to the seasonal data from both the Makhamisa and Masinda study areas and new density estimates of the number of rhino groups/km² $\pm$ 95% confidence intervals derived.

The combined profile was applied to the seasonal data for each study area by dividing the number of rhino groups seen/km walked in the study area (N_i) by the conversion ratio of the combined data set (CR).

$$DS_i = \frac{N_i}{CR}$$

The conversion ratio of the combined data set was the ratio used to convert the number of rhino groups seen/km walked (N) into the density of rhino groups/km² (DS).

$$CR = \frac{N}{DS}$$

This ratio was also applied to the 95% confidence intervals of the original density estimates derived by Distance 2.1 to determine the 95% confidence intervals of the combined data set.

Significant differences between the original and combined density estimates were determined by examining the overlap of the 95% confidence intervals. This was done as the density estimates were ratios and thus could not be tested for significance by using a binomial test for two proportions or a chi-squared goodness-of-fit test.

Despite the addition of unforeseen circumstances, data collected in July-August 1996, for both the Makhamisa and Masinda study areas, were utilised in the sample to determine the changes in the rhino populations. Prior to the July-August 1996 sampling session, Game Capture staff removed rhinos from the Makhamisa section of the reserve, while at the same time in Masinda, approximately one third of the study area was burned.

1.2.1 Age and sex classes

The age and sex of all white rhinos observed along each transect was recorded. The age of individual rhinos were classified as either, adult (>7 -10 years) individuals not reliably distinguishable from fully mature individuals; subadult (2-7 years for females, 2 up to 10 years for males), immature individuals not attached to an adult female, or in the age range of two to three years if with an adult female; or calf (<3 years) immature animals less than three years of age that are with an adult female (Hillman-Smith *et al.* 1986; Owen-Smith 1973). For immature white rhinos (calves and subadults) the height of the individual relative to an adult white rhino and the degree of horn development were used as indicators of age (Hillman-Smith *et al.* 1986; Owen-Smith 1973; Pienaar *et al.* 1991). When two or more white rhinos, less than or equal to 2-3 years of age, were seen with a single adult female the youngest animal present was recorded as the female's calf while the other individuals were recorded as subadults.

The proportion of male and female adults, subadults and calves in each study area were determined. These proportions were determined by dividing the mean number of male and female rhinos recorded per sampling session in each age class, by the sum

of the age class means. Age compositions of the white rhino populations in each study area were determined by dividing the mean number of adults, subadults and calves recorded per sampling session by the combined sum of the age means.

1.2.2 Data Analysis

Subadults are the most mobile age class of white rhinos (Owen-Smith 1973) and thus the age class most likely to move in and out of the vacuum zones. To get an indication of whether white rhinos were moving into or out of the vacuum zones, the mean number of subadult white rhinos in each season was compared using the nonparametric Mann-Whitney U test. The Mann-Whitney U test was used as the data for subadult numbers in the two study areas were not normally distributed.

To determine if there were significant differences between the densities of rhino groups in each season or between the two study areas, the 95% confidence intervals were compared. The confidence intervals were used as, like with the comparison of the original and new density estimates, the ratios could not be tested with a binomial test for two proportions or a chi-squared goodness-of-fit test.

As there were no significant differences in the visibility profiles between seasons or study areas, it was estimated that the changes in the number of rhino groups seen/day reflected changes in rhino density (see results). Due to this, the changes in the number of rhino groups seen/day were analysed for significance. A repeated measures ANOVA (Anon 1995a; Keppel & Zedeck 1989; Mead 1990) was used to determine if there were significant differences between the number of rhino groups seen/day in the sampling sessions, in the Makhamisa and Masinda study areas. The

repeated measures ANOVA was employed to analyse the data as the white rhino populations in the two study areas had been sampled repetitively over the different sessions during the study, whereas the normal ANOVA method would treat the data as independent observations. By using the repeated measures ANOVA, the estimate of the inherent variability was based on the within unit variability and not on the between unit variability as with a normal ANOVA.

In each study area, there were two repeated measures of the white rhino populations:

- 1) the seven different sampling sessions; and
- 2) the four times that the transects were walked per sampling session.

For each study area, the area sampled was divided into four independent sections consisting of two transects each. As two transects were walked per day it was felt that the individual transects could not be considered as replicates. However, as the same two transects were walked together consistently throughout the study, the sections containing the two transects were treated as replicates. As it took four days to walk the eight transects in each study area, the four sections (replicates) were sampled four times per sampling session.

To determine if the number of rhino groups seen per day over the course of the study differed significantly between the two study areas, the data were analysed using the nonparametric Mann-Whitney U test. The Mann-Whitney U test was used over a two sample T test as the data were not normally distributed and could not be transformed.

1.3 Results

The visibility profiles derived from perpendicular distance data were used to determine if:

- 1) the visibility profile for each study area differed significantly between the two seasons; and
- 2) the visibility profiles of the study areas in each season differed significantly.

When the data were tested using the Mann-Whitney U test, no significant differences were found between any of the visibility profiles (Table 1). As these values did not differ, the visibility profiles were assumed to be the same and thus a combined profile was used to estimate the density of rhino groups in both the Makhamisa and Masinda study areas.

When the combined visibility profile was applied to the two study areas, new estimates for the density of rhino groups area were derived. The density of white rhino groups/km² determined from the original data using Distance 2.1 (Laake et al. 1994) and the combined data using the conversion ratio (CR) resulted in ratios that could not be analysed by using a binomial test for two proportions or a chi-squared goodness-of-fit test. To determine if the density estimates from the two visibility profiles were significantly different, the 95% confidence limits were compared. When these estimates were compared, no significant differences were found at the $P < 0.05$ level (Fig. 3 a & b).

As the density estimates from the two visibility profiles did not differ significantly, the estimates from the combined visibility profile were applied to the Masinda study

area to compensate for the small sample size found in the original analysis. To ensure that the densities in the two study sites could be compared, the combined visibility profile was also applied to the Makhamisa study area. When the densities of rhino groups (Fig. 4) and individual white rhinos (Fig. 5) were compared using the 95% confidence intervals, Makhamisa was found to have a significantly higher density than Masinda in both the summer (wet) and winter (dry) seasons. When the densities in each study area were compared between seasons no significant differences were found in the changes in rhino groups. However, a significant increase was recorded in the density of rhinos during the dry season in the Makhamisa study area.

When the number of rhino groups seen per day over the course of the study were tested with the Mann-Whitney U test, significantly more white rhino groups were recorded per day throughout the study in the Makhamisa study area than in the Masinda study area ($Z=8.233$, $P<0.001$) (Fig. 6). When the data were analysed to determine whether the number of rhino groups seen per day differed between sampling sessions, no significant differences were found in the Makhamisa (ANOVA Repeated Measures (within subject designs, multiple factor analysis), $df= 6,18$; $F= 0.818$; NS, $df= 3,9$; $F= 1.013$; NS), or Masinda (ANOVA Repeated Measures (within subject designs, multiple factor analysis), $df= 6,18$; $F= 1.871$; NS, $df= 3,9$; $F= 3.834$; NS) study areas (Fig. 6).

1.3.1 Sex classes

The sample of the white rhino population in the Makhamisa study area comprised 43.4% male and 56.6% female adults ($N= 435$); 51.3% male and 48.7% female subadults ($N= 76$); and 47.4% male and 52.6% female calves ($N= 137$). In Masinda,

the sample of the white rhino population comprised 49.6% male and 50.4% female adults (N= 141); 79.0% male and 21.0% female subadults (N= 19); and 40.9% male and 59.1% female calves (N= 22) (Table 2).

1.3.2 Age composition

The sample of the white rhino population in the Makhamisa study area had an age composition comprising of 61% adults, 12% subadults and 27% calves (N= 742). While in Masinda, the sample of the white rhino population comprised 67% adults, 11% subadults and 22% calves (N= 188) (Table 3).

To get an indication as to whether white rhinos were moving into and out of vacuum zones and thus only utilising them as areas in which to obtain trophic resources, the changes in the number of subadults seen/day in each season in the two study areas were analysed. When the data were analysed using the Mann-Whitney U test, no significant differences were found in the number of subadults seen per season in either the Makhamisa ($Z= 0.139$, NS) or Masinda ($Z= 1.358$, NS) study areas suggesting that rhinos did not leave the vacuum zones during the study.

1.4 Discussion

The understanding of the movement patterns of white rhinos in relation to the vacuum zones is the key to understanding how well the sink management policy for white rhinos is working in the Umfolozi Game Reserve. By monitoring changes in the density of white rhinos in two of the vacuum zones, the study attempted to estimate whether white rhinos were immigrating in and emigrating out of the vacuum zones or remaining in them year round.

In trying to determine if the combined visibility profile could be applied to the two study areas, the density estimates of the two profiles were compared and found not to differ significantly. However, the two estimates for the Masinda study area seemed to predict that the rhino density peaked in different seasons. These differences were likely the result of the small sample size used to derive the original estimates. However, as the confidence intervals of the two estimates in the Masinda study area overlapped, it was assumed that the estimates were not significantly different.

The results of the repeated measures ANOVA and the changes in the mean number of rhinos seen/day $\pm$ SE, differed with regard to determining if the number of rhino groups seen/day changed between the sampling sessions. The repeated measures ANOVAs estimated that there were no significant changes between the sampling sessions, while the standard errors of the means did not overlap suggesting that the number of groups could have varied during the study. These findings raise questions as to whether the number of rhino groups did in fact change between the sessions, however, with the data available, these changes, if they did occur, can not be proven.

When looking at the changes in rhino density between the May-June and July-August 1996 sampling sessions, it would seem that the added manipulations to both study areas did not influence the number of white rhinos found in either study area. However, these results may be an artefact of the small sample size of the rhino groups found in the sample sessions. With the available data, it would be difficult to prove whether any changes took place as a result of the manipulations, as the small sample sizes of the data would reduce the power of any statistical test.

The hypothesis that the pattern of fluctuation in rhino density would be similar between the study areas can be rejected at two levels. Firstly, the patterns for the changes in the mean number of white rhinos groups seen/day differed between the different sample sessions. Secondly, when the seasonal changes in rhino density in the two study areas were compared, the density of rhinos in the Masinda study area did not change while the density of rhinos in Makhamisa increased in the dry season. However, the extent to which these differences were related to the different starting rhino densities in Makhamisa and Masinda cannot be determined. Other effects such as the differences in the grassland community compositions of the two study areas and the availability of the preferred grazing and water resources of white rhinos between the two study areas, could also have had an affect on these changes in white rhino density. These factors will be addressed in later chapters with the differences in the trophic resources (grass and water) of the study areas and how they changed over the course of the study (chapter two). While the effects that the changing condition of the trophic resources had on white rhino numbers in the two study areas is addressed in chapter three.

The finding that subadult numbers did not differ between the wet and dry season in either study area indicates that either rhinos do not move between the core and vacuum zones or that conditions during the study were such that the rhinos did not need to utilise the vacuum zones. If rhinos do not move into or out of the vacuum zones, and if the annual removals are removing more than just 'excess' rhinos, then other factors must be leading to the removal of too many rhinos from the reserve.

However, if the number of subadult white rhinos did not change, then why was there an increase in the density of rhinos in Makhamisa during the dry season? In Umfolozi, as the dry season progresses the Umfolozi rivers become the main sources of water in the reserve. A possible explanation for the increased density of rhinos could be that white rhinos outside of the study area (core and other vacuum zones) moved towards the river which enclosed the Makhamisa study area. When the water level was low, rhinos could have moved into the study area thus increasing density. During the study, white rhinos were observed moving between the study area and the core when the water level was down, however, as these observations were only made two or three times, and no data were collected on the white rhino population in the core, no definite conclusions can be drawn. Owing these findings, the hypothesis that white rhinos would use the vacuum zones more during the dry season than in the wet season cannot be rejected. Also, if rhinos were moving into Makhamisa during the dry season, then the possibility exists that some of the rhinos removed from Makhamisa during the capture season (April-August) may have been from the core.

The results of the study show that the pattern of change for the mean number of rhinos seen/day and the changes in the density of rhinos between the seasons differed for the two study areas. Because of this, the hypothesis that the fluctuations in rhino density in the two study areas would be the same is rejected. However, the hypothesis that white rhinos use the sinks as a source of trophic resources and do not maintain home ranges in them cannot be rejected. In Masinda, there were no changes in the density of rhinos, density of rhino groups or the number of subadults, which suggested that the hypothesis could be rejected. However, as the density of rhinos in Makhamisa was found to increase significantly during the dry season, this hypotheses cannot be

rejected. To be able to understand what went on in Makhamisa, the areas where the rhinos entering the study area originated from would need to be determined. If the rhinos were moving into Makhamisa from other vacuum zones, and not the core, then the hypothesis could be rejected.

Table 1. Results of the Mann-Whitney U test on the number of rhino groups seen/day between the seasons in each study area and between the study areas in each season. Non-significant results indicate that the visibility profiles of the areas or seasons did not differ.

Between seasons	Z	P
Makhamisa (wet & dry)	-0.051	NS
Masinda (wet & dry)	0.832	NS
Between study areas		
Wet (Makhamisa & Masinda)	0.226	NS
Dry (Makhamisa & Masinda)	-1.181	NS

Table 2. Mean number of individuals/sampling session and the percentage of male and female white rhinos in the Makhamsa and Masinda study areas. Percentages were estimated from the mean number of individuals recorded between the July-August 1995 and July-August 1996 sampling sessions. (N= total number of individuals recorded)

	Total	Male	Female
Makhamsa N= 639	5.7321	2.634 46%	3.098 54%
Masinda N=183	1.661	0.884 53%	0.777 47%

Table 3. Mean number of individuals/sampling session and the percentage of male and female white rhinos in each age class, in the Makhamisa and Masinda study areas. Percentages were estimated from the mean number of individuals/sampling session recorded between the July-August 1995 and July-August 1996 sampling sessions. (N= total number of individuals recorded)

Makhamisa	N	Mean	%
Adult	435		
Male	189	27.0	43.4
Female	246	35.0	56.6
Subadult	76		
Male	39	5.0	51.3
Female	37	5.0	48.7
Calf	137		
Male	65	9.3	47.4
Female	72	10.3	52.6
Masinda			
Adult	141		
Male	70	10.0	49.6
Female	71	10.1	50.4
Subadult	19		
Male	15	2.1	79.0
Female	4	0.6	21.0
Calf	22		
Male	9	1.3	40.9
Female	13	1.9	59.1

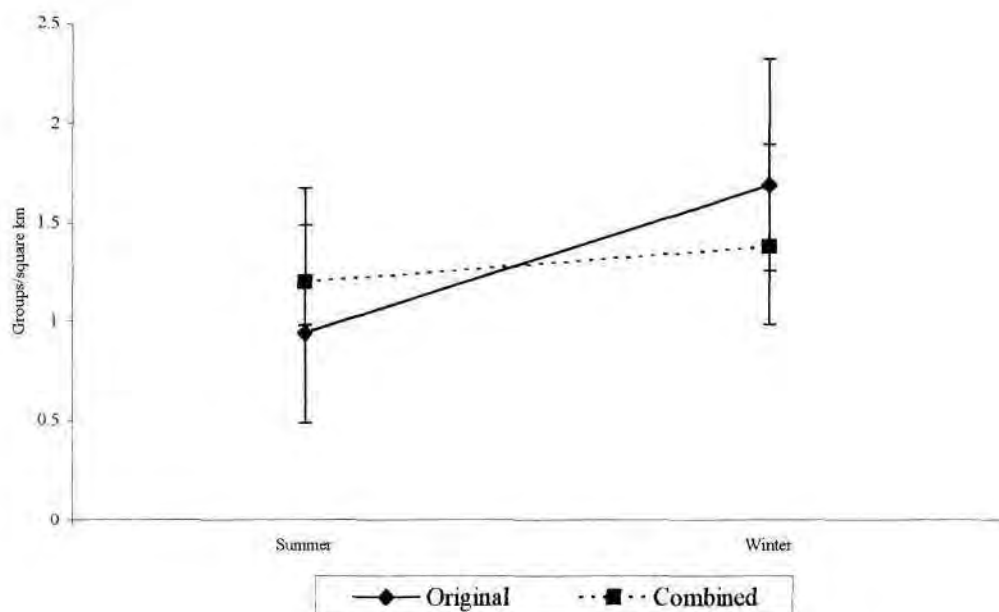
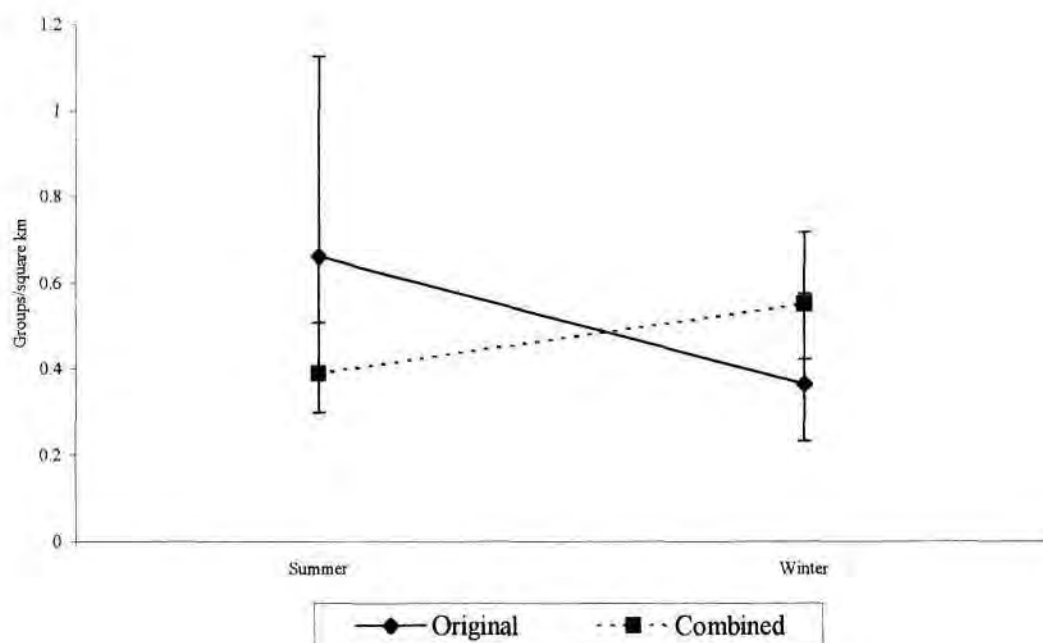
A.**B.**

Fig. 3. Mean density of rhino groups/km²/season $\pm$ SE derived using the original visibility profile (from Distance 2.1) and the combined visibility profile (from the combined seasonal data of both Makhamisa and Masinda) in the Makhamisa (A) and Masinda (B) study areas.

