

Diet choice of the black rhinoceros (*Diceros bicornis*) in the Double Drift Game Reserve, Eastern Cape Province, South Africa.

Feeding ecology of the black rhinoceros.



Frederik Winkel
October 2004

Supervisors:
Dr. W.F. de Boer
Dr. P. Lent



Introduction

Diet choice of the black rhinceros (*Diceros bicornis*) in the Double Drift Game Reserve, Eastern Cape Province, South Africa.

Feeding ecology of the black rhinoceros.

Msc. thesis Wageningen University, Resource Ecology Group.

Supervisors:

Dr. W.F. de Boer

Dr. P. Lent

October 2004

No part of this report may be reproduced in any form or by any means without authorization of the author or one of the supervisors.

Table of contents	
Abstract	
1. Introduction	1
1.1. Introduction and research objections	1
1.2. Research questions and hypotheses	3
1.3. Study area	4
1.4. Geology	4
1.5. Climate	4
1.6. Vegetation description	4
1.7. Study animal	6
1.8. Other browsers in the reserve	6
2. Methods	7
2.1. Diet choice	7
2.2. Biomass offtake of selected plant species	8
2.3. Forage availability	8
2.4. Preference indexes	9
2.5. Statistical analyses	9
2.6. Chemical analyses of plant species	10
3. Results	11
3.1. Regression equations for calculating dry matter offtake	11
3.2. Diet composition	12
3.3. Non characteristic bites	15
3.4. Dry matter offtake arranged along height classes	16
3.5. Vegetation availability and preference indexes	16
3.6. Chi-square test	18
3.7. Chemical analyses	19
3.8 Correlation between preference indexes and chemical analyses of plant species in Bushclump Karroid Thicket	20
3.8.1. Correlation between preference indexes and chemical analyses of plant species in Tall Euphorbia Thicket	21
4. Conclusion and discussion	23
4.1. Browse selection	23
4.2. Chemical analyses of plant species	24
4.3. Recommendations for future research	25
Literature	
Appendix 1	
Appendix 2	

Abstract

Apart from several other factors influencing foraging behavior, primary factors influencing foraging behavior of black rhinoceros are the annual forage quality, concentrations of plant secondary metabolites, available forage biomass, structure, and plant density of the vegetation. Knowledge of the mechanisms of resource exploitation is fundamental to our understanding of the population ecology of the consumers. In the case of the black rhinoceros of which the meta population is increasingly dependent on management in protected areas this knowledge can contribute to formulate optimal stocking rates. This research is aimed at describing the diet choice of the black rhinoceros in different vegetation types in the Double Drift Game Reserve and investigates possible selection criteria that the rhinos use when foraging during the wet season.

The diet choice of the black rhinoceros was investigated in three different vegetation types. The backtracking method was used to find plant species that were browsed by black rhinos. A total of 2273 bites from 54 different plant species were recorded from 24 backtracks.

In two vegetation types the forage availability was measured with the point centered quarter method. Preference for food items was calculated with the Ivlev's electivity index, depending on forage availability in the environment and the proportion of plant species in the diet. Twelve plant species were analyzed on N, P, cell wall constituents (NDF), digestibility, tannins and total phenolics.

Large mammals tend to go for mass instead of quality of forage material and it might be expected that one of the factors regulating forage intake is regulated by avoiding high levels of plant secondary metabolites (PSMs).

To investigate the hypotheses that forage selection patterns of black rhinos are not regulated by the quality of selected food items but by avoidance of high levels of secondary plant metabolites, outcomes of the chemical analyses are tested on correlation with the preference indexes of these plant species in two vegetation types.

The overall results indicate that black rhino foraging patterns are not the result of high nutritional quality of selected plant species, nor by the avoidance of PSMs.

1.1 Introduction and research objectives

Black rhinoceros population numbers have declined at a faster rate than any other large land mammal in recent times (Milliken et al. 1991). Deliberate translocation and management in protected areas are an important part in conservation strategies for this species. In 2000 the Double Drift Game Reserve participated in reintroduction of the Black rhinoceros and twenty animals were released into the area. The animals were translocated from the Hluhwe Umfolozi Complex, Kwazulu-natal.

All groups of animals possess different physiological and morphological adaptations in relation to their environment and foraging strategies. Diets reflect the interplay between the availability and quality of food items and the animal's ability to ingest and digest various food items. Dietary shifts occur when a species alters its diet in response to some intrinsic factor, and are often interpreted as an adaptive response to varying dietary availability (Smith, 1990). Several authors (Joubert & Eloff, 1971; Hall-Martin et al. 1982 and Oloo et al. 1994) refer to the tendency that rhinos concentrate on a few preferred species that form the bulk of their diet, although they feed on a wide variety of species. Oloo et al. (1994) concluded that rhinos fed less on each plant during the dry season. Hall-Martin concluded that less woody species were consumed during the dry season.

The diet breadth model (McArthur et al. 1966) approaches the question of how many food items should be included in the diet in terms of energy expenditure. The model assumes that the forager knows the profitability of the food item that is determined by the energy content per handling time. The energy content per handling time should be equal or greater than the mean expected energy intake during the foraging trip (De Boer et al. 2002). Decreasing quality and availability of bulk species can be interpreted in terms of a lower mean expected energy intake during the foraging trip. On a seasonal basis this could imply that more species which yield a lower mean energy intake are included as food items and that the diet becomes more diverse the dry season.

Apart from several other criteria herbivores may use two criteria in maximizing their nutritional intake when confronted with a range of food resources: a minimum digestibility and a minimum cropping rate. Minimum digestibility depends on plant chemical characteristics and minimum cropping rate should depend on the densities of plant items and their size e.g. mass. The theory on optimal foraging concludes that: Large bodied mammalian herbivores, because of greater digestive efficiency and lower metabolic demands per unit of body mass, can survive on foods of lower nutritional value than small bodied species (Belovsky 1997).

The study of home range dynamics tries to describe spatial occupation of habitats on a longer period of time, including seasonal variation (because of seasonal variation in forage availability). Seasonal variation in forage availability is mainly the result of lower precipitation levels during the dry season. Plant species possess different strategies to cope with lower precipitation levels. Drought coping strategies on a seasonal basis vary from leaf shedding, water storage in plant stems, translocation of nutrients and low stomatal conductance (with less photosynthesis as a consequence and hence less biomass increment). Plant species become less available (quantitative aspects) and/or the nutritional quality decreases.