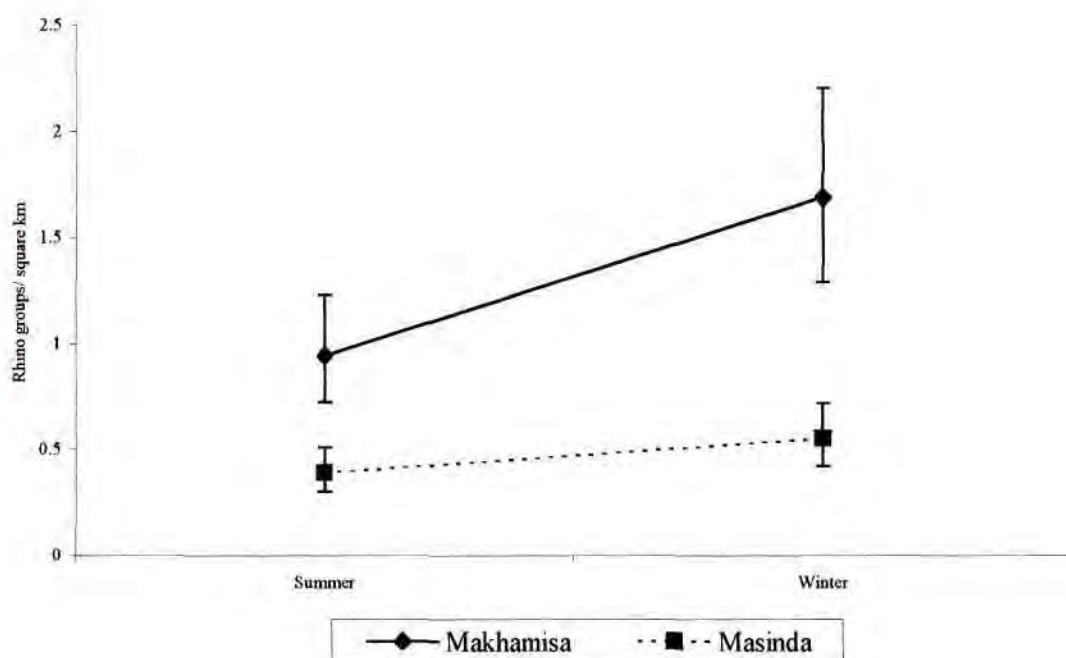


Fig.4. Density estimates of the number of white rhino groups/km² $\pm$ 95% confidence intervals in the Makhamisa and Masinda study areas. Estimates were derived using a combined visibility which that consisted of the seasonal data from both study areas.

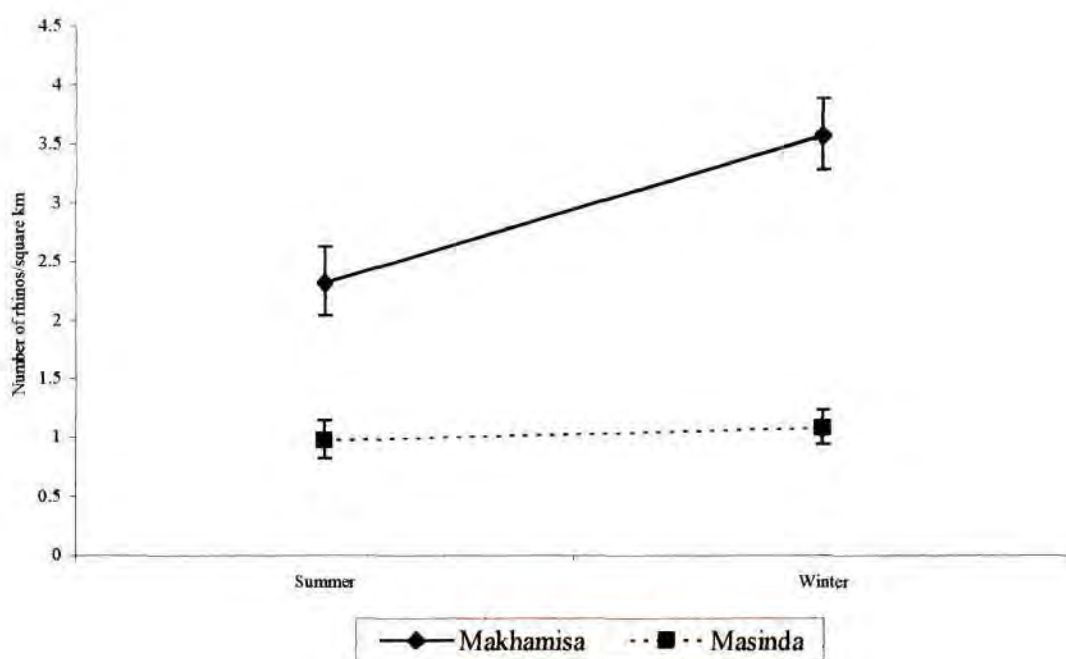


Fig. 5. White rhino density estimates $\pm$ 95% confidence intervals in the Makhamsa and Masinda study areas. Estimates were derived by multiplying the density of rhino groups/km² and the confidence intervals for each area in each season, by the average group size for the study area in the season.

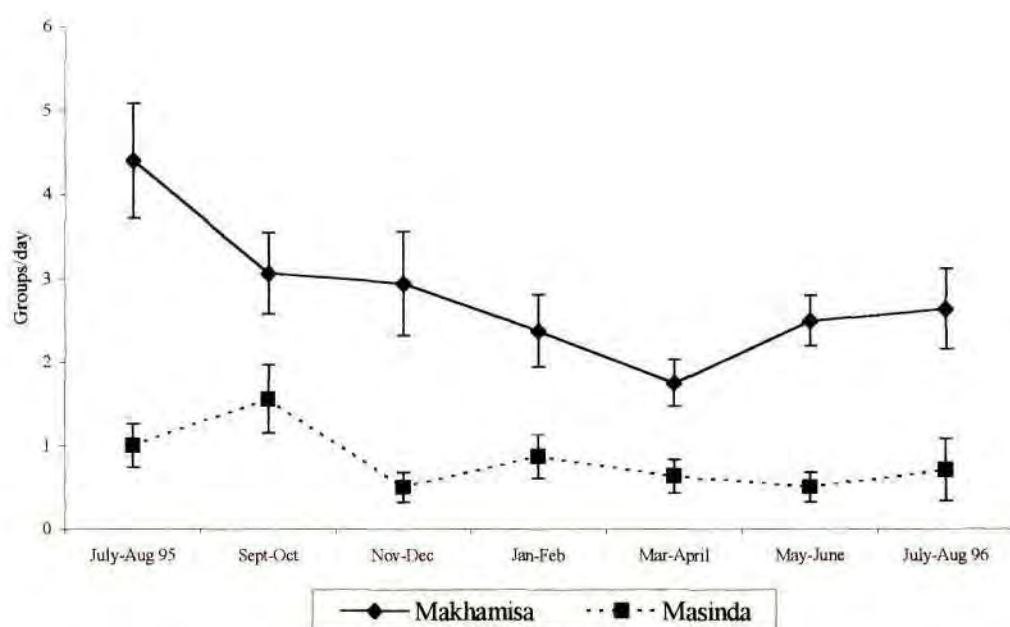


Fig. 6. Changes in the mean number of white rhino groups seen/day ($\pm$ SE) in the Makhamisa and Masinda study areas from July- August 1995 to July-August 1996.

Chapter 2

Trophic resources in the Makhamisa and Masinda study areas

2.1 Introduction

The grassland communities in the Umfolozi Game Reserve were classified by Downing (1972). Downing described nine different grassland communities in the reserve based on their floristic characteristics; Themeda, Themeda-Panicum, Themeda-Urochloa, Panicum coloratum, Themeda-Aristida, Panicum maximum, Trichoneura, Bothriochloa, and Cynodon. Owen-Smith (1973) then combined some of these communities physiognomically to form categories that were important to white rhino feeding ecology; Tall (Themeda, Themeda-Panicum), Short (Themeda-Urochloa, Panicum coloratum), Sandy (Themeda-Aristida) and Woodland (Panicum maximum). The remaining three grassland communities; Trichoneura, Bothriochloa, and Cynodon were not used in Owen-Smith's study as they were of limited occurrence in his study areas (Owen-Smith 1973).

[Owen-Smith (1973; 1988) described how white rhinos utilised different grassland communities at different times during the course of a year. The movement of white rhinos within and between territories and home ranges is governed by the changes in the condition and availability of the trophic resources in the grassland communities and water points (Owen-Smith 1973; 1988).] As the present study was concerned with how the density of white rhinos changed in the Makhamisa and Masinda study areas, it was important to establish how similar the two study areas were in regard to

grassland community composition and the availability of water, so as to be able to determine what effect density had on white rhino movement.

2.2 Materials and Methods

Data on the trophic resources in the Makhamisa and Masinda study areas were collected from September-October 1995 to July-August 1996. The eight transects in each study area were separated into the grassland communities found along them. The boundaries of these grassland communities were determined by a change in either grass species composition, slope or aspect. A Global Positioning System (GPS) position at the start of each community was recorded using a Trimble GeoExplorer. These positions, along with the GPS position for the start of the subsequent community, delineated the boundaries of the different grassland communities. Each grassland community was recorded as either a habitat, which was an area that was a minimum of 100m in length, or a grassland patch, which was less than 100m in length. This division was made as areas sampled that were 100m in length or longer could be plotted on a 1:50,000 scale map, however, some areas that were shorter than 100m were considered important for white rhino foraging (i.e. termite mounds found in the Tall grassland community (Owen-Smith 1973, 1988)). Each time a transect was walked the species composition of each grassland habitat was randomly sampled twice, while grassland patches were sampled only once. To generate a random sample, a 0.5 m² quadrat was thrown three times in different directions five metres either left or right of the transect from a random position within a habitat or patch. Data were recorded on grass species present, grass height and grass colour.

Data on the grass species composition of habitats and patches were analysed using the Dry-Weight-Rank method (Mannetje & Haydock 1963). This method was used to derive an estimate of the grass species composition of each grassland habitat or patch. In each quadrat thrown, the three most abundant grass species were ranked in as first, second or third place. The proportion of quadrats in which each grass species occurred in the three ranks was determined by adding the number of times a grass species fell into each rank and then dividing that number by the total number of times each rank was recorded in the habitat or patch. The proportions for each grass species were then multiplied by the factors, 70.19 for first place, 21.08 for second place and 8.73 for third place and the results for each grass species added to determine the percentage that the specie contributed to a habitat or patch (Mannetje & Haydock 1963). A description of how the factors 70.19, 21.08 & 8.73 were derived is given in Mannetje & Haydock (1963).

To determine the grassland communities found in each study area, the five most abundant grass species in each habitat and patch were first compared with the grass species list for each of Downing's (1972) grassland communities, and then these communities were placed into one of Owen-Smith's (1973) grassland categories. In Masinda, four grassland communities were discovered that did not fit into any of Downing's (1972) or Owen-Smith's (1973) communities (Table 4). These grassland communities were combined into the single category named 'Other'.

The grassland community composition for each study area was extrapolated from the lengths of the grassland habitats and patches recorded along each transect. The distances for the habitats and patches were determined by plotting their GPS positions

on the GIS programme Arcview 3. In each study area, the total distance for each grassland community was then calculated by adding the distances of the individual habitats and patches. The distance for each grassland community was then divided by the total distance of all the communities to estimate the percentage of the study area comprised by each grassland community.

2.2.1 Grassland condition

The seasonal condition of the habitats and patches were recorded as aspects of grass height and colour. In each quadrat the mean grass height was estimated from all grass plants (including emergent clumps where present) and the data recorded in one of three height categories; <10 cm, 10-30 cm, or >30cm. These categories were chosen to estimate different degrees of white rhino grazing pressure with the assumption of grazing pressure being inverse to grass height. The height of the grass was measured from the ground to the tallest standing part of the grass (i.e. top of the inflorescence). If the grass was leaning over, decumbent or procumbent, the height was taken from the ground to the tallest part of the grass plant without straightening the grass stem. If grass height was variable within a quadrat, five height measurements were taken, one in each corner and one in the middle, and the average of these measurements used as the height of the grass in the quadrat.

The overall grass colour for each quadrat was estimated and recorded in similar categories to those used by Owen-Smith (1973), which represented a typical orderly seasonal trend in the varying degrees of greenness, i.e. green (a combination of Owen-Smith's early green and late green categories), mainly green, mainly brown and brown.

2.2.2 Surface water

The presence of surface water in pans, streams and rivers was recorded while walking each transect. The size of each pan was categorised based on the diameter of the pan; <2m, 2-5m, 5-10m and >10m. The presence of surface water in each of these pans was recorded as either just water, a combination of mud and water, just mud or dry. Streams were categorised by width; <1m, 1-5m or >5m, while water in the streams and the Umfolozi rivers was recorded as either being present or absent.

2.2.3 Rainfall

Rainfall data were recorded on a monthly basis at the Makhamisa and Masinda ranger stations. The amount of rainfall recorded during the sampling sessions was derived by adding the data for the two months that coincided with each sampling session (i.e. The rainfall data recorded for July 1995 and August 1995 were added to give the total rainfall for the July-August 1995 sampling session.). The annual rainfall for each study area was determined by adding the rainfall from the twelve month period of July 1995 to June 1996. The annual rainfall of the combined study areas was determined by adding the total monthly rainfall from July 1995 to June 1996 from both study areas and then dividing by two (the number of study areas).

2.2.4 Data Analysis

A MANOVA was used to determine if there was a significant difference between the grassland community compositions of the two study areas. The eight transects in each study area were assumed to be replicate samples of the study areas and the data,

which were percentages of each grassland community found along each transect, and were Arcsine transformed prior to analysis. The MANOVA was performed using the statistical package Statistica (Statsoft 1995).

A paired sample T test was used to determine if the amount of rainfall recorded during the study differed significantly between the Makhamisa and Masinda study areas. The paired sample T test was used as the data were related by sample session. As with the MANOVA the paired sample T test was performed using the statistical package Statistica (Statsoft 1995).

Loglinear analyses (Anon 1995b; Bakeman *et al.* 1992; Knoke & Burke 1980; Sokal & Rohlf 1995) were performed with the computer package Statgraphics to determine if there were significant seasonal changes in grass condition and the availability of surface water in the Makhamisa and Masinda study areas. The loglinear analysis was chosen because it was considered more appropriate for analysing categorical data than an ANOVA, was more powerful, and did not have the stringent assumptions of the ANOVA (Bakeman *et al.* 1992). An explanation of loglinear analysis and an example of a study using loglinear analysis is given in Appendix II.

In the present study, the number of levels for each variable was limited to four or less except for the sampling sessions. For the variable sampling session, six levels, (September-October 1995, November-December 1995, January-February 1996, March-April 1996, May-June 1996 and July-August 1996) were used in the analysis. These six levels were used as the categorical data for; grassland habitat, grass height, grass colour, and the availability of surface water in pans and streams were collected

during these sampling sessions and thus the data were already separated into these levels.

To reduce the size of the cross tabulation and increase the power of the analysis, the independent samples from some of the variables were combined. Grassland habitats were combined into four broad levels, Tall (Themeda, Themeda-Panicum), Short (Themeda-Urochloa, Panicum coloratum), Woodland (Panicum maximum) and Other (Themeda-Aristida, Trichoneura, Bothriochloa, and Cynodon). Grass colour was reduced to three levels, green (early green, late green), transition (mainly green, mainly brown) and brown (brown), while grass height was left in three levels (<10cm, 10-30cm, >30cm). The independent samples of the variables for availability of surface water in pans were combined to form three levels, water (water, mud and water), mud (mud) and dry (dry), while the levels for streams remained as water and dry.

Loglinear analyses were conducted on the data from each of the four grassland communities to determine changes in grass height and grass colour in the grassland communities during the study. The variables used in each analysis were study area [A], grass colour [B], grass height [C], and sampling session [D]. The model used in an analysis was determined by comparing models generated from both forward and backward selection procedures. For the tall, short and other grassland communities, both procedures determined that the model that best fit the data was the saturated model [ABCD], while for the woodland community the model that best fit the data was [ABD] [ACD] [BCD].

The analysis of the seasonal changes in the availability of water conducted for pans and streams used the variables; area [A], session [B] and water availability [C]. Both the forward and backward selection procedures determined that the fully saturated model [ABC] best fit the two data sets.

2.3 Results

The grassland community composition for each study area was determined (Figs. 7&8). Ninety five percent of the grassland habitat in Makhamisa was attributed to the Tall, Short, Sandy and Woodland communities with the last five percent being divided between the Cynodon and Bothrichloa communities. The Tall community was the most common grassland community in Makhamisa, comprising 31 percent of the total study area. At Masinda, 76 percent of the study area was attributed to the Tall, Short, Sandy and Woodland communities, with the remaining 24 percent being divided between the Cynodon, Other, Trichoneura and Bothriochloa grassland communities. The most prevalent community found at Masinda was the Tall grassland community which comprised almost half of the entire study area, with 43 percent. When the lengths of the grassland communities along each transect in the two study areas were analysed with a MANOVA, the grassland community compositions of the two study areas were found not to differ significantly (Wilks' $\lambda = 0.3102$; $df=1,14$; $P>0.05$).

2.3.1 Grassland condition

Seasonal changes in the height and colour of the four grassland communities in the Makhamisa and Masinda study areas were recorded. The highest availability of green grass in both study areas was recorded during the summer (November-December

1995 and January-February 1996 sampling sessions) and the availability of green grass decreased as the year progressed into winter (Figs. 9&10).

2.3.1.1 Tall grassland community

For the tall grassland community, the saturated model [ABCD] ($L^2 = 19.762$; $df = 20$; $P > 0.05$) was fitted to the data ($N = 15,930$) and six significant interactions were found (Table 5). At Makhamisa there was:

- 1) significantly more green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly less green, <10cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 3) significantly more brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected.

At Masinda there was:

- 1) significantly less green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly more green, <10cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 3) significantly less brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected.

2.3.1.2 Short grassland community

For the short grassland community, the saturated model [ABCD] ($L^2 = 32.716$; $df = 20$; $P < 0.05$) was fitted to the data ($N = 5,965$) and ten significant interactions were found (Table 6). At Makhamisa there was:

- 1) significantly more green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly less green, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 3) significantly more green, >30cm tall grass recorded in the May-June sampling session than expected;
- 4) significantly more brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 5) significantly less brown, >30cm tall grass recorded in the July-August 1996 sampling session than expected.

At Masinda there was:

- 1) significantly less green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly more green, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 3) significantly less green, >30cm tall grass recorded in the May-June sampling session than expected;
- 4) significantly less brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 5) significantly more brown, >30cm tall grass recorded in the July-August 1996 sampling session than expected.

2.3.1.3 Woodland grassland community

For the woodland grassland community, the model [ABD] [ACD] [BCD] ($L^2=13.434$; $df=24$; $P>0.05$) was fitted to the data ($N=6,282$) and twenty seven significant

interactions were found (Table 7 a&b). Sixteen of these interactions were between the factors study area, grass colour and sample session [ABD], while no significant interactions were found between study area, grass height and sample session [ACD]. The remaining eleven interactions were for the interaction between the combined grass colour and grass height of the two study areas and sample session [BCD]. At Makhamisa there was:

- 1) significantly more green grass recorded in the September-October sampling session than expected;
- 2) significantly more green grass recorded in the January- February sampling session than expected;
- 3) significantly less green grass recorded in the July-August 1996 sampling session than expected;
- 4) significantly more transitional grass recorded in the March-April sampling session than expected;
- 5) significantly less transitional grass recorded in the May-June sampling session than expected;
- 6) significantly less brown grass recorded in the September-October sampling session than expected;
- 7) significantly more brown grass recorded in the May-June sampling session than expected; and
- 8) significantly more brown grass recorded in the July-August 1996 sampling session than expected.

At Masinda there was:

- 1) significantly less green grass recorded in the September-October sampling session than expected;

- 2) significantly less green grass recorded in the January- February sampling session than expected;
- 3) significantly more green grass recorded in the July-August 1996 sampling session than expected;
- 4) significantly less transitional grass recorded in the March-April sampling session than expected;
- 5) significantly more transitional grass recorded in the May-June sampling session than expected;
- 6) significantly more brown grass recorded in the September-October sampling session than expected;
- 7) significantly less brown grass recorded in the May-June sampling session than expected; and
- 8) significantly less brown grass recorded in the July-August 1996 sampling session than expected.

When the grass colour and grass height of the two study areas were combined there was:

- 1) significantly less green, <10cm tall grass recorded in the January-February sampling session than expected;
- 2) significantly more green, <10cm tall grass recorded in the May-June 1996 sampling session than expected;
- 3) significantly more green, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 4) significantly more green, >30cm tall grass recorded in the January-February sampling session than expected;

- 5) significantly less green, >30cm tall grass recorded in the July-August 1996 sampling session than expected;
- 6) significantly less transitional, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 7) significantly less transitional, >30cm tall grass recorded in the September-October sampling session than expected;
- 8) significantly more transitional, >30cm tall grass recorded in the July-August 1996 sampling session than expected;
- 9) significantly more brown, <10cm tall grass recorded in the March-April sampling session than expected;
- 10) significantly less brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 11) significantly more brown, >30cm tall grass recorded in the July-August 1996 sampling session than expected.

2.3.1.4 Other grassland community

For the other grassland community, the saturated model [ABCD] ($L^2= 42.243$; $df= 20$; $P<0.05$) was fitted to the data ($N= 9,335$) and sixteen significant interactions were found (Table 8). At Makhamisa there was:

- 1) significantly more green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly less green, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 3) significantly more green, >30cm tall grass recorded in the July-August 1996 sampling session than expected;

- 4) significantly less transitional, <10cm tall grass recorded in the November-December sampling session than expected;
- 5) significantly more transitional, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 6) significantly more transitional, >30cm tall grass recorded in the November-December sampling session than expected;
- 7) significantly less transitional, >30cm tall grass recorded in the July-August 1996 sampling session than expected; and
- 8) significantly more brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected.

At Masinda there was:

- 1) significantly less green, <10cm tall grass recorded in the November-December sampling session than expected;
- 2) significantly more green, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 3) significantly less green, >30cm tall grass recorded in the July-August 1996 sampling session than expected;
- 4) significantly more transitional, <10cm tall grass recorded in the November-December sampling session than expected;
- 5) significantly less transitional, <10cm tall grass recorded in the July-August 1996 sampling session than expected;
- 6) significantly less transitional, >30cm tall grass recorded in the November-December sampling session than expected;
- 7) significantly more transitional, >30cm tall grass recorded in the July-August 1996 sampling session than expected; and

8) significantly less brown, <10cm tall grass recorded in the July-August 1996 sampling session than expected.

The results of the loglinear analyses indicated that from the beginning of the study through the rainy season, there was significantly more green grass at the Makhamisa study area than at the Masinda study area. Firstly, in the September-October sampling session the woodland grassland community at Makhamisa was significantly greener than Masinda. Secondly, in November-December the tall, short and other grassland communities at Makhamisa all had more short green grass than Masinda. Finally, in January-February there was significantly more green grass in the woodland community of Makhamisa.

However, in March-April, when the amount of green grass started to decrease in the two study areas, the Masinda study area maintained a higher percentage of green grass while Makhamisa had significantly more transitional grass. Masinda continued to have a higher proportion of green then transitional grass than Makhamisa for the remainder of the study. In May-June significantly more transitional grass and significantly less brown grass was found in the Masinda study area. During the May-June sample session, however, there was significantly more green grass >30cm found in the short grassland community in Makhamisa. In July-August 1996, the Masinda study area had a significantly higher percentage of green grass in the woodland community and significantly more green grass that was less than 10cm in the tall, short, and other grassland communities.

During the study, as the seasons progressed from the dry season into the summer rainy season and then back into the dry season again, both study areas expressed similar patterns of change with regard to grass height. The largest percentages of short (<10cm) and medium (10-30cm) grass in both study areas was recorded in the September-October 1995 study session (Figs. 11&12). This height distribution was the result of a combination of grazing by the herbivores in Umfolozi reducing the height of the grasses and a reduced plant growth owing to the prolonged dry season in early 1995 (Fig. 13). Once the rains returned in November the promotion of new growth exceeded the grazing pressure and the overall grass height increased. Grass growth continued to be greater than the level of grazing pressure until May-June 1996 when the grazing pressure of the herbivores in Umfolozi started to decrease the overall height of the grass, thus increasing the amount of grass present in short and medium height categories.

2.3.2 Surface Water

A difference was found between the number of pans and streams located in the Makhamisa and Masinda study areas. During the study more pans were present in Makhamisa while there were more streams in Masinda (Table 9). The availability of surface water in both pans and streams changed over the course of the study (Figs. 14-17). Surface water in pans was at a maximum availability in both study areas during November-December 1995 (Figs. 14&15). Water levels remained high through the rainy season and then gradually decreased to the lowest level of availability in July-August 1996.

When the data for the pans in the two study areas were analysed using loglinear analysis ($N= 2472$), the saturated model [ABC] ($L^2= 102.862$; $df= 10$; $P<0.05$) was found to best represent the data. When this model was fitted to the data set twelve interactions were found to be significant (Table 10). At Makhamisa there was:

- 1) significantly more pans that contained water in September-October than expected;
- 2) significantly less dry pans in September-October than expected;
- 3) significantly less pans that contained water in November-December than expected;
- 4) significantly less pans that contained water in March-April than expected;
- 5) significantly more dry pans in March-April than expected; and
- 6) significantly more dry pans in May-June than expected;

At Masinda were was:

- 1) significantly less pans that contained water in September-October;
- 2) significantly more dry pans in September-October than expected;
- 3) significantly more pans that contained water in November-December than expected;
- 4) significantly more pans that contained water in March-April than expected;
- 5) significantly less dry pans in March-April than expected; and
- 6) significantly less dry pans in May-June than expected;

For streams and rivers the availability of water peaked in March-April 1996 with 44% of the streams at Makhamisa and 75% at Masinda having water (Figs. 16&17). The water availability in the streams then declined to its lowest level in September-October 1995. Both the Black and White Umfolozi Rivers retained water through

September-October 1995, however, the availability of water differed. Surface water in the Black Umfolozi river during September-October 1995 was found in a small stream flowing between interspersed large pools while the White Umfolozi river only had water in a few pools that were <2m in diameter. When the saturated model [ABC] from the loglinear analysis was fitted to the stream data from the two study areas ($L^2= 31.307$; $df= 5$; $P<0.05$; $N= 1670$), no significant interactions were found. This indicates that the availability of water in the streams throughout the study did not differ significantly from what was expected.

2.3.3 Rainfall

The average annual rainfall for the UGR approximates 700mm (Walker *et al.* 1987). The present study was conducted during a year in which the UGR experienced above average rainfall with an average annual rainfall from July 1995 to June 1996 of 1020 mm for the two study areas (Fig. 13). When the rainfall data collected in the two study areas was analysed using a paired sample T test, Masinda was shown to have experienced a significantly higher amount of rain than Makhamisa during the study ($T=-2.692$, $df=6$, $P<0.05$).

2.4 Discussion

An understanding of the movement of white rhinos with regard to the vacuum zones requires a knowledge of how factors such as trophic resources including grass and surface water, change seasonally in the vacuum zones. The analysis of the grassland communities along the transects indicate that the Makhamisa and Masinda study areas did not differ significantly with regard to grassland community composition. These results seemed to differ from Figs. 7 & 8, however, when the variances and standards

errors of the grassland communities were examined, these descriptive measurements supported the findings of the MANOVA (Table 11).

The results of the loglinear analysis suggest that the Makhamisa study area had a higher availability of favourable grassland (i.e. green and <10cm) and water resources from September-October 1995 through to the end of the rainy season in February 1996. However, as the study progressed into the dry season, the delayed shift from predominantly green grass to predominantly brown grass at the Masinda study area created a higher availability of favourable grassland resources at Masinda than at Makhamisa. The persistence of green and transitional grass at the Masinda study area into the dry season was due to the larger amounts of rainfall experienced at Masinda during the study.

During the July-August 1996 sampling session, the increase in the amount of green grass <10cm in height and the decreases in the amount of brown grass that was <10cm in height, in the grassland communities of the Masinda study area were most likely the direct result of the burns conducted just prior to the July-August 1996 sampling session. This explanation is evident as first, the only significant increase in green grass in Makhamisa during the July-August 1996 sampling session was an increase in grass >30cm in the other grassland community. Second, after the first rains in July-August 1996 the increase in the growth of green grass was recorded mainly in areas that had previously been burnt.

Results indicate that the Masinda study area maintained a larger amount of available surface water than Makhamisa for most of the study. In the Makhamisa study area, a

larger number of pans was recorded, however, these pans only maintained a significantly greater amount of water than Masinda in the September-October sampling session. Masinda, however, had more streams than Makhamisa and a greater number of these streams retained water for the duration of the study.

Water becomes an important and critical resource at the end of the dry season when its availability is limited. During the study, the time period when the water resources in both study areas were at their lowest level was September-October 1995. During the September-October 1995 sampling session, the lowest water levels for both the Black and White Umfolozi rivers were recorded. The White Umfolozi, which borders Makhamisa, had only a few small pools that were <2m in diameter. At the same time, the Black Umfolozi, bordering Masinda, maintained a small stream flowing between large pools for most of the dry season, before it dried up and only the pools remained. The presence of a larger amount of water available in the Black Umfolozi River, the pans in Masinda having significantly more water than Makhamisa in the March-April sampling session, and that Masinda had more rainfall during the dry season, suggests that Masinda had a higher availability of surface water during the dry season.

It is evident from these results that the two study areas differed in the composition of trophic resources for white rhinos (grass and water). The grassland community compositions of the two study areas were not significantly different, however, the rate at which the indicators of quality (height and colour) varied, did differ. If rhinos were utilising the vacuum zones only as sources of grassland resources then one would expect a larger number of white rhinos to be present at Makhamisa during the rainy season while more rhinos would be present in Masinda during the dry season. The

results from chapter one showed that the white rhino density and the number of subadults in the Masinda study area did not vary between the two seasons. Makhamisa, however, differed from Masinda in that the density of white rhinos differed between the wet and dry seasons.

If only grassland resources attracted white rhinos into the Makhamisa vacuum zone, then one would expect an increase in white rhino density in the wet season, when the availability of green grass was high, and not during the dry season. The inverse pattern expressed at the Makhamisa vacuum zone suggests that the surface water present in the White Umfolozi River was what attracted rhinos to the study area, however, this hypothesis cannot be tested with the available data. One way of better understanding the movement of white rhinos with regard to the vacuum zones would be to determine the manner in which the different grassland communities in the vacuum zones are utilised by the white rhinos. In chapter three, the question of white rhino utilisation of the grassland resources at the Makhamisa and Masinda study areas is addressed.

Table 4. Grassland species list for the four grassland communities placed into the 'Other' grassland category. These communities are unique to the study as they were not described by either Downing (1972) or Owen-Smith (1973). Communities are named either for the grass species unique to the community (*Trichoneura*), the most prevalent grass species (*Bothriochloa*) or for the condition of the terrain in which the community is found (Disturbed & Marsh). The Marsh community is found in areas with a high soil water content, while the disturbed community is found along primarily along rocky hill slopes and erosion areas. Species are listed in alphabetical order and not according to prevalence.

Trichoneura community

Aristida diffusa
Brachiaria serrata
Brachiaria spp.
Chloris gayana
Eragrostis spp.
Eragrostis superba
Heteropogon contortus
Panicum maximum
Panicum schinzii
Paspalum scrobiculatum
Perotis patens
Pogonarthria squarrosa
Sporobolus nitens
Sporobolus fimbriatus
Themeda triandra
Trachypogon spicatus
Trichoneura grandiglumis
Tristachya leucothrix
Urochloa mosambicensis

Disturbed community

Cymbopogon plurinodis
Eragrostis spp.
Eragrostis nindensis
Heteropogon contortus
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

Bothriochloa community

Aristida diffusa
Bothriochloa insculpta
Cenchrus ciliaris
Digitaria ternata
Diplachne eleusine
Enneapogon cenchroides
Panicum maximum
Panicum deustum
Panicum schinzii
Sporobolus nitens
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

Marsh Community

Trachypogon spicatus
Eragrostis spp.
Eragrostis superba
Perotis patens
Setaria sphacelata
Tristachya leucothrix
Themeda triandra
Paspalum scrobiculatum

Table 5. Significant interactions from a loglinear analysis performed on data from the tall grassland community (N=15,930). The model found that best fit the data was the saturated model [ABCD]. Factors and variables in the model are: area [A] (1= Makhamisa, 2= Masinda), grass colour [B] (1= Green, 2= Transitional, 3= Brown), grass height [C] (1= <10cm, 2= 10-30cm, 3= >30cm) and sampling session [D] (1=Sept-Oct, 2= Nov-Dec, 3=Jan-Feb 1996, 4= Mar-April, 5= May-June, 6= July-Aug). Significant interactions are indicated by an absolute z-value larger than 1.96 and a 95% confidence interval (CI) which did not include zero.

Factor ABCD	Coefficient	SE	Z-value	Lower and 95% CI	Upper
1112	0.485	0.213	2.274	0.067	0.903
1116	-0.747	0.248	-3.008	-1.233	-0.260
1316	0.460	0.212	2.173	0.045	0.875
2112	-0.485	0.213	-2.274	-0.903	-0.067
2116	0.747	0.248	3.008	0.260	1.233
2316	-0.460	0.212	-2.173	-0.875	-0.045

Table 6. Significant interactions from a loglinear analysis performed on data from the short grassland community (N=5,965). The model found that best fit the data was the saturated model [ABCD]. Factors and variables in the model are: area [A] (1= Makhamisa, 2= Masinda), grass colour [B] (1= Green, 2= Transitional, 3= Brown), grass height [C] (1= <10cm, 2= 10-30cm, 3= >30cm) and sampling session [D] (1=Sept-Oct, 2= Nov-Dec, 3=Jan-Feb 1996, 4= Mar-April, 5= May-June, 6= July-Aug). Significant interactions are indicated by an absolute z-value larger than 1.96 and a confidence interval (CI) which did not include zero.

Factor ABCD	Coefficient	SE	Z-value	Lower and 95% CI	Upper
1112	0.504	0.229	2.203	0.056	0.953
1116	-0.887	0.285	-3.114	-1.446	-0.329
1135	0.403	0.193	2.083	0.024	0.782
1316	0.611	0.199	3.075	0.222	1.00
1336	-0.476	0.202	-2.358	-0.872	-0.080
2112	-0.504	0.229	-2.203	-0.953	-0.056
2116	0.887	0.285	3.114	0.329	1.446
2135	-0.403	0.193	-2.083	-0.782	-0.024
2316	-0.611	0.199	-3.075	-1.00	-0.222
2336	0.476	0.202	2.358	0.080	0.872

Table 7 a&b. Significant interactions from a loglinear analysis performed on data from the woodland grassland community (N=6,282). The model found that best fit the data was [ABD] [ACD] [BCD]. Factors and variables in the model are: area [A] (1= Makhamisa, 2= Masinda), grass colour [B] (1= Green, 2= Transitional, 3= Brown), grass height [C] (1= <10cm, 2= 10-30cm, 3= >30cm) and sampling session [D] (1=Sept-Oct, 2= Nov-Dec, 3=Jan-Feb 1996, 4= Mar-April, 5= May-June, 6= July-Aug). Significant interactions are indicated by an absolute z-value larger than 1.96 and a confidence interval (CI) which did not include zero. Significant interactions from the analysis were found in interactions [ABD] (Table 7A) and [BCD] (Table 7B) but not in [ACD].

A.