In response to changes in forage availability rhinos have to adapt their foraging strategies. Foraging strategies are a trade-off between energy spent during foraging and energy intake from the different food

items. Rhino foraging patterns and spatial occupation of vegetation types might change, because the potential energy intake from plant species per ha is less during the dry season. Plants have a lower nutritional quality in terms of energy, and intake rates might be divided over more plants from the same species and/or the diet becomes more diverse. It is expected that the rhinos have to cover a greater distance during the dry season to meet nutritional requirements. Trends in dietary shifts can be described by comparing food preference differences during different seasons in relation to home range dynamics. Preference indexes are based on availability and their proportional contribution to the diet.

Resistance of terrestrial plants against herbivory may take three forms. Plants can avoid damage by defense, tolerate, or escape herbivory in time and space (Rosenthal et al. 1994). It is assumed that few plant species invest simultaneously in more than one mechanism to avoid herbivore induced damage (Rohner 1997). Defense mechanisms can be divided into physical, chemical and growth strategies. The role of secondary plant metabolites may involve deterrence and/anti-feedent activity, toxicity or acting as precursors to physical defense systems. Tolerance is often expressed in increased intrinsic growth rates, and flexibility of photosynthetic rates (Bennet et al 1994). Growth strategies include growing to tall for the leaves to be eaten, changes in plant architecture and low nutrient content.

The theory of optimal defense aims to relate the benefits of production of defensive traits to the costs of producing them. It proposes that investments in physical and chemical defense are positively related with risk of herbivore damage, and limited by the cost of producing the particular defensive trait in terms of resources that could be directed to other sinks such as growth and reproduction (Gowda 1996).

For the Black rhinoceros, being a large mammalian herbivore, total forage intake is expected to be more important than nutritional value of food items, however it is not clear to what extent nutritional quality regulates selection patterns in foraging behavior. The literature regularly states two hypotheses to explain patterns of food selection by herbivores.

- Forage selection patterns are the result of avoidance of plant secondary compounds (psc) that are antagonistic to vertebrate herbivore fitness (Bryant et al. 1980).
- Plants are spatially and temporally variable in nutritional value, and food selection is the result of acquiring an adequate balance of nutrients (Pulliam 1975).

Plant secondary metabolites vary greatly in structural types, and are often specific to a particular species or genera. Among the most prevalent are numerous classes of phenolics, terpenoids and steroids, cyanogenic compounds, and alkaloids (Molyneux et al. 1992).

This research focuses on diet choice of the black rhinoceros in different vegetation types and investigates possible selection criteria that the rhinos use when foraging during the wet season.

1.2 Research questions and hypotheses

1. Which plant species are part of the diet of the black rhinoceros in the different vegetation types?

2. What is the proportion of the foraged species in the diet in terms of bites and dry matter off take?
3. What are the important browse species in different vegetation types?
4. Is the selection of available browse based on avoidance of secondary plant compounds or on the selection of plant species with a high nutritional quality?

Hypotheses

1. Preferred plant species are positively correlated with low levels of secondary plant metabolites (tannins and total phenolics).
2. Preferred plant species are not positively correlated with high nutritional quality (N, P, digestibility and cell wall content. Cell wall constituents (NDF) are expected to be negatively correlated with preference indexes.

1.3 Study area

The Double Drift Game Reserve is located in the Mid Fish River valley and catchment area in the Eastern Cape Province. It occupies an area of 25000 ha. In 1982 former commercial farms were transferred to the Ciskei Government and used to establish the Double Drift Game Reserve. Together with the Sam Knott Nature Reserve and Andries Vosloo Kudu Reserve it forms a combined conservation area of 45000 ha. The Great Fish River cuts the reserve in half and acts a moving barrier for

the Black rhinoceros. Geographically the region extends from 32°50'S, 26°30'E and 33°15' S, 27°15' E. Bordering lands to the reserve can be divided into commercial and communal rangelands.

1.4 Geology

The Mid Fish River valley has a characteristic undulating nature valley with a great range in elevation over a relatively short distance (Palmer et al. 1994). The elevation of the area ranges from 170 m above sea level at the river up to 800 m at the ridges. The area comprises of the Middelton formation which is a Adelaide subgroup of the Beaufort group, Karoo supergroup, and predominantly consists of red and grey mudstone. Soils are apedal, and are described as clay or sandy clay loams.

1.5 Climate

The differences in elevation influence temperature and rainfall totals. Rainfall varies from 250 mm to over 650 mm (Birch et al. 1999). Lower elevation sites have a lower mean annual rainfall and higher mean annual temperatures, which result in a hot semi-arid environment. Higher elevation sites experience wetter and cooler conditions. Position of the slopes also contributes to variety in climatic conditions. South-facing slopes are cooler and have higher moisture levels than north-facing slopes (Evans et al. 1997). Dry forest is mostly found on the southern slopes. Mean annual rainfall is 434 mm, with peaks in October and March. According to the Koppen classification the area may be described as *Cfa*.

- C, warm temperate climate and coldest month 18°C to -3°C.
- f, sufficient annual precipitation during all months.
- a, maximum temperature over 22°C.

1.6 Vegetation description

Several authors have described the vegetation in de GFRR. Ackocks (1953) referred to the vegetation as Valley Bushveld. It was later renamed it into Xeric Succulent Thicket. At the biome level it was considered to be a part of the Savanna Biome. Low et al. (1996) concluded floristic and structural differences from earlier studies and nowadays the area is referred to as Thicket Biome. The following paragraphs briefly summarize the main conclusions of some of these studies on vegetation classification within the area.

Evans et al. (1997) used twinspan and direct gradient analyses to classify the vegetation into different vegetation types. In the nature conservation area 111 vegetation releves were made in ten by ten meter plots. The vegetation was classified into Medium Succulent Thicket (MST), Mesic Bushclump Savanna (MBS), Grasslands of the Mesic Bushclump Savanna (GMBS) and the Succulent Bushclump Savanna (SBS). Table 1 gives an overview of these vegetation communities

Table 1, overview of vegetation types and important species

Community	Community description	Important/common species
MST	Vegetation 2.0 to 2.5 m tall. Sandy clay to clay soils. Mainly present on north facing slopes, but also found on west and south facing slopes	<i>Portulacaria affra</i> <i>Euclea undulata</i> <i>Grewia robusta</i>

MBS	Dense bush clumps, consisting of up to eight different species, are separated by small patches of open grassland. Height > 2.5 m Soils are shallow sandy clays on sandstone. Found on flat to north facing slopes.	<i>Scutia myrtina</i> <i>Accacia karoo</i> <i>Digitaria eriantha</i> <i>Sporobolus fimbriatus</i> <i>Helichrysum degreanum</i>
GMBS	Grassland comprises most of the vegetation cover (70-80%). The species composition of the bushclump is the same as in the MBS, however the number and size of the bushclumps are smaller in diameter and consist of two or three species	<i>Acacia karoo</i> <i>Digitaria eriantha</i> <i>Eragrostis obtusa</i> <i>Sporobolus fimbriatus</i> <i>Scutia myrtina</i>
SBS	Mostly restricted to north facing slopes. Height is between 1 and 2 m. Little or no ground cover occurs between the small succulent bushclumps.	<i>Portulacaria afra</i> <i>Euphorbia tetragona</i> <i>Kalanchoe rotundifolia</i> <i>Delosperma calycinum</i>

Fabricius et al. (2002) analyzed satellite imagery and concluded that the higher diversity of landscape patches in the nature reserve areas are the result of disturbances caused by wildlife grazing, and low natural stocking rates. The lower diversity in the communal rangelands is due to continuous and heavy grazing by livestock in combination with intensive fuel wood harvesting.

The main conclusion on the vegetation in the Great River Fish basin is that the vegetation is heterogeneous and patchy, classification is based on different approaches and there is a clear gradient in degradation due to former and present land use forms, which might explain the patchy structure of the vegetation in certain areas.

A plant species list of the Samknot and Andries Vosloo nature reserve complex describes 80 plant families, 251 genera and 389 species of which 6.7 % are alien species. One species is a naturalized indigenous species. Leaf stem and root succulents (including geophytes) account for 35 % of the flora. Climbing, scrambling and species which do not exceed 100 cm. in height account for approximately 77 % of the flora.

For the purpose of studying the diet choice in relation to forage availability in the Great Fish River Reserve Trollope et al. (2002) identified 12 vegetation types and described the dominant plant species that occur in each vegetation type. In this study backtracks were recorded in Bushclump Karroid Thicket characterised by *Rhus spp.*, *Scutia myrtina* bushclumps and a karroid herbaceous layer. Bushclump Savanna characterised by dense thornvelds dominated by *Rhus spp.* and *Scutia Myrtina* and Tall Euphorbia Thicket which is characterised by tall growing *Euphorbia triangularis* and *Euphorbia tetragonia*.

1.7 Study animal

The black rhinoceros (*Diceros bicornis*) is the only survivor of a genus whose ancestry reaches back some ten million years ago in North and sub-Saharan Africa, Southern Europe, and the Near and Middle East. The Black rhinoceros belongs to the class of the

Mammalia, order of the Perissodactyla; odd-toed ungulates and family of the Rhinocerotidae. The Black rhinoceros is divided into five subspecies and the studied animals belong to the *minor* species. The animal has a relative narrow mouth with a prehensile lip. They are browsers, feeding mainly on woody vegetation, and have the ability to feed on coarser material than most other herbivores (Oloo et al. 1994). Grazing may also occur (Mabinya et al. 2002). Mukinya (1977) recorded two feeding

peaks, one in the morning and the other in the afternoon. Drinking mostly takes place at night.

Habitats of Black rhinoceros generally exist of grasslands, savannahs and tropical bush lands. The most suitable habitat seems to be thick shrub and bush land, often with some woodland, which supports the highest densities between 1.4 rhinoceros/km² and 1.6 rhinoceros/km². This habitat has the smallest home range size of 2.6 km². Open grassland supported densities as low as 0.04 rhinoceros /km² and home ranges up to 100 km². The most important factors affecting habitat suitability are availability of water, food, cover, and absence of human disturbance (Tatman et al. 2000). Table 2 gives an overview of bodyweight, height, length and horns of Black rhinoceros.

Table 2, body features of Black rhino

Weight	800-1350 kg.
Height	1.4-1.7 m. tall at shoulder
Length	3.0-3.8 length of head and body
Horns	anterior 0.5-1.3 m. posterior 2-55 cm.

An average body weight of 1075 kg corresponds more or less with 1.3 % of body mass for daily food intake rates (Owen-Smith, 1988). Data is based on the regression equation $6.0M^{-0.191}$, $R^2 = 0.647$ $p < 0.01$. The x-axis represents body weight and the y-axis represents the daily dry matter intake rate as a percentage of body weight. Daily forage intake is estimated at $0.013 * 1075 \text{ kg} = 14 \text{ kg dry mass}$.

1.8 Other browsing species in the reserve

Several other browsers and selective grazers are present in the reserve. Other browsers are the Cape kudu (estimated at 669 animals) and the Giraffe (16). Selective browsers are the Bushbuck (504), Grey duiker (48), Eland (17) and the Steenbuck (20). Selective browsers complement browsing with grazing in their foraging strategies. The number of animals is based on actual counts and a correction factor (pers. com W. Erlank 2004). The correction factor depends on vegetation type, size of the area, type of animal and previous experiences in game counts.

2 Methods

2.1 Diet choice

Three main methods (Barnes, 1976) on studying diet choice are considered.

1. Analyses of ingested or faeces of animals
2. Direct observation of feeding.
3. Measurement of previously browsed vegetation (plant based methods).

All methods have their limitations depending on local prevailing conditions. Black rhinos browse vegetation in a very distinct manner, clipping of twigs and shoots cleanly (Oloo et al. 1994), but this may not always be the case, for example non-thorny species are browsed in a way similar to Kudu and Giraffe. The diet of the black rhinoceros mainly consists of browsed plant species, but the diet can consist of other species than woody species alone. By using faecal analyses it is difficult to make quantifications on consumed biomass, however faecal analysis can complement method two and tree because certain plant species might be overlooked using method two and or tree. Previous studies in the reserve found that *Euphorbia* species form an important part of the diet. The growth form of *Euphorbia* species makes it difficult to quantify browsed biomass. In this case faecal analyses can be of practical help by defining the ratios in the faeces between *Euphorbia* and species were it is possible to quantify browsed biomass with plant based methods.

Limitations to the observer using plant based methods are that certain plant species, particularly for the succulent genera, such as *Euphorbia* and *Aloe* it is difficult to measure offtake. The length of the scleroids of these genera does not vary proportionally with the diameter. Herbaceous species such as forbs might be overlooked, because of their small size and uncharacteristic bites. Drying out of plant parts can cause doubt on which animal was responsible for browsing. More information and examples on this topic are well described by Kotze and Zacharias (1993).

Places where rhinos stopped to forage are called feeding stations, forming a rough semicircle in front of the browsing rhino (Goddard 1968). Feeding on plant species was quantified by counting the number of freshly browsed stem tips. A browsed stem tip can be due to several or one bite. Mukinya (1977) recorded two feeding peaks, one in the morning and the other in the afternoon.

With the backtracking method a feeding black rhino was located early in the morning or afternoon. When possible a located black rhino is approached in a cautious way to identify the animal and when the rhino has moved a safe distance its tracks are followed backwards to search for browsed plant species. The browsed plant species were then recorded followed by the number of bites and the height of each bite. A bite was recorded for twigs bitten off at the same level within a hypothetical circle of 10 cm.