Factor ABD	Coefficient	SE	Z-value	Lower and 95% CI	Upper
111	0.415	0.199	2.083	0.024	0.806
113	0.473	0.171	2.764	0.138	0.808
116	-0.706	0.205	-3.449	-1.107	-0.305
124	0.487	0.166	2.942	0.163	0.812
125	-0.210	0.102	-2.064	-0.409	-0.011
131	-0.336	0.134	-2.513	-0.598	-0.740
135	0.292	0.123	2.386	0.052	0.532
136	0.818	0.143	5.687	0.536	1.099
211	-0.415	0.199	-2.083	-0.806	-0.024
213	-0.473	0.171	-2.764	-0.808	-0.138
216	0.706	0.205	3.449	0.305	1.107
224	-0.487	0.166	-2.942	-0.812	-0.163
225	0.210	0.102	2.064	0.011	0.409
231	0.336	0.134	2.513	0.074	0.598
235	-0.292	0.123	-2.386	-0.532	-0.052
236	-0.818	0.144	-5.686	-1.099	-0.536

Table 7 a&b (cont.)

B.

Factor BCD	Coefficient	SE	Z-value	Lower and 95% CI	Upper
113	-0.977	0.248	-3.942	-1.463	-0.492
115	0.444	0.191	2.318	0.069	0.819
116	1.609	0.278	5.782	1.064	2.155
133	0.626	0.233	2.688	0.170	1.082
136	-1.381	0.310	-4.451	-1.990	-0.773
216	-0.566	0.182	-3.102	-0.924	-0.208
231	-0.339	0.154	-2.203	-0.640	-0.373
236	0.490	0.183	2.677	0.131	0.848
314	0.738	0.350	2.108	0.052	1.424
316	-1.043	0.214	-4.877	-1.463	-0.624
336	0.892	0.203	4.396	0.494	1.289

Table 8. Significant interactions from a loglinear analysis performed on data from the other grassland community (N=9,335). The model found that best fit the data was the saturated model [ABCD]. Factors and variables in the model are: area [A] (1= Makhamisa, 2= Masinda), grass colour [B] (1= Green, 2= Transitional, 3= Brown), grass height [C] (1= <10cm, 2= 10-30cm, 3= >30cm) and sampling session [D] (1=Sept-Oct, 2= Nov-Dec, 3=Jan-Feb 1996, 4= Mar-April, 5= May-June, 6= July-Aug). Significant interactions are indicated by an absolute z-value larger than 1.96 and a 95% confidence interval (CI) which did not include zero.

Factor ABCD	Coefficient	SE	Z-value	Lower and 95% CI	Upper
1112	0.598	0.209	2.857	0.188	1.009
1116	-1.116	0.288	-3.876	-1.680	-0.552
1136	0.702	0.320	2.192	0.074	1.329
1212	-0.551	0.238	-2.313	-1.018	-0.084
1216	0.666	0.183	3.634	0.307	1.025
1232	0.477	0.221	2.157	0.044	0.911
1236	-0.409	0.178	-2.295	-0.759	-0.060
1316	0.450	0.205	2.199	0.049	0.851
2112	-0.598	0.209	-2.857	-1.009	-0.188
2116	1.116	0.288	3.876	0.552	1.680
2136	-0.702	0.320	-2.192	-1.329	-0.074
2212	0.551	0.238	2.313	0.084	1.018
2216	-0.666	0.183	-3.634	-1.025	-0.307
2232	-0.477	0.221	-2.157	-0.911	-0.044
2236	0.409	0.178	2.295	0.060	0.759
2316	-0.450	0.205	-2.199	-0.851	-0.049

Table 9. Number of pans (A) and streams (B) found along the transects in the Makhamisa and Masinda study areas. Pans are divided into size categories determined by diameter while streams are categorised by width.

A.

Pans	<2m	2-5m	5-10m	>10m
Makhamisa N= 75	6	20	27	22
Masinda N= 43	2	19	10	12

B.

Streams	<1m	1-5m	>5m
Makhamisa N= 25	5	18	2
Masinda N= 48	8	32	8

Table 10. Significant interactions from a loglinear analysis performed on data from the pans in the two study areas (N= 2472). The model found that best fit the data was the saturated model [ABC]. Factors and variables in the model are: area [A] (1= Makhamisa, 2= Masinda), sampling session [B] (1= Sept-Oct, 2= Nov-Dec, 3= Jan-Feb, 4= Mar-April, 5= May-June, 6= July-Aug 1996) and pans [C] (1= water, 2= mud, 3= dry). Significant interactions are indicated by an absolute z-value larger than 1.96 and a confidence interval (CI) which did not include zero.

Factor ABC	Coefficient	SE	Z-value	Lower and 95% CI	Upper
111	0.437	0.136	3.21	0.170	0.704
113	-0.476	0.105	-4.539	-0.681	-0.270
121	-0.351	0.141	-2.482	-0.628	-0.074
141	-0.527	0.089	-5.902	-0.702	-0.352
143	0.319	0.089	3.568	0.144	0.494
153	0.188	0.086	2.178	0.019	0.357
211	-0.437	0.136	-3.205	-0.704	-0.170
213	0.476	0.105	4.539	0.270	0.681
221	0.351	0.141	2.482	0.074	0.628
241	0.527	0.089	5.902	0.352	0.702
243	-0.319	0.089	-3.568	-0.494	-0.144
253	-0.188	0.086	-2.178	-0.357	-0.019

Table 11. The mean, variance and standard error of the grassland communities along the eight transects in the Makhamisa and Masinda study areas. The descriptive statistics support the findings of the MANOVA in indicating that the grassland community compositions of the two study areas do not differ significantly.

	N	Mean	Variance	Standard Error
Makhamisa				
Tall	8	0.308	0.046	0.076
Short	8	0.241	0.031	0.062
Woodland	8	0.258	0.040	0.071
Sandy	8	0.143	0.019	0.049
Cynodon	8	0.024	0.003	0.019
Trichoneura	8	0	0	0
Bothriochloa	8	0.026	0.003	0.020
Other	8	0	0	0
Masinda				
Tall	8	0.473	0.043	0.073
Short	8	0.120	0.007	0.029
Woodland	8	0.147	0.010	0.035
Sandy	8	0.085	0.008	0.032
Cynodon	8	0.077	0.040	0.071
Trichoneura	8	0.051	0.010	0.035
Bothriochloa	8	0.006	0.0003	0.006
Other	8	0.040	0.002	0.016

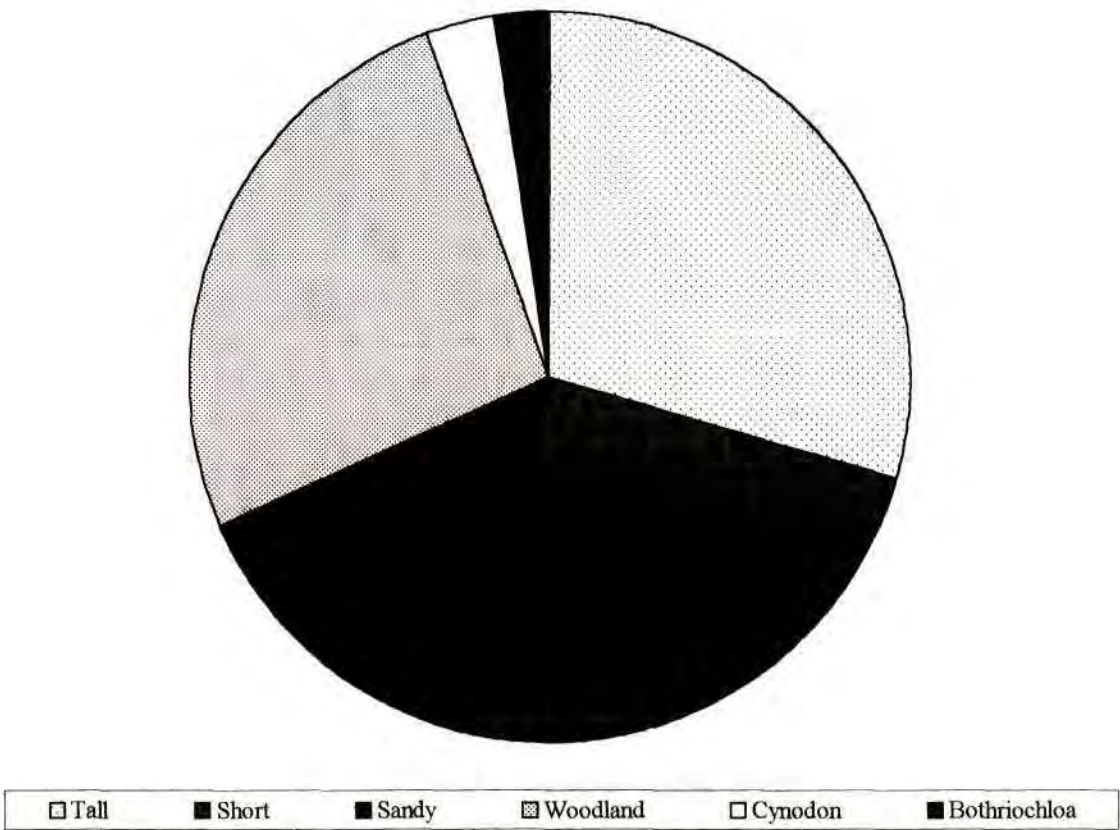


Fig. 7. The grassland community composition of the Makhamisa study area. Grassland communities are classified according to the grassland communities established for the Umfolozi Game Reserve by Downing (1972).

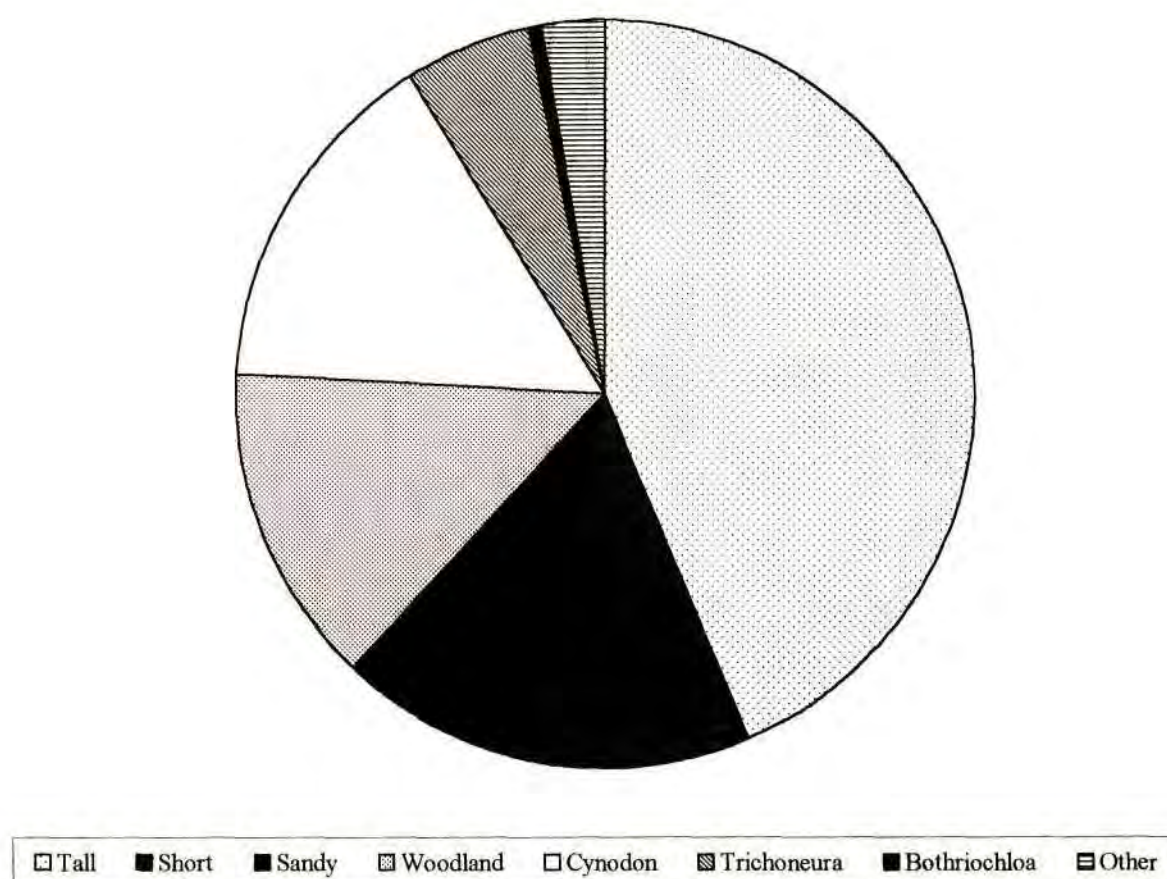


Fig. 8. The grassland community composition of the Masinda study area. Grassland communities are classified according to the grassland communities established for the Umfolozi Game Reserve by Downing (1972).

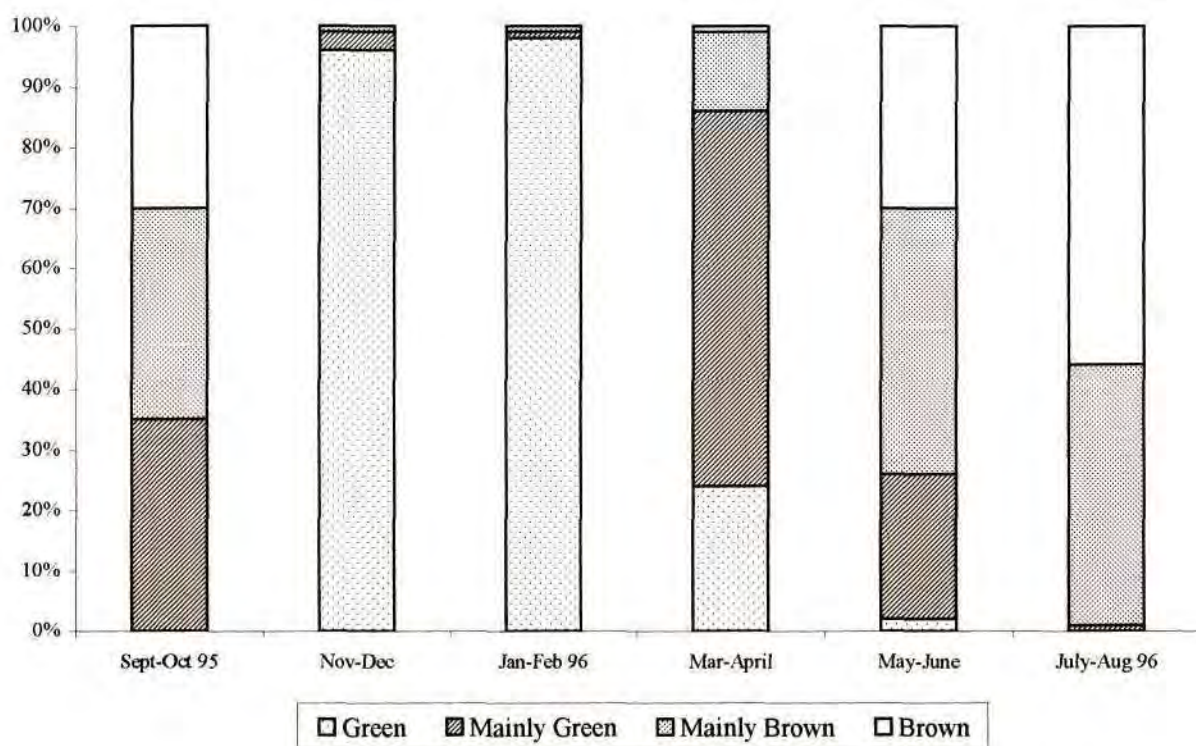


Fig. 9. Seasonal changes in the percentage of sampled grass found in each colour category in the Makhamisa study area, between the September-October 1995 and July-August 1996 sampling sessions. Grass colour is divided into four colour categories, green, mainly green, mainly brown and brown.

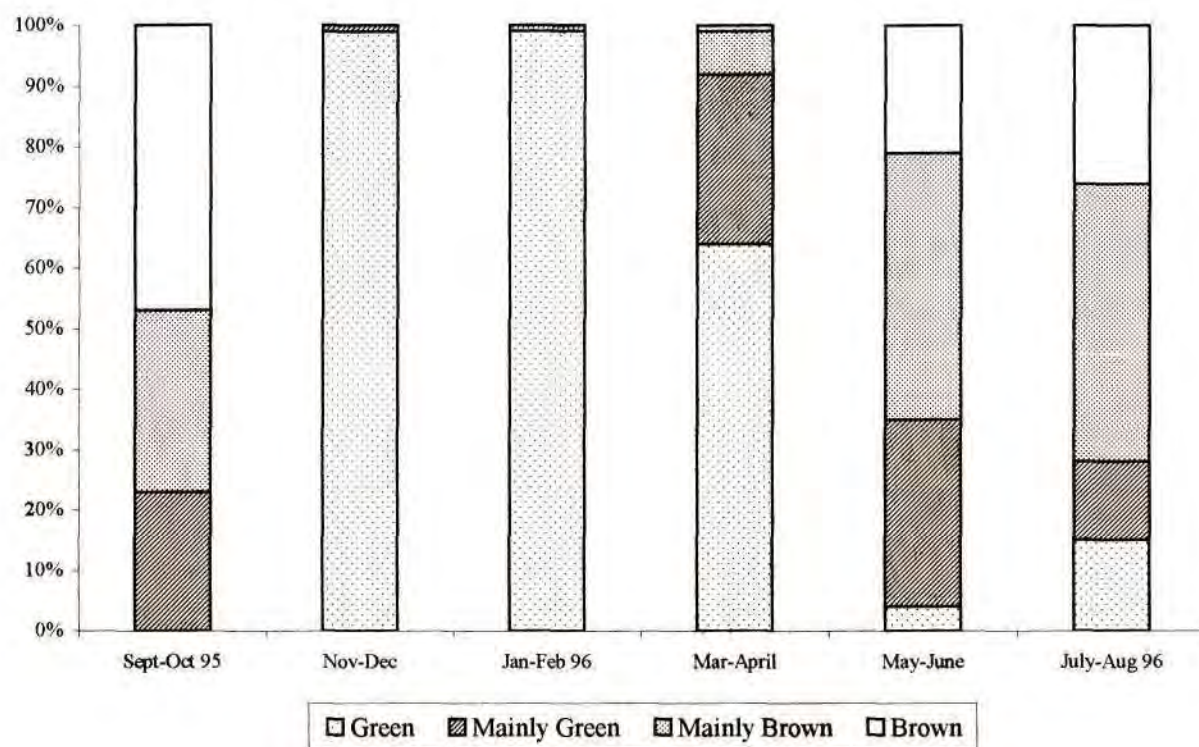


Fig. 10. Seasonal changes in the percentage of sampled grass found in each colour category in the Masinda study area between the September-October 1995 and July-August 1996 sampling sessions. Grass colour is divided into four colour categories, green, mainly green, mainly brown and brown.