In this study method three (plant based observation) was used. A bite was recorded for twigs bitten off at the same level within a hypothetical circle of 10 cm and each plant where fresh bite marks were encountered, data was collected on plant species, number and diameter of browsed twigs per bite, number and height of bites, level of utilization of each plant (consumed biomass in percentages) and previous browsing using a subjective scale from one to four. One stands for not browsed before and four heavily browsed. Total height of each plant and distance between each browsed species.

2.2 Biomass offtake of selected plant species

Quantifying biomass off take was carried out by selecting twenty twigs for different diameter classes from important plant species. The average weight of the twigs is measured and plotted in a graph with the x-axis representing twig diameter and the y-axis representing weight. The regression line is then used to calculate biomass off take based on measured twig diameter from different plant species during fieldwork. A combined regression curve is used for the rest of the species that occur in the diet of the Black rhino.

2.3 Availability

Measuring forage availability was done with the point centered quarter method after Trollope et al. (2002) Two parallel transects of 110 and 120 m are laid out, locating 12 and 13 recording points at 10 m intervals. Each recording point is divided into 4 quadrants. In the first two quadrants the nearest species < 2 m are recorded. In the third quadrant the nearest species taller than 2 m is recorded. In the fourth quadrant the tallest species is recorded. All recordings of plant species takes place within a 10m radius from the recording point. In case were no plant species within 10m are found nothing is recorded. One transect records a 100 plant species in. A total of 8 transects were recorded, four in Tall Euphorbai Thicket and four in Bushclump Karroid thicket. Recorded plant species are measured on height, distance from recording point, lower canopy height, maximum canopy height and the height of the maximum canopy diameter.

Data from the transects was analyzed to calculate the percentage browse volume per plant species and their occurrence in numbers in each of the vegetation types. The following formulas describe the procedures to calculate browse volumes

- $RAD = [(Ht-H1)/2]+R]/2$
RAD is average radius of canopy (m)
Ht is plant height (m)
H1 is height of canopy bottom from ground level (m)
R is average horizontal radius of canopy
- $Vol = [(4/3)*(22/7)*(RAD^3)]$
Vol is canopy volume (m³)
- $B vol = [(22/7)*(h^2)/3]*[(3*(RAD))-h]$
B vol is browseable volume (m³)
h is (1.80-H1) (m), 1.80 is the maximum browse height for black rhinos

When recording the transects the maximum horizontal canopy diameter was measured. To obtain the average horizontal radius this value was divided by 2 and multiplied with 0.75. The last formula is used when the 1.80 m maximum browse level is less than or equal to the mid canopy height of the plant species. When this is not the case the formula is used to calculate the unbrowseable volume above 1.80 m and this is then subtracted from the total canopy volume (Vol). All species with a lower canopy of > 1.80 m were excluded from the data, with the exception of *Cussonia spicata*, *Euphorbia tetragonia* and *Euphorbia triangularis*, because the rhinos push them over. When recording the transects the maximum horizontal canopy diameter was measured. To obtain the average horizontal radius this value was divided by 2 and multiplied with 0.75.

Densities of plant species were calculated with the formula $10000 m^2/D^2$ after Cottam et al. (1959), with D as the average distance for the different categories from the recording point. The density of plants is expressed in plants per ha.

2.4 Preference indexes

If a plant is abundant in one area it could be more advantageous for browsers to consume this species instead of spending more time and energy searching for more preferred species (Stephen et al. 1986). Principal foods are food items that the animals eat most, preferred plant species reflect the nutritional requirements of the animals. Preference indexes are based on the ratio between proportion of the species in the diet and the proportion of plant species available in the environments. This ratio can vary from 0 to infinity unless preference indexes in this research are calculated with the Electivity index.

- $E_i = r_i - n_i / r_i + n_i$

E is Ivlev's electivity measure for species i

r_i is Percentage of species i in diet

n_i is Percentage of species i in environment

Values of the electivity index vary from -1 to 1 , with values between 0 and 1 indicating preference and values between 0 and -1 indicating avoidance.

2.5 Statistical analyses

Correlation describes and measures the direction and strength of the linear relationship between two quantitative variables. The relationship can be positive or negative and the correlation coefficient is a number between -1 and 1 . Correlation coefficients near 0 indicate a very weak linear relationship. The relation between species in the diet their preference index values and the results of the chemical analyses from these plant species is described with statistical analyses using correlation.

Chi-square a nonparametric test, was used for measuring observed and expected values between the number of bites and available browse and the observed and expected values between number of bites and plant density.

2.6 Chemical analyses of plant species

Twelve plant species were collected for chemical analyses. In each vegetation type samples were collected from three plants. The samples were dried in an oven at 60°C . Fresh/dry weight and leaf twig ratios were measured. Leafs and twigs were grinded separately for separate analyses. The plant species were analyzed on N, P, cell wall constituents (NDF), digestibility, tannins and total phenolics.

Total nitrogen and phosphorus were determined after a modified Kjeldahl destruction. Total nitrogen and phosphorus concentrations were measured colourimetrically using a continuous-flow analyser (Skalar SA-4000). Digestability was determined by imitating the digestion process of ruminants after Tilley et al (1963). The samples were incubated with pens liquid followed by incubation with a pepsin/HCl solution. The cell wall fraction was determined by boiling the sample with neutral detergent fiber. The cell content dissolves and the cell wall fraction (NDF) remains. Tannins and phynolics were measured with aquamate vis. V4.60 and it translates the absorbsion of a wavelenght of 550 nm which is send through the sample

into the concentrations of tannins and polyphenolics. Phenolics are known to interfere with the intestinal absorption of minerals, while Tannins are perceived as important digestion inhibitors of fiber (Bryant et al. 1992).

3Results

3.1Regression lines for calculating dry matter off take

Table three describes the regression lines for individual species. R^2 values are high and indicate a good fit. Dry matter off take is calculated for all twigs in a bite per plant species and the sum gives the dry matter off take per bite per plant species.

Table 3, regression equations developed from measurements on twig diameter and dry matter weight of 7 plant species (source Brown 2003)

Species	Regression line	R ² values
<i>Coddia rudis</i>	$Y=0.0439x^{2.7275}$	0.9308
<i>Euclea undulata</i>	$Y=0.2409x^{2.4296}$	0.9539
<i>Grewia robusta</i>	$Y=0.0345x^{3.1127}$	0.879
<i>Jatropha capensis</i>	$Y=0.0258x^{2.577}$	0.8539
<i>Plumbagho auriculata</i>	$Y=0.0619x^{2.8286}$	0.8764
<i>Schotia afra</i>	$Y=0.0542x^{2.6551}$	0.8671
<i>Euhporbia bothea</i> (green stems)	$Y=0.1244x^{1.2024}$	0.5128
<i>Euphorbia bothea</i> (grey stems)	$Y=0.2011x^{1.0322}$	0.6614

The diameter of *Euphorbia* scleroids do not vary proportionally with the length of the stems and the regression lines are assessed with scleroids at a fixed length of 50 mm.

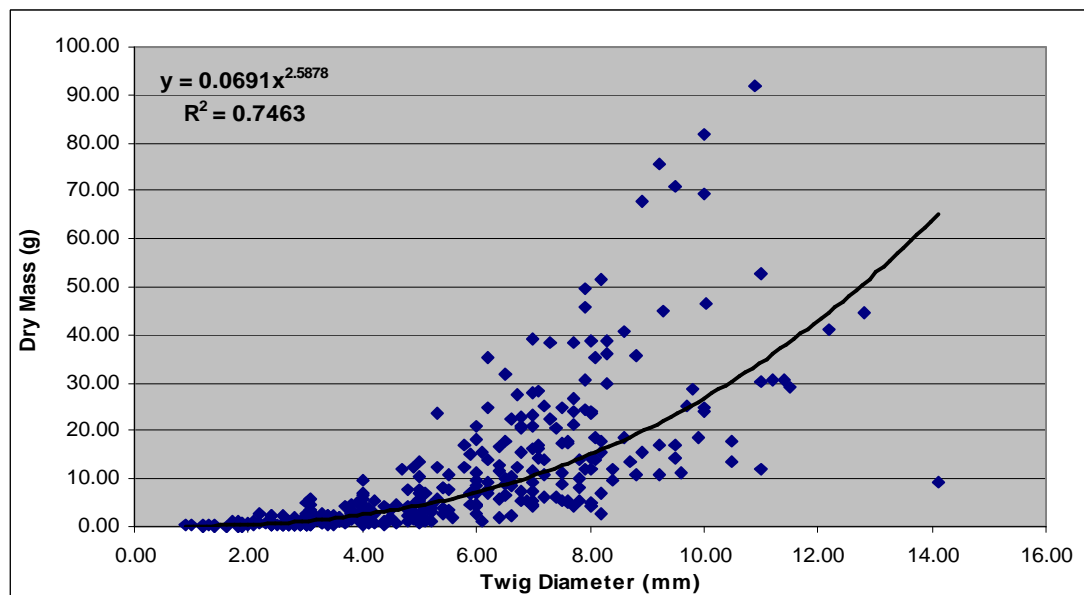


Figure 1, combined regression line of 7 plant species between twig diameter and drymass (source Brown 2003)

Figure 1 shows the combined regression line of the plant species in table 3. The combined regression line is calculated without the *Euphorbia* regression lines. The R² value is lower than the individual lines, but still indicates a relatively good fit between twig dry mass and twig diameter.

3.2 Diet composition

Data was analyzed separately for different vegetation types. A total of 2273 bites from 54 different plant species were recorded from 23 backtracks. The total biomass off take was 16055 gr. dry weight. Fig 2 shows the cumulative number of plant species against the number of backtracks. The last four backtracks contributed with 2 new species to the diet. The flattening end of the curve indicates that the diet is adequate described with the 23 backtracks in terms of number of different plant species, but it does not mean that all potential species of the diet are recorded.

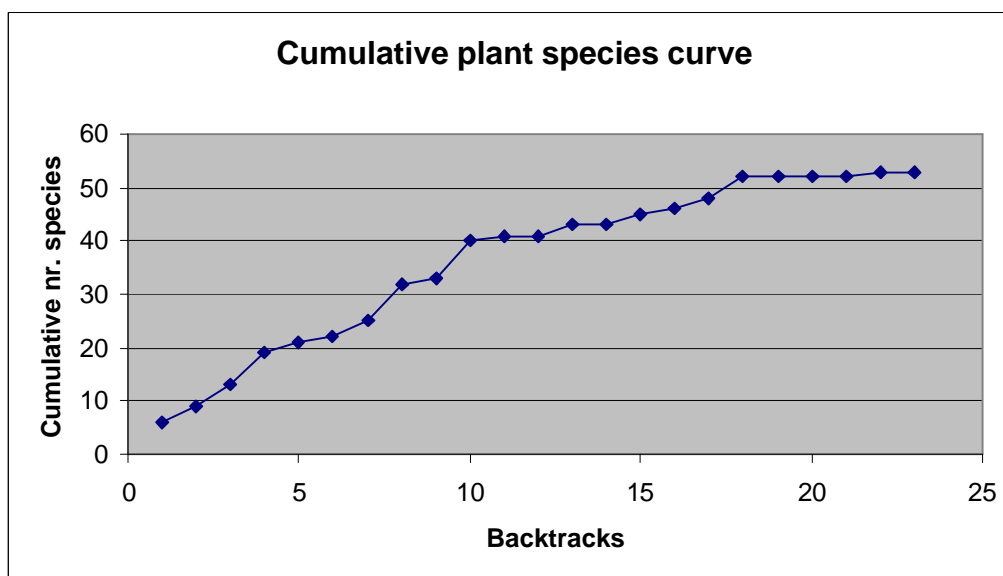


Figure 2, cumulative number of plant species against the number of backtracks

Table 4, 5, 6 and 7 describe the observed number of bites, estimated biomass off take and the contribution of each plant species to the diet in percentages. Species with a contribution of less than 2 percent are not mentioned separately. Appendix 2 shows results for species with a contribution to the diet of less than 2 percent. In Bushclump Savanna vegetation three plant species (*Coddia rudus* 31.4 %, *Euclea undulata* 14.5 % and *Plumbagho auriculata* 10.5 %), contribute more than 50 % to biomass consumption. Eighth plant species with a contribution of less than 2 % make up for 6.4 % of the consumed biomass in Bushclump Savanna.

Table 4, diet composition in Bushclump Savanna for species with a contribution of more than 2 % dryweight consumption . The contribution of plant species is described in number of bites, dryweight consumption and the percentage dryweight consumption.