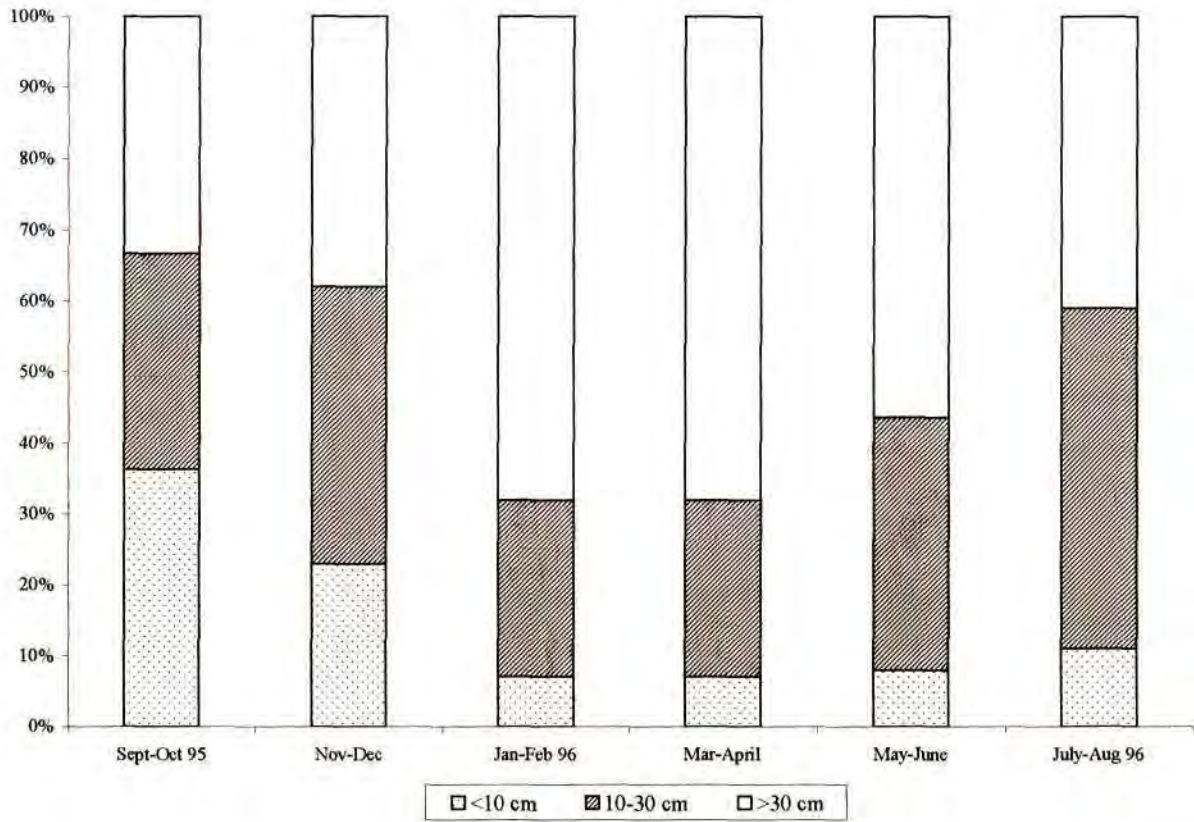


Fig. 11. Seasonal changes in the percentage of sampled grass found in each height category in the Makhamisa study area between the September-October 1995 and July-August 1996 sampling sessions. Grass heights are divided into three classes: less than 10cm, 10-30cm and greater than 30cm.

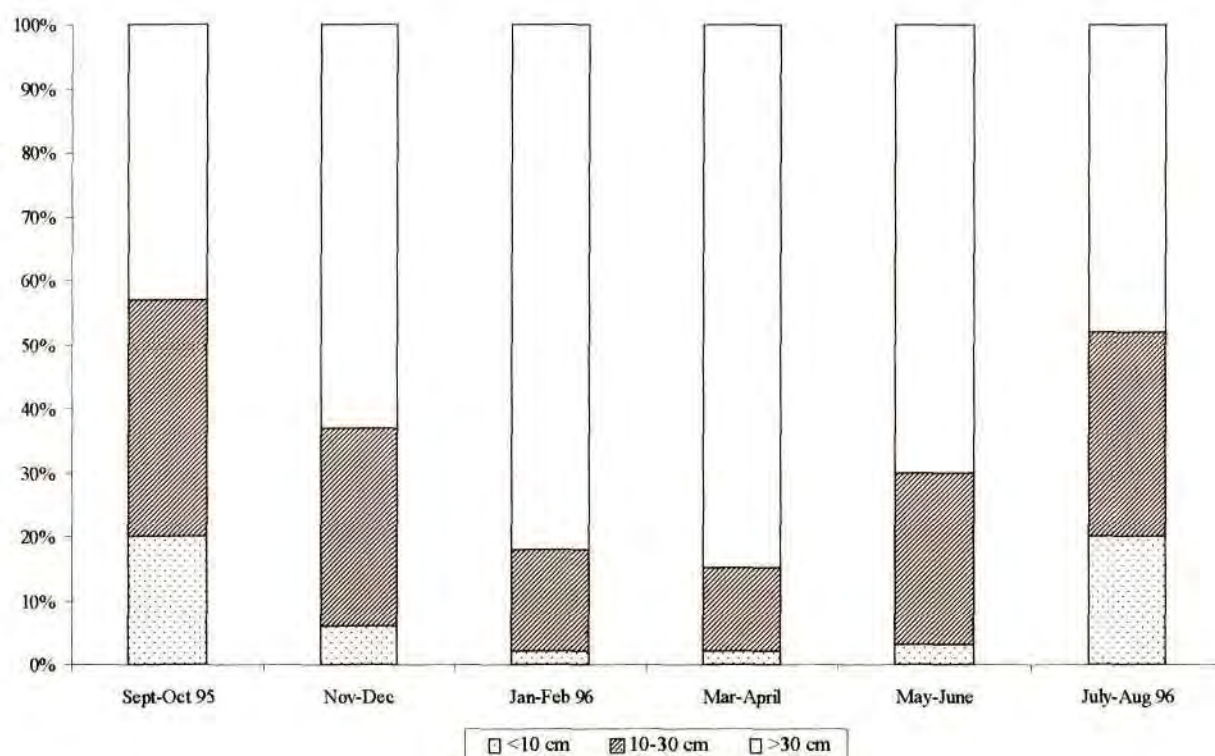


Fig. 12. Seasonal changes in the percentage of sampled grass found in each height category in the Masinda study area between the September-October 1995 and July-August 1996 sampling sessions. Grass heights are divided into three classes: less than 10cm, 10-30cm and greater than 30cm.

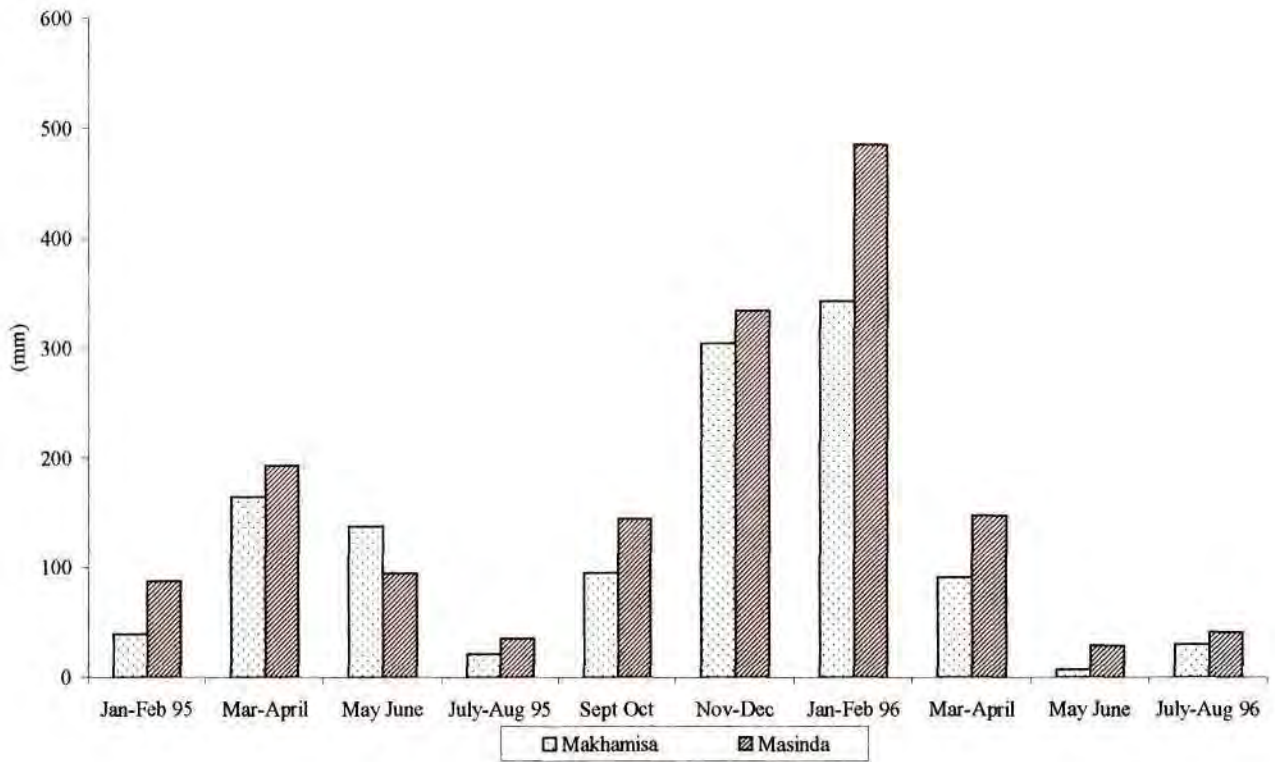


Fig. 13. Seasonal changes of rainfall, in millimeters, for the Makhamisa and Masinda study areas from January 1995 to August 1996. Rainfall data was collected at the Section Ranger outposts for both study areas and then combined into bimonthly categories.

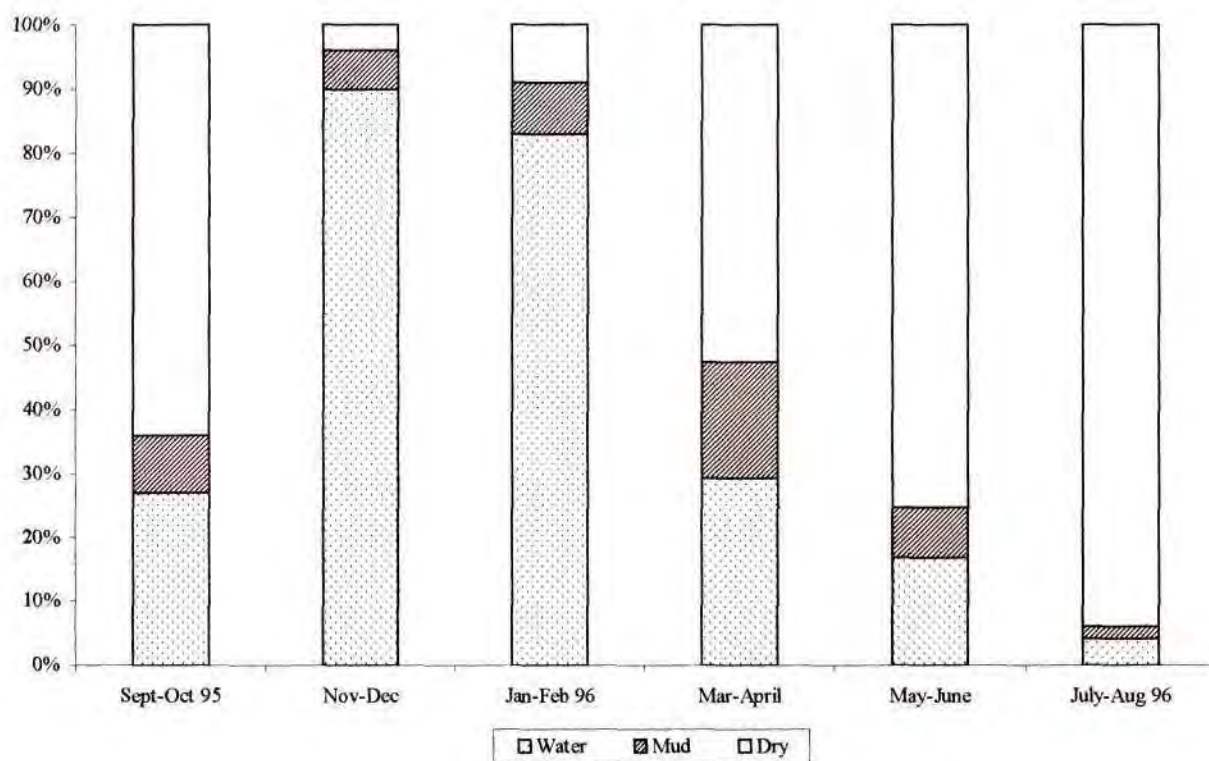


Fig. 14. Seasonal changes in water availability of the pans in the Makhamisa study area between the September-October 1995 and July-August 1996 sampling sessions. Water availability in pans is divided into three categories, dry, mud and water.

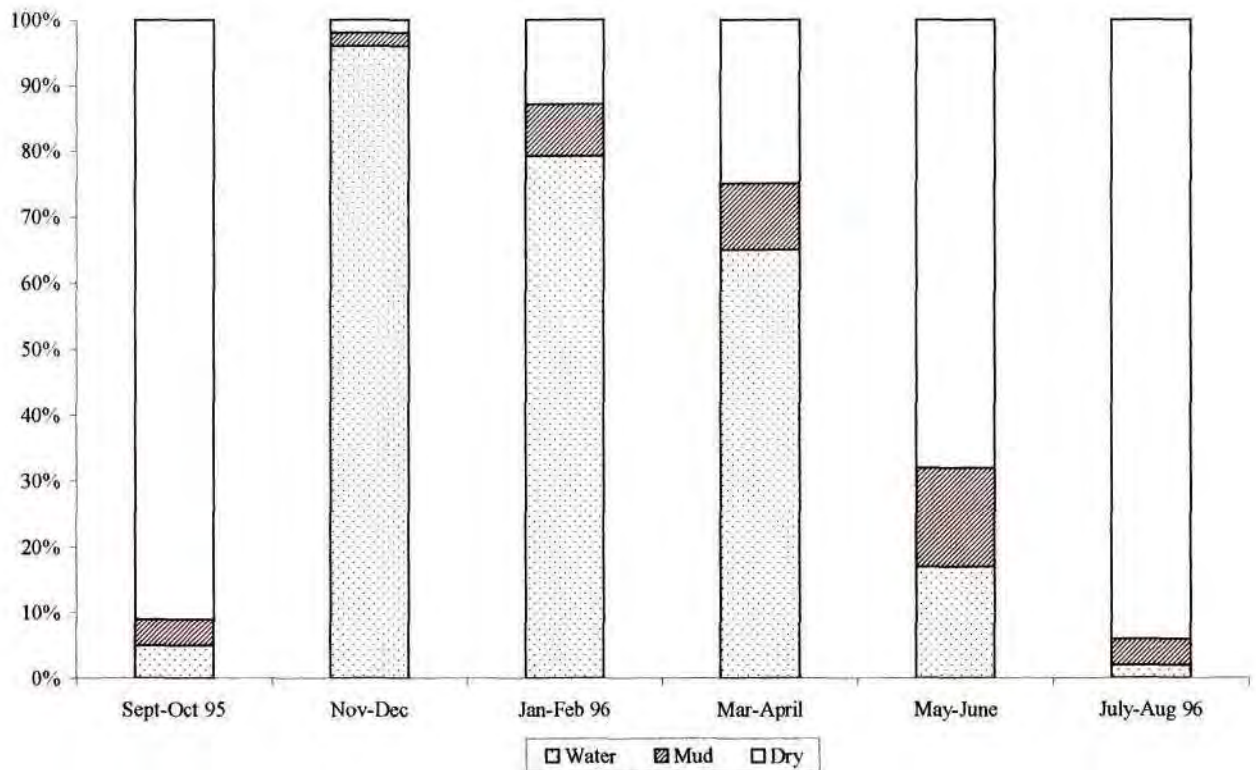


Fig. 15. Seasonal changes in water availability of the pans in the Masinda study area between the September-October 1995 and July-August 1996 sampling sessions. Water availability in pans is divided into three categories, dry, mud and water.

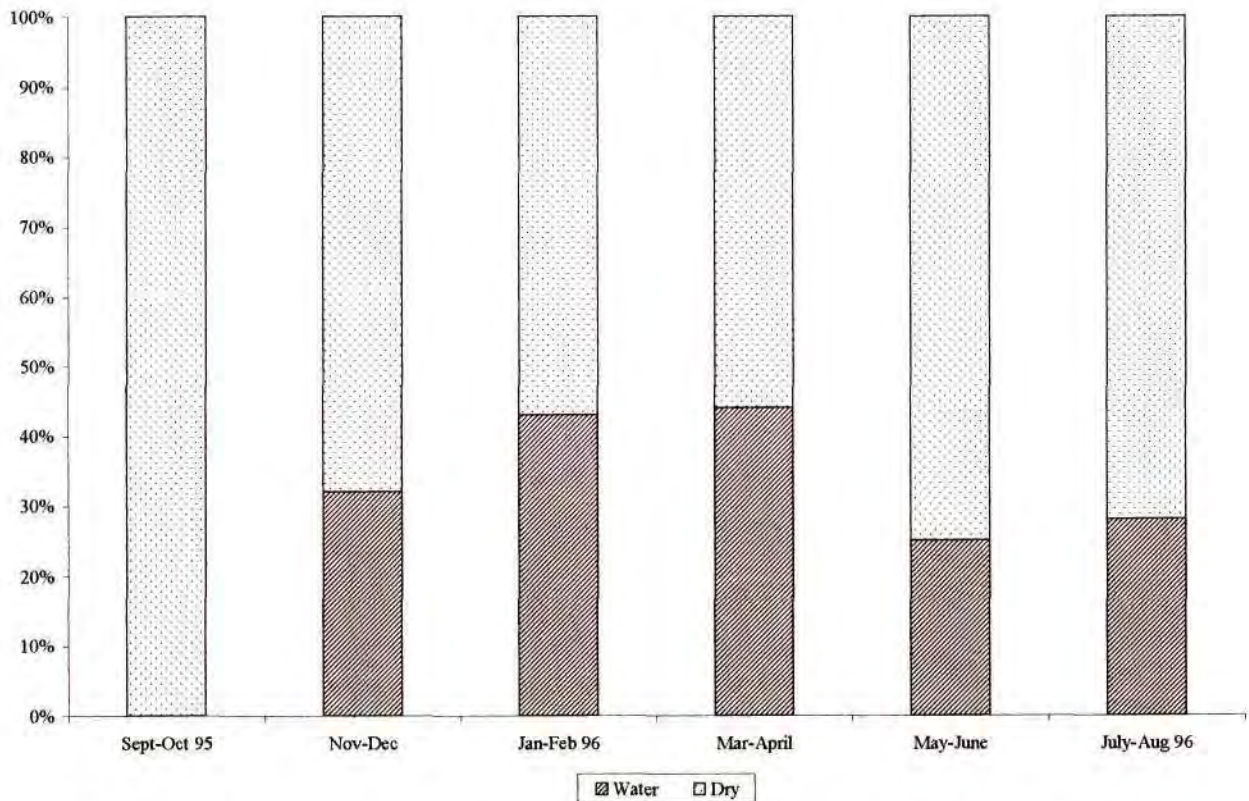


Fig. 16. Seasonal changes in water availability of streams in the Makhamisa study area between the September-October 1995 and July-August 1996 sampling sessions. Water availability for streams is divided into two categories, dry and water.