Plant species	Bites	Dryweight gr	Percentage
<i>Coddia rudis</i>	86	690	31.4
<i>Euclea undulata</i>	24	318.2	14.5
<i>Plumbagho auriculata</i>	45	229.8	10.5
<i>Maytenus capitata</i>	18	144.5	6.5

<i>Azima tetracantha</i>	21	112.8	5.1
<i>Asparagus striartis</i>	38	99	4.5
<i>Rhus refracta</i>	16	75.3	3.4
<i>Jatropha capensis</i>	18	72.4	3.3
<i>Cassine crocea</i>	6	68.9	3.1
<i>Brachylaena elliptica</i>	6	55.6	2.5
<i>Buddlega saligna</i>	11	53.7	2.4
<i>Grewia robusta</i>	18	47.7	2.2
<i>Jasminum angulare</i>	18	45.4	2.1
<i>Euphorbia tetragonia</i>	11	45.2	2.1
Other species n = 8	48	139.5	6.4
Total	348	2198	100

Four plant species (*Azima tetrachanta* 17.6 %, *Coddia rudus* 16.1 %, *Euclia undulata* 14.8 %, *Grewia robusta* 9.7 %) make up for more than 50 % of the biomass offtake in Bushclump Karroid Thicket. A total of 16 % biomass consumption comes from plant species with a contribution of less than 2 % to the diet.

Table 5, diet composition in Bushclump Karroid Thicket for species with a contribution of more than 2 % dryweight consumption. The contribution of plant species is described in number of bites, dryweight consumption and percentage dryweight consumption.

Species	Bites	Dryweight gr	Percentage
<i>Azima tetracantha</i>	80	560	17.6
<i>Coddia rudis</i>	84	511	16.1
<i>Euclia undulata</i>	26	472	14.8
<i>Grewia robusta</i>	46	309	9.7
<i>Plumbago auriculata</i>	46	292	9.2
<i>Gnidia cuneata</i>	23	139	4.3
<i>Ozoroa mucronata</i>	15	126	4
<i>Maytenus capitata</i>	14	103	3.2
<i>Brachalaena elliptica</i>	13	92	2.9
<i>Brachalaena ilicifolia</i>	8	68	2.1
Other species n = 19	88	505	16.1

Total	443	3177	100
-------	-----	------	-----

In Tall Euphorbia Thicket four plant species (*Euphorbia tetragonia* 21.4 %, *Euclia undulata* 20.5, *Euphorbia triangularis* 11.7) contribute more than 50 % of the biomass off take. The contribution of individual plant species less than 2 % is 16 %.

Table 6, diet composition in Tall Euphorbia Thicket for species with a contribution of more than 2% dryweight consumption. The contribution of plant species is described in number of bites, dryweight consumption and percentage dryweight consumption.

Plant species	Bites	Dryweight gr	Percentage
<i>Euphorbia tetragonia</i>	417	1614	21.4
<i>Euclea undulata</i>	100	1546	20.5
<i>Euphorbia triangularis</i>	208	881	11.7
<i>Azima tetracanta</i>	92	592	7.8
<i>Ozoroa mucronata</i>	44	440	5.8
<i>Coddia rudis</i>	85	435	5.8
<i>Asparagus striartis</i> *	47	221	2.9
<i>Jatropha capensis</i>	85	206	2.7
<i>Grewia occidentalis</i>	28	176	2.3
<i>Brachalaena ilicifolia</i>	23	165	2.2
<i>Maytenus capitata</i>	20	155	2.1
Other species = 24	219	1100	14.8
Total	1368	7531	100

* Bites on *Asparagus striartis* are mostly found on open spots and are associated with TET

In non identified vegetation types *Euclia undulata* 18.5 %, *Azima tetrachanta* 15.7 %, *Plumbago auriculata* 13.6 %, *Euphorbia tetragonia* 11.7 % contribute more than 50 % to the diet choice of the black rhinoceros, however the diet composition as described in table 7 cannot be interpreted as the diet choice in a particular vegetation type, because it is the result of recordings in different vegetation units. *Euclia undulata* and *Azima tetrachanta* appear as important plant species in all 3 vegetation types. Although the number of bites does not vary proportionally exactly with the biomass consumption, such as *E.undulata* in table 7 it gives a good indication of the contribution to the diet.

Table 7, diet composition in non identified vegetation types for species with a contribution of more than 2 % dryweight consumption. The contribution of plant species is described in number of bites, dryweight consumption and percentage dryweight consumption.

Plant species	Bites	Dryweight gr	Percentage
<i>Euclea undulata</i>	32	583	18.5
<i>Azima tetracantha</i>	86	494	15.7
<i>Plumbago auriculata</i>	91	428	13.6
<i>Euphorbia tetragonia</i>	95	368	11.7
<i>Euphorbia triangularis</i>	70	315	9.9
<i>Grewia robusta</i>	20	131	4.2
<i>Acacia karoo</i>	5	105	3.3
<i>Maytenus peduncularis</i>	18	104	3.3
<i>Ozoroa mucronata</i>	14	92	2.9
<i>Maytenus polycantha</i>	13	92	2.4

<i>Scutia myrtina</i>	11	64	2
Other species = 19	113	373	12.5
Total	568	3149	100

3.3 Non characteristic bites

Euphorbia sp. have a different growth form compared to woody species, each bite on a scleroid is recorded separately as one bite. On three backtracks browse on *Cussonia spicata* was encountered. Rhinos push the tree over and browse on the branches, which tend to be soft on the inside, leaves are not eaten. One was recorded in TET with a bite on branch of 6 cm. in diameter. The two other ones were recorded on backtracks in NIVT with bites on two branches of respectively 4.7 and 5.5 cm. and the latter one on branches of 8 and 6 cm in diameter. Three bites on three different leaves of one *Opuntia sp.* were recorded during one backtrack in Bushclump savanna. Appendix 2 provides an overview of selected plant species with a proportional contribution of less than two percent to the diet.

3.4 Dry matter off take arranged along height classes

Browsing takes place on different heights. Different browsing animals might browse on the same plant species along different heights. Figure 3 presents an overview of browsing in different height classes. Biomass off take is the highest between 31-60 cm and most off take (> 65 %) takes place below 1 m.