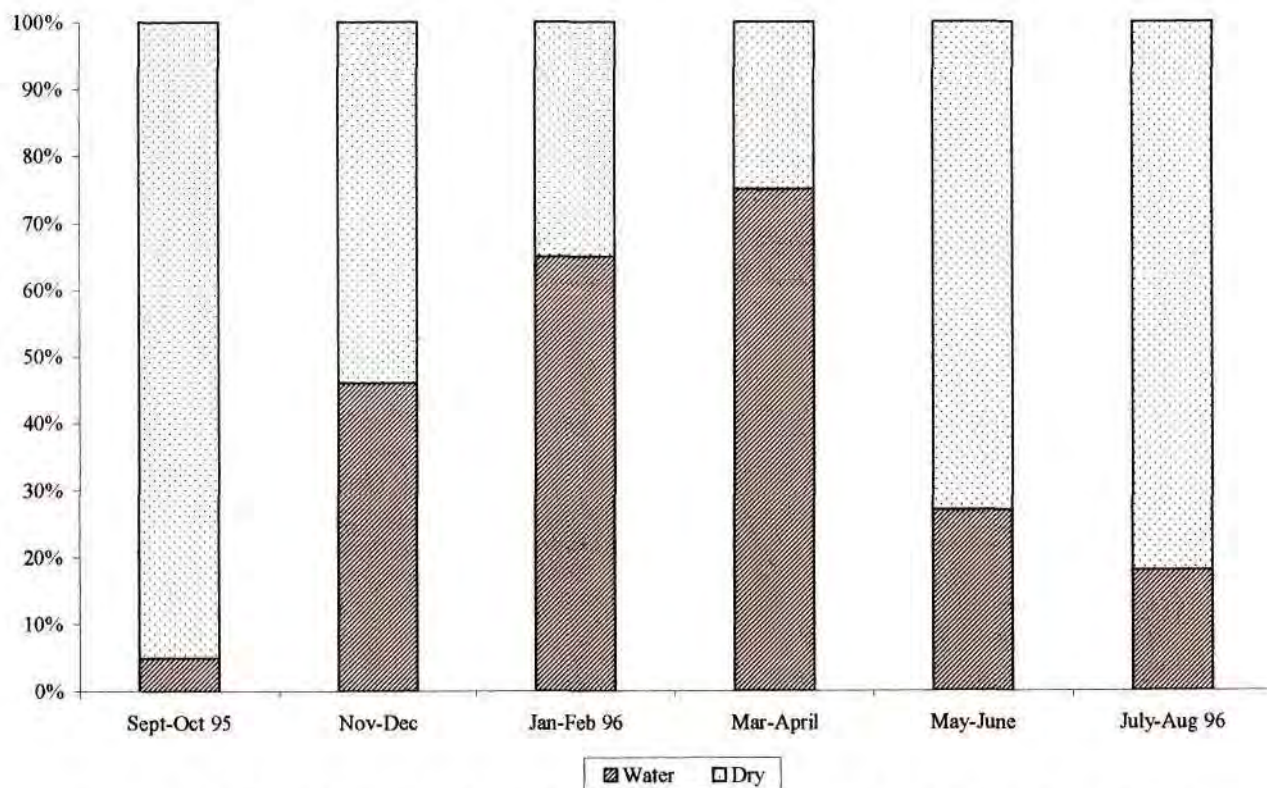


Fig. 17. Seasonal changes in water availability of streams in the Masinda study area between the September-October 1995 and July-August 1996 sampling sessions. Water availability for streams is divided into two categories, dry and water.

Chapter 3

Utilisation of the grassland communities by white rhinos

3.1 Introduction

During an animal's life it will seek food, water, shelter and access to mates from the environment in which it lives (Brown 1988; Coltman *et al.* 1997; Dunning *et al.* 1992; Fryxell & Sinclair 1988; Melton 1987). How an animal utilises the habitats available to it can be viewed as a direct expression of attempts to satisfy these various needs (Putman 1986). During the different stages in an animal's life the requirements of these various resources change, as does the availability of the resources. However, one of the most important attributes of an environment for an animal is the relationship between the quantity and quality of foods (Demment 1983). One aim of the present study was to determine how white rhinos in the vacuum zones reacted to the seasonal changes in resource availability (food and water) and to compare these utilisation patterns with the availability of resources and the utilisation pattern previously described by Owen-Smith (1973; 1988). In this chapter, I will integrate the findings of chapters one and two, and then combine them with data on the utilisation of the grassland communities by the white rhinos in the two study areas.

Optimal foraging theory (Pyke 1984; Schluter 1981) provides a functional approach for examining grazing behaviours, including diet selection, patch selection and movement (Bailey *et al.* 1996). The initial ideas of optimal foraging theory came from interactions between predators and their prey (Abrams 1997; Krebs 1978; Stevens & Krebs 1986) while more recently, attention has been directed to application of the theory to herbivores and their abundant yet low quality food (Bailey *et al.* 1996;

Belovsky 1997; Belovsky & Schmitz 1991; Jiang & Hudson 1993; Owen-Smith & Novellie 1982; Owen-Smith 1985, Owen-Smith 1991).

Herbivores encounter trophic resources at several levels of ecological resolution (Bailey *et al.* 1996; Senft *et al.* 1987; Kotliar & Wiens 1990; Laca & Ortega 1995). These levels can be collectively called a nested ecological hierarchy (Fig 18). A nested ecological hierarchy can be defined as the division of an animal's environment into distinct spatial sub-units, with the boundaries between these sub-units being determined, not by physical structures (Allen & Star 1982; O'neil *et al.* 1986; Spalinger and Hobbs 1992), but by an animal's foraging behaviour (Laca & Ortega 1993; Senft *et al.* 1987). Each level in the hierarchy not only has a distinct spatial scale attached to it, but also a distinct temporal scale (Table 12) (Laca & Ortega 1993; Senft *et al.* 1987).

In a nested ecological hierarchy, the upper levels comprise the levels below them (Allen & Star 1982; O'neil *et al.* 1986). As a herbivore forages through its environment the food resources it encounters can be considered in these different levels. With white rhinos in the Umfolozi Game Reserve, the most observable utilisation of the spatial scales of an ecological hierarchy range from bites to landscapes. Each landscape, whether it has man-made boundaries or not, comprises a group of vegetation communities termed habitats (Owen-Smith in press). A habitat is defined by its biotic properties (i.e. plant species composition, vegetation physiognomy or phenology) and areas that differ with regard to these properties constitute distinct habitat types (Owen-Smith in press). The areas that, together, make up a habitat are termed foraging sites. These sites have similar biotic properties yet

can differ with regard to their physical properties (i.e. slope or aspect). Each foraging site comprises a group of patches. The spatial scale of a patch is determined by an individual animal. The spatial boundaries of a single grazing patch are defined by the point at which the animal starts to graze, the distance it travels while it continually grazes, and ending at the point where the animal stops grazing (Jiang & Hudson 1993; Owen-Smith in press). The movement from one patch to another occurs when an animal stops grazing, moves a certain number of steps, then recommences grazing in a new spot within the foraging area (Jiang & Hudson 1993; Owen-Smith & Novellie 1982; Owen-Smith in press). Each patch comprises feeding stations which are defined as the area that can be exploited by a herbivore without it moving its front feet (Goddard 1968; Novellie 1978). Each feeding station comprises a collection of the smallest units called grains (Kotliar & Wiens 1990) which for herbivores are synonymous with bites (Bailey *et al.* 1996; Laca & Ortega 1995).

As a herbivore forages it can be viewed as making decisions on whether to move or stay in each level of the hierarchy. As the seasons progress, ungulates must respond to seasonal changes in the abundance, and quality of food resources (Owen-Smith & Cumming 1993). A herbivore must be able to utilise the information obtained from foraging in the lower levels (bites, feeding stations, patches) in order to make decisions concerning where to forage in the higher levels (foraging areas, habitats and landscapes) during the different seasons (Bailey *et al.* 1996).

Many studies have focused on the utilisation of patches by herbivores through different seasons and have put forward many reasons to explain the foraging strategies expressed by these herbivores. These foraging strategies have been explained by

changes in; foraging efficiency (Langvatn & Hanley 1993), intake rate (Illius *et al.* 1992; Laca & Demment 1991; Laca *et al.* 1993; Vivas *et al.* 1991), nutrients and crude protein of the vegetation (Cooper *et al.* 1990), fitness potential (Newman *et al.* 1995; Rosenzweig 1985) and the ratio between the depletion of a patch from utilisation and the rate of the vegetation regrowth (Owen-Smith in press).

Many of the explanations of the foraging strategies in the above studies are based on the underling assumption of the marginal value theorem (Charnov 1976). Foraging decisions of animals based on the marginal value theorem deal with decisions between whether to remain, move to another location on the same hierarchical level or to proceed to the next highest level (Laca & Ortega 1995). For example, if gains in a patch fall below the expectations of the gains of other patches in the same foraging area an animal can decide either to remain in that patch, move to another patch, or if the gains in all the patches of the foraging area are lower than other foraging areas, it may decide to move to a new foraging area.

During dry or cold seasons, plants become dormant and food availability decreases for herbivores in both quantity and quality (Owen-Smith 1982b). In their study of kudus (*Tragelaphus strepsiceros*), Owen-Smith and Cooper (1989; Owen-Smith 1994) found that as the dry season progressed the diet of kudus expanded to incorporate food types that were not eaten during the rainy season (i.e. palatable and unpalatable evergreen woody plants and unpalatable deciduous species). At the habitat level, when resources in a preferred grassland community become sufficiently depleted, herbivores can either expand their habitat utilisation to exploit multiple habitats or switch to using another habitat (Owen-Smith in press). The shifts

observed between habitats may be the result of changing nutritional value owing to phenophase, previous defoliation, and changes in leaf:stem and green:brown leaf ratios (O'Reagin & Schwartz manuscript). Thus, the species and habitats favoured in the wet season may not be favoured during the dry season (Owen-Smith in press).

A herbivores' change in diet may ultimately result in herbivores transferring between habitats on a seasonal basis (Owen-Smith in press). The expansion of a herbivore's diet breadth at the species and patch levels will have direct implications on which grassland communities are utilised by the herbivore. Owen-Smith (1979) found that kudus forage commonly in plains savannas during the wet season while in the dry season they concentrate their foraging in the hill base ecotone.

Over the course of a year, as a herbivore moves through its environment, it may ingest a wide range of food types and forage in many habitats. Owen-Smith (in press) lists six generic resource types of which I will use some to describe the grassland communities utilised by white rhinos: the high quality component, the staple component, high quality components with restricted intake rates, the reserve component the buffer component and the bridging component. These resource types vary in nutritional value, eating rates yielded, wet season availability and dry season attrition (Owen-Smith in press).

Pienaar *et al.* (1992, 1993) demonstrated that white rhinos in the Kruger National Park display preferences for certain landscapes. Owen-Smith (1973;1988) found that white rhinos utilised four broad grassland communities throughout the year. In the summer rainy season, when there was a high availability of short green grass, white

rhinos were found to forage primarily in the Short grassland community (Panicum coloratum and Themeda-Urochloa). As the dry season progressed, white rhinos reduced the time spent foraging in the Short grassland community and increased the time spent foraging in the Woodland (Panicum maximum) community and the Tall grassland community (Themeda and Themeda-Panicum) found on the flats. If the dry season continued to where the available resources in the Tall grasslands on the flats declined the white rhinos were found to shift and forage in the Tall grassland community (Themeda and Themeda-Panicum) found on hill slopes.

Following Owen-Smith's (in press) classification, the resource types that reflect the grassland habitats utilised by white rhinos in the Umfolozi Game Reserve are the: staple (short grass community), reserve (tall grassland community on flats) and buffer (tall grassland community on hill slopes). The woodland community could possibly be considered a bridging resource. However, it will depend on how important a role the woodland community plays in the foraging of white rhinos in the transition period between the wet and dry seasons.

A wide range of grass species and grassland communities are able to be utilised by white rhinos owing to the morphological and physiological traits of the rhinos. White rhinos are able to exploit short nutritious grass owing to their wide lips, which are used to pluck grass, while still being able to tolerate taller more fibrous grass owing to their large body size which increases the retention time of grass in the digestive tract (Hanley 1982; Owen-Smith 1988; Owen-Smith & Cumming 1993).

To test the hypothesis that the utilisation of the grassland communities by the populations of white rhinos in Makhamisa and Masinda would be similar, the interactions of white rhinos and resources were monitored at the habitat level. Any differences found in the utilisation patterns of the grassland communities by the white rhino populations in the two study areas would help determine if density affects the way in which white rhinos utilise grassland communities. These results then may also provide insight into why the rhino density in Masinda did not change between the seasons while the rhino density in Makhamisa did.

3.2 Materials and Methods

Data collection methods used to record the number of white rhinos found in each of the grassland communities in the two study areas were described in chapter one. The methods on how the different grassland communities were determined and sampled were described in chapter two.

3.2.1 Data Analysis

The number of rhinos recorded in each grassland habitat were analysed using a G-test (likelihood ratio test) for goodness of fit (Sokal & Rohlf 1995) and Bonferroni confidence intervals (Byers & Steinhorst 1984) to determine whether white rhinos utilised grassland habitats based on availability. The data were not analysed using loglinear analysis as the data set for rhinos was extremely small compared to the habitat data and thus too many zeros would have been present for the analysis.

White rhinos utilising the grassland communities in proportion to availability would indicate that the rhinos were not selecting grassland communities in which to forage

but were moving through the communities randomly. White rhino groups were used in the analysis rather than the total number of individuals to insure that the data points were independent. This was done as white rhinos moving in a group would not be moving independently of each other, and thus, each rhino would not be making independent decisions about the habitat in which to forage (Byers & Stienhorst 1984).

The utilisation of the grassland communities by white rhinos for the duration of the study and independently in the wet and dry seasons, relative to availability, was determined for the populations in the two study areas. In the analysis of utilisation at Makhamisa, six grassland communities were analysed; Tall, Short, Woodland, Sandy, Cynodon and Bothriochloa. In Masinda the same grassland communities were used except that the Bothriochloa community was replaced with a combination of the Trichoneura, Bothriochloa and Other grassland communities. These three grassland communities were combined as the sample sizes for each were small, which resulted in expected values that were less than five, which is insufficient as the G or χ^2 test requires an expected value of five or greater (Fowler & Cohen 1992; Koehler & Larntz 1980; Roscoe & Byars 1971; Sokal & Rohlf 1995).

The utilisation of the grassland communities by white rhinos in each sampling session could not be analysed. The removal of white rhinos prior to the study created a population in Masinda that was too small for statistical analysis. This circumstance, however, was not determinable prior to the commencement of the study. To generate suitable sample sizes for the grassland communities in both the Makhamisa and Masinda study areas, the data were divided into wet (October 1995 - March 1996) and dry (July 1995 - September 1995 & April 1996- August 1996) seasons.

3.3 Results

The utilisation of the grassland communities by white rhinos in both study areas differed significantly from the availability of the communities (Makhamisa, $G=98.693$, $df=5$, $P<0.001$; Masinda, $G=17.551$, $df=5$, $P<0.05$). In the Makhamisa study area, white rhinos utilised the Tall and Bothriochloa communities less than expected by chance while the Short and Cynodon community were utilised more than expected (Table 13). In Masinda, all the grassland communities were utilised in proportion to their availability except for the Sandy community which was utilised more than expected by chance (Table 13).

When the data were divided into seasons, the utilisation of the grassland communities by white rhinos in Makhamisa differed significantly to availability in both the wet ($G=68.290$; $df=5$; $P<0.001$) and dry ($G=44.592$; $df=5$; $P<0.001$) seasons. In Masinda, utilisation of the grassland communities differed to availability only in the wet season ($G=31.847$; $df=5$; $P<0.001$) but not in the dry season ($G=10.891$; $df=5$; NS). During the wet season white rhinos in the Makhamisa study area utilised the Tall and Bothriochloa grassland communities less than expected by chance, the Short and Cynodon grassland communities more than expected by chance and the Woodland and Sandy grassland communities in proportion to their availability (Table 14). During the dry season, the white rhinos in Makhamisa continued to utilise the Tall grassland community less than was expected by chance, the short grassland community more than expected by chance and the Woodland and Sandy in proportion to their availability, while the rhinos switched and started utilising the Cynodon and Bothriochloa grassland communities in proportion to their availability (Table 14).

In Masinda, during the wet season only the Tall grassland community was utilised by white rhinos less than expected by chance, while the Sandy grassland community was utilised more than expected by chance and the Short, Woodland, Cynodon and Bothriochloa grassland communities were utilised in proportion to their availability (Table 14). While in the dry season, the rhinos utilised all the grassland communities in proportion to their availability.