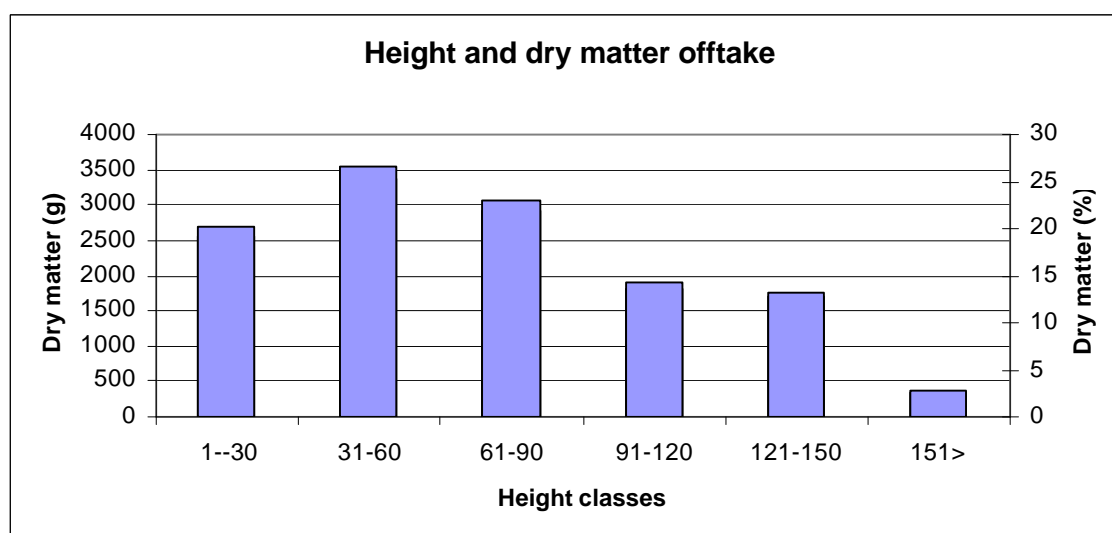


Figure 3 dry matter off take of browsed plant species arranged along height classes in all vegetation types.

3.5 Vegetation availability and preference indexes

Table 4 describes the proportional presence of plant species with a contribution of more than 2 percent in the diet in Bushclump Karroid Thicket and Tall Euphorbia Thicket. Appendix 2 describes preference indexes for species with a contribution to the diet of less than 2 percent. Column number 3 shows the browse volumes in terms of canopy volume taking into consideration the maximum browse height of the black rhinoceros. The next column shows plant density per ha, followed by biomass consumption in % and the last column displays the preference indexes. In BKT 7 out of the 10 important plant species show moderate to high preference indexes. In TET with the exception of *E. tetragonia* and *M. Capitata* all important plant species show moderate to high preference indexes and this is an indication that the black rhinos are well provided with their preferred plant species in these vegetation types. The implications of the preference indexes should be interpreted in combination with at least one other parameter such as biomass consumption, because the results can be misleading. For example in TET the value of the preference index of *E. tetragonia* is -0.4035 with a biomass consumption of 21.4 %, compared to *L. capensis*, with a biomass consumption of only 0.10 % and a preference index of 0.9719.

Table 4, vegetation availability and preference indexes in Bushclump Karroid Thicket and Tall Euphorbia Thicket as calculated with the Ivlev's electivity index. For detailed description of columns see text above.

vegtype	species	%bvol	nrspecies	%diet	preference index
BKT	<i>A. tetracantha</i> *	0.0012	11	17.6	0.9999
	<i>C. ruddis</i> *	0.5559	640	16.1	0.9332
	<i>E. undulata</i> *	4.9443	480	14.8	0.5003
	<i>G. robusta</i> *	3.9123	1401	9.71	0.4257
	<i>P. auriculata</i> *	1.0829	614	9.19	0.7891
	<i>G. cuneata</i>	0.0012	11	4.3	0.9994
	<i>O. mucronata</i>	1.2306	12	4	0.5295
	<i>M. capitata</i>	11.083	1042	3.2	-0.5519
	<i>B. elliptica</i>	4.9289	455	2.9	-0.2591
	<i>B. ilicyfolia</i>	6.2997	1014	2.1	-0.4999
	<i>P. verricussus</i>	0.1828	175	1.85	0.8200
	<i>A. karoo</i> *	6.0458	870	0.48	-0.8556
	<i>E. rigida</i> *	17.322	1394	0.32	-0.9634
TET	<i>E. tetragonia</i>	50.354	534	21.4	-0.4035
	<i>E. undulata</i> *	0.9356	860	20.5	0.9128
	<i>E. triangularis</i>	3.6550	54	11.7	0.5239
	<i>A. tetracantha</i> *	0.4805	811	7.86	0.8847
	<i>O. mucronata</i>	1.3320	143	5.8	0.6265
	<i>C. ruddis</i> *	0.0177	449	5.78	0.9939
	<i>A. striartis</i> *	0.0014	206	2.9	0.9999
	<i>J. capensis</i>	0.0149	864	2.7	0.9890
	<i>G. occidentalis</i>	0.1540	6727	2.3	0.8745
	<i>B. ilicyfolia</i>	0.0014	42	2.2	0.9987
	<i>M. capitata</i>	1.2588	408	2.1	0.2504
	<i>G. robusta</i> *	0.0028	243	1.76	0.9967
	<i>P. afra</i> *	0.1247	542	1.66	0.8602
	<i>P. verricosus</i> *	0.0078	724	0.17	0.9161
	<i>I. capensis</i> *	0.0014	243	0.10	0.9719

<i>E. rigida</i> *	0.5578	3237	0.07	-0.7761
<i>P. obliquum</i> *	5.2464	4257	0.03	-0.9874

* are plant species used in chemical analyses

3.6 Chi-square test

In each of the two vegetation types it was tested whether the number of bites corresponded with the proportion of browse volume/density of plant species. The expected value for browse volumes and plant densities are calculated as the total number of bites multiplied with the proportion (%) of browse volumes/densities. Table 6 presents an overview of the X^2 values for browse volumes and plant density in Busclump Karrroid Thicket and Tall Euphorbia Thicket. The 3rd collum describes the number of bites followed by browse volumes in percentages. The 5th collum describes the expected values of available browse volumes. The chi-square value is the sum of values in collum number 6. Plant density is expressed in % followed by the expected values and the chi-square value.

Table 6 X^2 values chi-square test for plant species with more than 2 % contribution to the diet. Chi-square values are calculated for the observed and expected values of browse volume for the relation with the number of bites and observed and expected values of plant densities in relation to the number of bites.

veg type	plant species	bites	browse volumes			plant density		
			% bvol	expected	X	% species	expected	X
BKT	<i>A. tetraacantha</i>	80	0.003728	0.013234	483442.7	0.191176	0.678674	9270.833
	<i>C. ruddis</i>	84	1.633335	5.798339	1054.699	11.2676	39.99998	48.40006
	<i>E. undulata</i>	26	14.52473	51.56279	12.67302	8.448025	29.99049	0.530968
	<i>G. robusta</i>	46	11.49326	40.80106	0.662459	24.66669	87.56675	19.73117
	<i>P. auriculata</i>	46	3.181287	11.29357	106.6568	10.80837	38.36973	1.517369
	<i>G. cuneata</i>	23	0.003728	0.013234	39926.8	0.191176	0.678674	734.1399
	<i>O. mucronata</i>	15	3.615179	12.83389	0.365599	0.207074	0.735113	276.8107
	<i>M. capitata</i>	14	32.55862	115.5831	89.27886	18.3474	65.13326	40.14248
	<i>B. elliptica</i>	13	14.47955	51.40241	28.69019	8.012304	28.44368	8.385247
	<i>B. ilicyfolia</i>	8	18.50658	65.69837	50.67252	17.86018	63.40365	48.41306
		355		355	$X^2=524713$		355	$X^2=10449$
TET	<i>E. tetragonia</i>	417	88.44034	956.9244	304.641	5.091189	55.08667	2377.731
	<i>E. undulata</i>	100	1.643607	17.78382	380.0926	8.213456	88.86959	1.39402
	<i>E. triangularis</i>	208	6.401414	69.2633	277.8943	0.514536	5.567278	7360.69
	<i>A. tetrachanta</i>	92	0.844237	9.134642	751.7172	7.730151	83.64023	0.835551
	<i>O. mucronata</i>	44	2.339951	25.31827	13.78478	1.361351	14.72982	58.1639
	<i>C. ruddis</i>	85	0.031104	0.33654	21298.78	4.285099	46.36477	32.1943
	<i>J. capensis</i>	85	0.026306	0.284632	25213.94	8.241445	89.17243	0.195231