3.4 Discussion

During the study, white rhinos at both the Makhamisa and Masinda study areas selected specific communities in which to forage which indicated that the rhinos did not forage randomly in the grassland communities in the two study areas. These findings indicate that the hypothesis that white rhinos in the Makhamisa and Masinda study areas utilise the grassland communities in proportion to their availability can be rejected.

During the study, neither the white rhinos at the Makhamisa or Masinda study areas utilised the grassland communities in the pattern described by Owen-Smith (1973;1988). As the white rhinos in both study areas consistently used the Short grassland community throughout the year and did not switch to mainly using the Tall grassland community it indicates that there was not a shortage of resources during the study. The most likely explanation for rhinos not needing to extensively utilise Other grassland communities is that the rhinos' staple grassland community, the Short grassland community, in both study areas, did not start to senesce until late in the dry season owing to the above average rainfall. At Makhamisa, this was evident as in

both the wet and dry seasons white rhinos utilised the Short grassland community more than what was expected and the Tall grassland community less than was expected. At Masinda, the fact that the white rhinos utilised the Short grassland community equal to its availability in the wet and dry season and never utilised the Tall grassland community more than what was expected indicated that the rhinos at Masinda also did not shift and forage primarily in their reserve or buffer communities.

The differences recorded in the utilisation of the grassland communities by white rhinos in the Makhamisa and Masinda study areas do not suggest that rhino density influenced how white rhinos utilise grassland communities. The utilisation of the grassland communities by the white rhinos in the two study areas were similar. White rhinos in both study areas never reduced their utilisation of the staple grassland community, the short grassland community, or switch and forage mainly in the reserve or buffer communities, the tall grassland communities on flats and hill slopes respectively.

Unexpectedly, white rhinos in the Masinda study area preferred the Sandy grassland community during the wet season. The utilisation of the Sandy community during the wet season was unexpected as its utilisation in the wet season was not recorded in Owen-Smith's study (1973;1988) or in the Makhamisa study area. An explanation as to why rhinos were attracted to the Sandy community in Masinda, but not at Makhamisa, may be that something was present in the Sandy community at Masinda that was not present at Makhamisa. When the grass species compositions of the Sandy communities in the two study areas were compared, it was found that the Sandy grassland community in each study area had grass species unique to each study

area (Table 15). When these grass species were compared with the grass species found to be relatively important in the diet of white rhinos in Owen-Smith's study (1973;1988), two grass species were found that were only present at Masinda; *Enteropogon monostachyus* and *Digitaria* spp. The possibility exists that the presence of these two grass species were what attracted white rhinos to the Sandy grassland community, however, as no data were recorded in the present study on the species composition of the diet of the rhinos diets no definite conclusions can be drawn.

At Masinda, the white rhinos' pattern of utilisation of the grassland communities was similar to that at Makhamisa, even though significant selection of the grassland communities could not be shown in most cases owing to the limited sample sizes. As the utilisation patterns of the grassland communities by the white rhinos in the two study areas were not sufficiently different, the hypothesis that rhinos in the two study areas utilised the grassland communities in a similar pattern is not rejected. The only distinct difference found in the utilisation of the grassland communities between the white rhinos in the two study areas was the utilisation of the Sandy community by the white rhinos at Masinda during the wet season.

The seasonal utilisation of the grassland communities by the white rhinos does not clear up or suggest a reason as to why there was an increase in rhino density recorded during the dry season in the Makhamisa study area. The possible explanation, as suggested in chapter one, is that rhinos were attracted to the availability of surface water in the White Umfolozi River during the dry season and crossed the river into the Makhamisa study area, while the water level was low, and foraged in the

grassland communities found in Makhamisa. With regard to subadults, it is evident from the utilisation patterns of the grassland communities that there was never a shortage of resources during the study and thus subadults most likely did not either enter or leave the study areas to search for grassland resources.

The findings of the study suggest that because of the above average rainfall during the study, rhinos were able to continue to utilise their staple grassland community, the short grassland community for the duration of the year. There is, however, a possibility that the differences in the utilisation of the grassland communities were not only the result of the study being conducted during a year that had above average rainfall. When Owen-Smith (1973;1988) conducted his study in Umfolozi, the white rhino population in the Hluhluwe-Umfolozi Park was estimated at around 2000 individuals. For the fraction of the population located in Owen-Smith's study area, in the western section of the Umfolozi Game reserve, the white rhino density was estimated to be as high as 5.7 per km² in local pockets with an overall density of 3.6-4.0 per km². In the present study the white rhino population in the Hluhluwe-Umfolozi game reserve was estimated to be substantially lower with 1350 individuals and the highest density recorded in the study areas being around 3.6 ± 0.3 per km². It is possible that the smaller white rhino population estimated for the present study, coupled with the above average rainfall, created a situation where the white rhinos could not deplete the resources in the grassland communities in the core of the reserve. Because of this, it is unlikely that during the study white rhinos would have dispersed into the vacuum zones or entered the vacuum zones and study areas, to search of trophic resources.

Table. 12. Utilisation time scale of the different levels of a nested ecological hierarchy. Time scale incorporated from Bailey *et al.* (1996); Laca & Ortega (1993); Owen-Smith (in press) and Sneft *et al.* (1987).

Level	Temporal scale
Region	Life time
Landscape	Years
Habitat	Months
Foraging Station	Hours
Patch	Minutes
Feeding Station	Seconds/Minutes
Bite	Seconds

Table 13. Total utilisation of six grassland communities by white rhinos in the Makhamisa and Masinda study areas. Utilisation is based on the number of white rhino groups recorded in the two study areas from July-August 1995 to July-August 1996. (* indicates a difference at the $P < 0.05$ level of significance, † indicates that the utilisation of the grassland community is greater than what is available and • indicates that the significant utilisation of the grassland community is less than what is than available)

Study Area		Expected proportion of usage	Actual proportion of usage	Bonferroni intervals for P_i
Grassland communities				
Makhamisa				
Tall	N= 40	0.296	0.129	$0.079 \leq P \leq 0.179^* \bullet$
Short	N= 124	0.252	0.399	$0.326 \leq P \leq 0.467^{*\dagger}$
Wood	N= 73	0.263	0.235	$0.172 \leq P \leq 0.298$
Sandy	N= 40	0.134	0.129	$0.079 \leq P \leq 0.179$
<u>Cynodon</u>	N= 32	0.031	0.103	$0.057 \leq P \leq 0.149^{*\dagger}$
<u>Bothriochloa</u>	N= 2	0.024	0.006	$0 \leq P \leq 0.018^* \bullet$
Masinda				
Tall	N= 37	0.436	0.330	$0.213 \leq P \leq 0.447$
Short	N= 18	0.105	0.161	$0.069 \leq P \leq 0.253$
Wood	N= 18	0.139	0.161	$0.069 \leq P \leq 0.253$
Sandy	N= 22	0.079	0.196	$0.097 \leq P \leq 0.295^* \dagger$
<u>Cynodon</u>	N= 11	0.153	0.098	$0.024 \leq P \leq 0.172$
<u>Bothriochloa</u>	N= 2	0.088	0.054	$0 \leq P \leq 0.110$

Table 14. Utilisation of the six grassland communities by white rhinos in the wet and dry seasons in the Makhamisa and Masinda study areas. Utilisation is based on the number of white rhino groups recorded in the study area from July-August 1995 to July-August 1996. The combination community in Masinda is a combination of the *Trichoneura*, *Bothriochloa*, and Other grassland communities. (* indicates a difference at the $P < 0.05$ level of significance, † indicates that the utilisation of the grassland community is greater than what is available and • indicates that the significant utilisation of the grassland community is less than what is than available)

Grassland communities		Expected proportion of usage	Actual proportion of usage	Bonferroni intervals for P_1
Makhamisa				
Wet season				
Tall	N= 7	0.2967	0.078	$0.004 \leq P \leq 0.151^{*•}$
Short	N= 36	0.252	0.400	$0.266 \leq P \leq 0.534^{*†}$
Wood	N= 20	0.263	0.222	$0.108 \leq P \leq 0.336$
Sandy	N= 9	0.134	0.100	$0.018 \leq P \leq 0.182$
<u>Cynodon</u>	N= 18	0.031	0.200	$0.090 \leq P \leq 0.310^{*†}$
<u>Bothriochloa</u>	N= 0	0.024	0.000001	$0 \leq P \leq 0.00028^{*•}$
Dry season				
Tall	N= 33	0.296	0.149	$0.125 \leq P \leq 0.173^{*•}$
Short	N= 88	0.252	0.398	$0.313 \leq P \leq 0.484^{*†}$
Wood	N= 53	0.263	0.240	$0.165 \leq P \leq 0.315$
Sandy	N= 31	0.134	0.140	$0.080 \leq P \leq 0.201$
<u>Cynodon</u>	N= 14	0.031	0.063	$0.021 \leq P \leq 0.106$
<u>Bothriochloa</u>	N= 2	0.024	0.009	$0 \leq P \leq 0.026$

Table 14 (cont.)

Grassland communities		Expected proportion of usage	Actual proportion of usage	Bonferroni intervals for P_1
Masinda				
Wet Season				
Tall	N= 10	0.436	0.208	$0.056 \leq P \leq 0.361^* \bullet$
Short	N= 7	0.105	0.146	$0.013 \leq P \leq 0.278$
Wood	N= 8	0.139	0.167	$0.027 \leq P \leq 0.307$
Sandy	N= 16	0.079	0.333	$0.156 \leq P \leq 0.510^* \dagger$
<u>Cynodon</u>	N= 5	0.153	0.104	$0 \leq P \leq 0.219$
Combination	N= 2	0.088	0.042	$0 \leq P \leq 0.117$

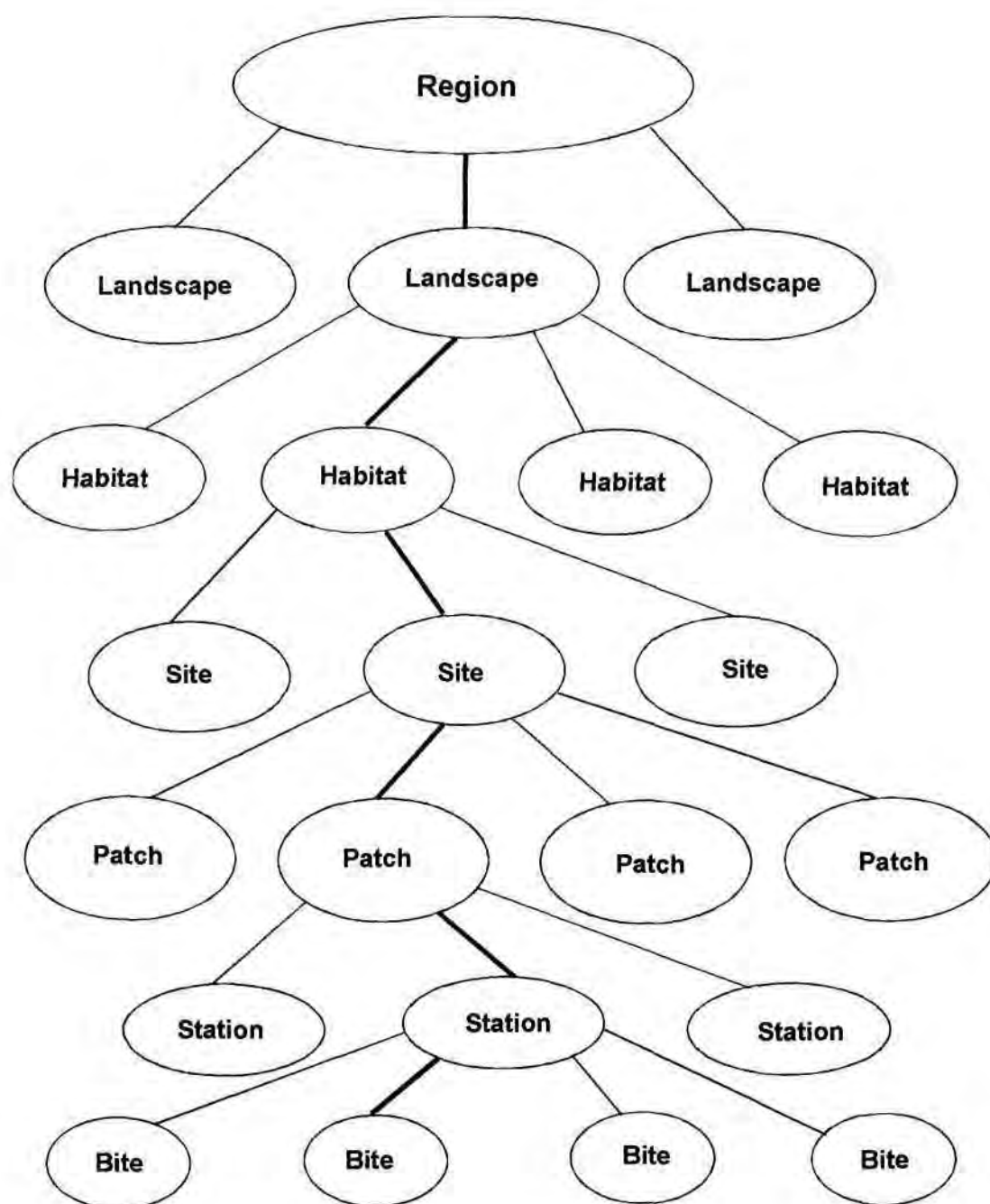


Fig. 18. A nested ecological hierarchy for large herbivores consisting of regional, landscape, habitat, foraging site, patch, feeding station and bite levels. Hierarchy derived from Bailey *et al.* (1996), Laca & Ortega (1995) and Sneft *et al.* 1987.

Chapter 4

Conclusion: A summary of the findings of the study

The purpose of this project was to assist the Natal Parks Board and the management staff of the Umfolozi Game Reserve in determining how white rhinos utilised the low density vacuum zones. Information was to be provided that would assist the Natal Parks Board in assessing the sink management policy, by monitoring the changes in the number of white rhinos in two vacuum zones and determining how the white rhino populations utilised available trophic resources under different density situations.

In the preceding three chapters questions were posed in an attempt to provide answers to the numerous aims and hypotheses of the study. In chapter one, the changes in rhino numbers were monitored and the age and sex classes of the white rhino populations in each study area determined. Chapter two sought to describe the trophic resources in the two study areas and determine how these resources differed between the study areas. Chapters one and two developed the basis on which the results of chapter three could be interpreted. In chapter three the overall utilisation of the grassland communities by the white rhinos in Makhamisa and Masinda were established along with the utilisation of the grassland communities in the wet and dry seasons in both study areas. Together these findings help to provide answers to the questions that management had regarding the utilisation of the vacuum zones by white rhinos.

Presented below is a list of the objectives of the study and the hypothesis that were tested. Under each, the findings from the previous chapters related to the objective or

hypothesis are provided along with a discussion of these findings. It is hoped that this format will allow easy access to the results of the study. However, the previous chapters will need to be referenced to obtain the explanations of the methods and statistical tests employed to obtain these results.

4.1 Main objective of the study

Determine the effect that different white rhino densities have on the utilisation of the grassland communities available to white rhinos in the low density vacuum zones.

The utilisation patterns of the grassland communities recorded in the Makhamisa and Masinda study areas were not sufficiently different to suggest that the high and low rhino densities in the study areas influenced the pattern in which the communities were utilised. The utilisation pattern of the grassland communities by white rhinos in both study areas differed to the pattern described by Owen-Smith (1973; 1988). The reason for this difference was that the above average rainfall experienced in both study areas during the study prevented the grass in the rhinos' staple grassland community, the short grassland community, from senescing early in the dry season and thus the rhinos remained in the short grassland community for the entire year. The only definite difference in the utilisation of the grassland communities between the two study areas was the preference for the sandy community exhibited by white rhinos in the wet season in Masinda. This preference, could have been caused by the presence of *Digitaria* spp. and *Enteropogon monostachyus* in the sandy communities of Masinda, however, this could not be demonstrated as the study did not focus on the grass species selected by the white rhinos when they foraged.

4.2 Auxiliary objectives

1. Determine the movements of the white rhinos in each study area.

The changes in the number of rhinos seen per day in the two study areas revealed that the number of rhinos did not change significantly between the sampling sessions in the two study areas. However, the standard errors of the means for all the sampling sessions did not overlap which indicated that the number of rhino groups seen could have varied during the study. These changes, if they did occur, could not be tested with the available data.

The changes in white rhino density, which were used as an indicator of the immigration and emigration of white rhinos into and out of the study areas, showed that the density of white rhino groups recorded in each study area did not differ significantly between the wet and dry seasons. The density of white rhinos in Masinda also did not change between seasons, however, the density of individuals in Makhamisa increased during the dry season. No definite explanation could be found for this increase, however, a possible explanation was that rhinos outside the study area (core and other vacuum zones) moved toward the White Umfolozi River and crossed the River while the water level was low. However, white rhinos were observed crossing the Umfolozi River only on two or three occasions during the dry season thus, these observations may have only been isolated instances.

2. Determine the seasonal utilisation of the grassland communities by the white rhinos in the Makhamisa and Masinda study areas.

White rhinos at Makhamisa and Masinda utilised the available grassland communities in a pattern different to the one described by Owen-Smith (1973; 1988). Throughout the year, white rhinos in both study areas foraged mainly within their staple grassland community, the short grassland community and were not observed to switch and forage primarily in their reserve or buffer communities, the tall grassland communities on flats and hillslopes respectively. The difference in the utilisation pattern of the grassland communities expressed by the rhinos in the present study was most likely caused by the above average rainfall experienced during the study. Owing to this rain, the grass in the short grassland community did not senesce early in the dry season and thus white rhinos were able to obtain the resources they required from the short grassland community throughout the year.

3. Determine if rhinos utilise different grassland communities at specific times of the year.

As stated above, white rhinos in both study areas did not change from foraging primarily in the short grass community owing to the above average rainfall experienced during the study. In the wet season, white rhinos in Makhamisa foraged primarily in the communities that contained short green grass (the short grassland community and the Cynodon community) and avoided communities that were either tall (Tall grassland community) or that comprised primarily grass species that had low grazing value (low nutritive value, low digestibility, etc.) (Bothriochloa community)

(Oudtshoorn 1992). During the dry season, the rhinos at Makhamisa did not drastically change their foraging patterns and continued to forage primarily in the short grassland community and avoid the tall grassland community.

The white rhinos in the Masinda study area utilised the available grassland communities similarly to the rhinos in Makhamisa. During the wet season, the rhinos foraged significantly less in the tall grassland community compared to what was available, while they foraged in the short grassland community in proportion to its availability. The difference observed in the utilisation of the short grassland community between rhinos at Makhamisa and Masinda was most likely an artefact of the sample size in Masinda being too small to determine if the rhinos in Masinda expressed a preference for the short grassland community. During the dry season, the white rhinos at Masinda utilised all the grassland communities in proportion to their availability. This, however, was not considered a drastic shift in the utilisation of the grassland communities as white rhinos continued to utilise the short grassland community in proportion to its availability while they did not utilise the tall grassland community in greater proportion than its availability.

A surprising discovery during the wet season was the preference displayed by white rhinos at Masinda for the sandy grassland community. A possible explanation for this is that there were grass species present in the sandy community at Masinda that were not present at Makhamisa and that these grass species attracted rhinos to the sandy community at Masinda. The species compositions of the sandy communities in the two study areas showed that there were two grass species only present at Masinda that were found by Owen-Smith (1973; 1988) to be relatively important in the diets of

the white rhinos; *Enteropogon monostachyus* and *Digitaria* spp. The possibility exists that these grass species attracted the rhinos to the sandy community, however, as no data were collected on the grass species composition of the diets of white rhinos during the study, no conclusions can be drawn.

These results indicate that owing to the above average rainfall, rhinos at Makhamisa and Masinda were not forced to utilise a broad range of grassland communities as the year progressed from the wet into the dry season. However, in years with average or below average rainfall the white rhinos in the Umfolozi game reserve would most likely utilise the grassland communities in a pattern similar to the one described by Owen-Smith (1973; 1988).

4. Predict which grassland communities white rhinos are most likely to occupy at any specific time of the year.

The data from the present study indicate that during years with above average rainfall white rhinos may not need to shift from utilising their staple grassland community, the short grassland community. Owen-Smith (1973; 1988) observed that white rhinos shifted between four grassland communities as the year progressed from the wet season into the dry season. These findings suggest that in years with average or below average rainfall, rhinos will shift between their staple, reserve and possibly their buffer communities. However, during years that have above average rainfall white rhinos may only need to utilise a few of these resource communities.

4.3 Hypotheses

1. The fluctuations in the density of white rhinos in the vacuum zones are similar for the two study areas through out the year.

This hypothesis was rejected for two reasons. First, the changes in the mean number of white rhino groups seen per day over the course of the study differed between the Makhamisa and Masinda study areas. Second, when the seasonal changes in rhino density in the two areas were compared, the density of rhinos at the Masinda study area did not change between the wet and dry seasons while the density of rhinos at Makhamisa increased in the dry season.

There are two possible explanations as to what influenced the changes in densities of white rhinos in the two study areas. First, the different initial white rhino densities and second, the changes in the trophic resources experienced during the study. If the different initial densities were the main factors that influenced how the density of white rhinos fluctuated during the study then one would expect that the patterns of change displayed by the different white rhino populations would not vary with the changing availability or condition of the trophic resources.

If, however, resources were the main factor that influenced the changes in the density of white rhinos, then one would expect that white rhino density would vary with changes in the availability of the trophic resources in and around the study areas. The results of the present study seem to suggest that the availability of surface water could have played a greater role in influencing the changes in white rhino density than either grassland resources or the different initial densities. The present study was conducted

in a year with above average rainfall, and thus the availability of grassland resources in the study area, and most likely the rest of the reserve, were not limited during the dry season. This was evident as rhinos did not shift from primarily foraging in their staple grassland community as the dry season progressed. The initial densities were not seen to influence the changes in white rhino density as the pattern in which the white rhinos utilised the grassland communities in the two study areas did not differ. As listed previously, it is possible that the increase in rhino numbers during the dry season at Makhamisa was owing to rhinos moving toward the White Umfolozi River to search for available surface water. However, to be certain that it was the water resources that influenced the movement of the white rhinos, a study would need to be conducted that focused on the movements of individual animals in the core and vacuum zones in relation to changing trophic resources.

2. White rhinos in both the Makhamisa and Masinda study areas utilise the grassland communities in proportion to their availability.

This hypothesis was rejected as over the course of the study, and in the wet and dry seasons particularly, white rhinos in both the Makhamisa and Masinda study areas utilised some of the grassland communities significantly different to their availability. These findings indicate that white rhinos did not just forage randomly through the available grassland communities but selected specific communities in which to forage while avoiding other communities.

3. The utilisation of the grassland communities by white rhinos is similar in the two study areas.

Even though the utilisation patterns of the grassland communities were not exactly the same, this hypothesis could not be rejected. The selection of the grassland communities by the white rhinos in the two study areas were similar in that during the dry season, rhinos did not decrease the utilisation of the short grassland community, their staple grassland community, or favour the tall grassland community, their reserve grassland community, over the short grassland community. These utilisation patterns of the grassland communities cannot be considered different, as the lack of selection of some of the grassland communities at Masinda, was most likely an artefact of the small sample sizes obtained. It is not very surprising that the white rhinos in the two study areas displayed similar patterns of utilisation of the grassland communities as the grassland community compositions of the two study areas were not significantly different, and owing to the above average rainfall there was not a shortage of grassland resources during the study.

In a direct attempt to answer management's question of how white rhinos utilise the vacuum zones, two hypotheses were tested:

- 1) White rhinos utilise the vacuum zones more during the dry season than in the rainy season; and
- 2) White rhinos use the vacuum zones only as a source of trophic resources.

4. White rhinos utilise the vacuum zones more during the dry season than in the rainy season.

This hypothesis can not be rejected as the white rhino density at Makhamisa increased significantly during the dry season, while the density at Masinda did not change significantly. The reason for this increase is not evident from the data as the availability of the grassland resources in the two study areas and thus presumably the majority of the reserve, did not decrease significantly. This is demonstrated by the fact that the rhinos in both the Makhamisa and Masinda study areas were able to forage mainly in the short grassland community, their staple grassland community, for the entire study. One possible explanation for this increase in density is that rhinos could have been attracted to the surface water that was available mainly in the White Umfolozi River during the dry season. During the dry season the water level in the Umfolozi dropped and rhinos were observed crossing the river into the study area. However, as it is likely that the grassland resources were equal in quality and quantity on both sides of the river, it is unclear why the rhinos would want or need to cross into the study area.

5. White rhinos use the vacuum zones only as a source of trophic resources.

This hypothesis could not be rejected as the white rhino density at Makhamisa increased in the dry season. The reason the hypothesis could not be rejected was that none of the results could explain why the white rhino density in Makhamisa increased in the dry season and thus it could not be ruled out that rhinos may have moved into the vacuum zone to obtain resources. However, it is unlikely that white rhinos

entered the study area looking for grassland resources for two reasons. First, the availability of resources in the grassland communities in the two study areas, and thus most likely for most of the game reserve, was high throughout the year. It is unclear why rhinos would need to cross into the study area as the availability grassland resources were most likely very similar on both sides of the White Umfolozi River.

Second, there were no significant differences recorded between the number of subadults in the wet and dry seasons in either study area. Subadults are the most mobile age group of white rhinos (Owen-Smith 1973; 1981) and thus the ones most likely to respond first to changes in resource availability. The lack of movement by the subadults suggests that there was not a shortage of resources during the study and that the subadults did not need to move far to obtain them.

However, the findings of the study may not represent the way in which rhinos respond to changes in trophic resources in other years. First, the study was conducted during a year that had above average rainfall and thus resources were not a limitation during the dry season. From the results of the study it would be difficult to determine if white rhinos would utilise the grassland communities in a similar manner in years that have average or below average rainfall. Second, in the present study the white rhino population in the Hluhluwe-Umfolozi Park was lower than it has been in the past. If the white rhino population increases in size then rhinos may move into the vacuum zones to obtain resources if the resources in the core are depleted through grazing. The smaller white rhino population estimated for the present study may not have been able to sufficiently deplete the grassland resources to where the rhinos would need to move into the vacuum zones.

The results of the study suggest that white rhinos outside of the study areas do not significantly utilise the vacuum zones as areas of trophic resources. However, as the study was conducted during a year that experienced above average rainfall the results do not indicate whether white rhinos in the Umfolozi Game Reserve would utilise the vacuum zones under drought conditions.

Recommendations

1. That the sink management policy continue to be utilised for the management of white rhinos in the Umfolozi Game Reserve. The findings of the study do not indicate that the policy is not working or that the vacuum zones are utilised by white rhinos just as areas of trophic resources. However, as the study was conducted in a year of above average rainfall these findings may not reflect the manner in which white rhinos utilise the vacuum zones in years with average or below average rainfall.

2. That a large scale project be initiated to determine if white rhinos move between the core and vacuum zones. A large number of rhinos will need to be monitored as dispersal of white rhinos is not a large scale event and may not happen every year.

3. That a survey be conducted to determine the age composition and sex ratio of the present white rhino population in the Hluhluwe-Umfolozi Park. The present study was conducted in only a small proportion of the Umfolozi Game Reserve, and the estimated age composition and sex ratio of the study areas were not meant to reflect the entire white rhino population. Once this survey is conducted, the results could be used to:

- 1) Determine if the estimates of the present study reflected the overall population;
- 2) Establish whether the removal policy has created a difference between the age and sex composition of the white rhino populations in the core and vacuum zones of the Hluhluwe-Umfolozi Park; and
- 3) Assist Research and Game Capture to determine what age and sex classes

should be removed from the park.

4. That a study be conducted to determine if the movement patterns of white rhinos differ between the core and vacuum zones. As the present study focused solely on the movement of rhinos in the vacuum zones, nothing is known about how white rhinos in the core respond to seasonal changes in trophic resources. By conducting a study that monitors rhino movements in both areas the factors that influence movements in and between the core and vacuum zones could be determined.

5. That a future study be conducted that focuses on the specific decisions an individual rhino makes while foraging. In the present study the specific reasons for the immigration of white rhinos into the Makhamisa study area during the dry season could not be determined. However, had the study focused on the specific foraging decisions made by white rhinos this immigration may have been explained. By conducting a study that monitors specific foraging decisions, answers to the following questions could be determined:

- 1) What triggers a rhino to move from one grassland community to another?;
- 2) Under what conditions do rhinos leave their staple grassland communities and forage in reserve and buffer grassland communities?;
- 3) Is the utilisation of the grassland communities by white rhinos similar in the core and vacuum zones?;
- 4) How sensitive are white rhinos to changes in the quality and quantity of trophic resources?; and
- 5) How far do rhinos travel while searching for trophic resources?

6. That the future study should focus on subadults and females with calves as they are the mobile age and sex classes of a white rhino population. As these age and sex classes are the most mobile, it is more likely that they will cross the management boundaries between the core and vacuum zones. By conducting a study that focuses on the subadults and females with calves, the conditions that prompt rhinos to move between the core and vacuum zones could be determined.

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Appendix I

Line Transect Method

The line transect method was used to determine the density of white rhinos in the two study areas. Line transects were chosen in preference to strip transects as observer visibility was estimated to vary between the different habitats along the transects. With strip transects, long narrow strips of defined lengths and widths are censused, while with line transects only a narrow strip around the centreline of the transect is censused and the remaining area sampled (Buckland *et al.* 1993). With differing visibility along each transect it was unlikely that the main assumption of strip transects, that all objects within the strip are detected, would be met. A benefit of using the line transect method was that only a portion of the population in the area being surveyed needed to be counted in order to give an accurate density estimate (Buckland *et al.* 1993).

Buckland *et al.* (1993) listed the assumptions of the line-transect method as follows:

- 1) objects on the centreline are always detected;
- 2) objects are detected at their initial location, prior to any movement in response to the observer;
- 3) the lines are random with respect to the distribution of objects in the population;
- 4) the transect line is straight;
- 5) the detection of each object is an independent event; and
- 6) distances (and angles where relevant) are measured accurately.

To insure that the line transect method was effective in estimating the density of white rhinos in the study areas, every attempt was made to meet these assumptions.

The first assumption, that all individuals on the line were seen, was met as it was unlikely that a megaherbivore, like a white rhino, would be missed if it was on or near the centreline of the transect. The assumption that objects were recorded at their initial location was met by walking silently and unobtrusively along each transect. Extraneous noise such as talking, radio communication, etc. was kept to a minimum so as not to alert the rhinos to the observers' presence. Binoculars were used to detect and observe the rhinos to help ensure that a large portion of the rhinos were sighted prior to any possible effect from the observer. In the instance where rhinos were detected moving due to the observers' presence, measurements were taken from the location from which the rhinos had moved.

The transects in the two study areas were placed randomly with respect to the distribution of the white rhinos by establishing them on a 1:50,000 scale map prior to arriving in the reserve. A compass bearing was used to insure that the transect was maintained while it was walked. Before the start of each transect, the map was orientated and the compass aligned with the transect. The compass was then checked while walking to insure that the centre line of each transect was maintained. No permanent markers were allowed to mark the transects in the Makhamisa study area as it was located in the Wilderness section of the game reserve. To be consistent in the two areas, none of the transects in the Masinda study area were marked. However, in both study areas, landmarks were noted and used, along with the compass bearing, to insure that the centreline was maintained.

Walking a straight line through thorn veld proved to be an almost impossible task. While walking, the transect was maintained as best as possible, however, when thorn bushes and trees became obstacles, they were circumvented and the transect resumed on the other side.

When the transects were walked, the number of white rhino groups seen were recorded rather than the total number of individuals to insure that the observations were independent. The size of the groups in the study varied from 1 to 10 individuals and were well defined (i.e. they were not loose aggregations). To insure that the detection of the groups was not a function of group size a regression was performed on the data in both study areas between the log of the cluster size and the detection probability. When tested, the slopes of the regressions were found to all have P-values greater than 0.05 ensuring that the rhino sightings in both study areas were independent of group size.

When a group of rhinos was seen measurements were recorded for the distances and angles to the groups from the centreline by using a range finder and an angle board respectively. It was suggested that distance measurements be made from the centre of the rhino groups, however, as the range finder needed to be focused on an object to determine distance, measurements were consistently made from the closest rhino.

The angle board used to estimate the sighting angles consisted of a plastic protractor of 180° with a movable pointer attached to the middle of the lower edge. The pointer was able to move through the 180° and thus to be used to indicate sighting angles.

When a rhino group was sighted, the angle board was placed on a flat surface next to the compass which had been orientated with the centreline of the transect. By placing the angle board next to the compass, it aligned with the centre line of the transect and made it possible for accurate measurements of the sighting angle to be determined.

Once the data for each season had been recorded, data from each study area were loaded into the computer program Distance 2.1 (Laake *et al.* 1994). Distance 2.1 used these data to determine the density of the rhino groups (D_s) in the study area. The density of the groups (D_s) was then multiplied by the average group size ($E(s)$) for that study area to determine the density of individuals in the study area (D) (Buckland *et al.* 1993).

$$D = D_s \cdot E(s)$$

Appendix II

AII.1 Loglinear analysis

Loglinear analysis is a non-parametric statistical test that uses cross-tabulation to test for associations between three or more variables (Anon 1995b). In the cross tabulation, variables (e.g. sampling session, grass colour, etc.), the levels of each variable (e.g. green, transition and brown for the variable grass colour) and their interactions (e.g. The differences in grass colour between the different sampling sessions) are tested for statistical significance (Anon 1995b; Bakeman *et al.* 1992; Knoke & Burke 1980; Sokal & Rohlf 1995). The loglinear analysis determines the expected cell frequencies in the cross-tabulation for the interactions between the levels of the different variables and then evaluates whether the difference between these frequencies and the observed frequencies is greater than what would be expected due to chance. The differences between the expected and observed frequencies in the cross-tabulation is assessed with the maximum likelihood Chi-squared statistic (L^2).

The loglinear analysis is similar to the G and Chi-squared (χ^2) tests, in that the power of the test is reduced if there is a large number of expected values that have values less than five. To reduce the number of expected values in the cross-tabulation that are less than five, either a large sample size is required or the cross-tabulation can be made smaller by limiting the number of levels for each variable.

To test the interactions of the different variables, a model that best describes the data is fitted to the data set. A model is defined as a statement of the relationship between

the variables being tested (Knoke & Burke 1980). The first step in loglinear analysis is to determine the model which includes the minimum number of parameters yet adequately describes the data. The model that best describes the data is determined by using either a forward or backward variable selection method. Forward selection starts with no variables in the model and variables are added until there is no significant difference between the model and the data set. Backward selection, however, starts off with all the variables in the model and variables are removed until no variables can be removed without making the model significantly different from the data set.

Once the model is determined, it is then fitted to the data and estimates for the parameters of each combination of cells are obtained. These parameters determine if observations in each cell are significantly higher or lower than the expected values for the cells. The computer program Statgraphics does not give a p-value for each interaction (as the test is approximate). However, a z-value and the approximate confidence interval are given, either of which can be used to determine which interactions are significantly different from zero. Significance is determined for each interaction if the absolute z-value is greater than 1.96 and the confidence interval does not include zero.

AII.2 Example of loglinear analysis

A hypothetical study of black rhinos will be used to help illustrate the workings of the log-linear analysis. In this study we are interested in whether the number of black rhinos in the study area fluctuates over the course of a year. In the study area, data are

recorded for the variables; season (levels-winter, spring, summer, and autumn), rhino presence (levels-present or absent) and woodland habitat type (levels-deciduous, evergreen and mixed).

The log-linear notation for each variable is represented with a single letter or number surrounded by braces ([]). In this example, letters will be used, as the statistical package Statgraphics, which was used to analyse the data for the white rhino project, utilises letters. The notation [A] will be used to represent the season, [B] status of rhinos and [C] the woodland habitat type. The interaction of these levels, called first order interactions, are represented by placing both letters, in any order, within the same pair of braces (i.e. [AB] for the interaction of season and rhinos presence).

Once the data for the different variables have been collected, a model that has the least number of variables yet still adequately describes the data is fitted to the data set. This model is found by using both forward and backward selection procedures and comparing the models determined with the two procedures (Knoke & Burke 1980). Once the model is determined, the fit of the model is then tested using a maximum likelihood Chi-squared test (L^2).

For this example let us assume that the model that best fits the data is the fully saturated model [ABC], with variables [A] season, [B] status of rhinos and [C] woodland habitat type. Once the model is fitted to the data, parameters for each interaction are generated. These parameters (coefficient, standard error, Z-value, and the 95 percent confidence interval) can be used to determine if the number of