<i>G. occidentalis</i>	28	0.270572	2.927594	214.7243	64.15916	694.2021	639.3314
<i>B. ilicyfolia</i>	23	0.002473	0.026762	19720.82	0.403618	4.367148	79.49883
	1082		1082	$X^2=68176$		1082	$X^2=10550$

Table 7 chi-square test results

		X^2	df	P values
BKT	Browse volume	524713	9	$p < 0.01$
	Plant density	10449	9	$p < 0.01$
TET	Browse volume	68176	8	$p < 0.01$
	Plant density	10550	8	$p < 0.01$

The large X^2 values for both browse volume and plant density in relation to the number of bites indicate a great difference in expected and observed values. It indicates that the black rhinoceros is selective in its foraging behavior. The relative smaller X^2 values for the relation between plant density and number of bites might be an indication that foraging behavior is influenced more by the actual plant density than browse volumes.

3.7 Chemical analyses

Table 5 describes the results of the chemical analyses of the plant species. Leaves and twigs were analyzed separately, the first cell of the plant species describes the results for *Coddia rudus* leafs and the second one the results of the twigs. Each following plant species starts with leaves followed by twigs. Leaf twig ratio is highest for *E. undulata*, 082 and lowest for *C.ruddus* 0.21. Column number 3 and 4 describe the % N and P. Digestibility of the plant samples is described in the next column. The NDF column describes the cell wall constituents. And the final 2 columns present the result of tannin and total phenolics content. Leavetwig ratios vary from 0.16 to 0.82. For all plant species N and P content are higher in the leaves than the twigs. Cell wall constituents (NDF) are lower in leaves for all plant species and the digestibility of leaves is higher for all plant species. From a nutritional quality point of view it might be assumed that higher leaftwig ratios are more favarouble. Two important plant species *P. auriculata* (9.2 % biomass consumption in BKT) and *E. undulata* (14.8 % and 20.5 % biomass consumption in BKT and TET) have the lowest digestability values and contain the highest concentrations of tannins.

Table 5, leaftwig ratios, nitrogen and phosphorus content (% drymatter), digestability (% organic matter), NDF (% cell walls in organic matter), tannins and phynolics (equivalents in quebracho tannins) of leaves and twigs per analysed plant species.

plant species		leaftwigratio	% N	% P	digestibility	NDF	tannins	phynolics
C. rudus	L	0.21	1.82	0.169	75.65	31.02	1.051	0.559
	T		0.58	0.108	54.14	55.90	0.546	0.263
L. capensis	L	0.36	3.69	0.231	84.88	31.45	0.487	1.062
	T		1.17	0.171	33.88	63.57	0.304	0.287
P. auriculata	L	0.16	2.58	0.146	30.00	36.72	5.3	2.49
	T		0.94	0.060	27.60	68.12	6.08	2.132
P. vericossus	L	0.18	2.49	0.190	71.87	22.18	1.404	2.51
	T		1.00	0.097	30.52	69.34	1.802	1.147
A. tetrathanta	L	0.57	2.41	0.111	75.24	31.13	0.468	0.471
	T		1.41	0.072	42.14	62.05	0.362	0.067
P. afra	L	0.61	1.07	0.099	41.11	54.92	2.411	1.001
	T		0.64	0.070	29.49	69.01	2.71	0.875

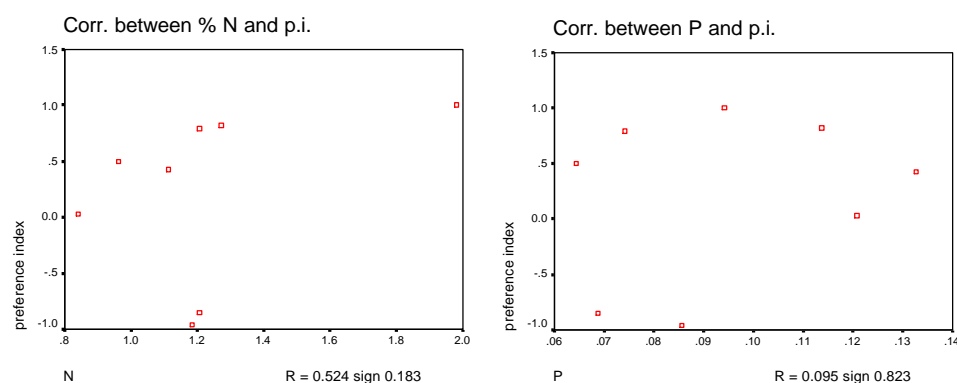
G. robusta	L	0.23	2.39	0.249	42.16	53.49	1.935	2.200
	T		0.73	0.098	29.91	72.33	1.701	0.957
A. striartis	L	0.51	1.48	0.106	38.20	66.34	0.266	0.545
	T		0.86	0.082	28.65	71.93	0.258	0.439
P. obliquum	L	0.62	3.05	0.185	59.99	39.65	1.045	1.638
	T		1.29	0.112	50.86	57.84	0.349	0.370
E. undulata	L	0.82	1.04	0.066	29.71	52.46	2.99	2.254
	T		0.63	0.056	23.35	64.85	5.03	1.947
A. karoo	L	0.27	2.36	0.128	32.69	51.83	0.322	2.102
	T		0.78	0.047	29.89	67.00	2.283	2.372
E. rigida	L	0.30	2.18	0.149	45.27	54.73	3.56	0.214
	T		0.76	0.059	28.40	65.47	1.1267	0.572

3.8 Correlation between preference indexes and chemical analyses of plant species

Correlation coefficients are calculated with the Spearman method, because the sample distribution is non parametric. Correlation between preference indexes and the results of the chemical analyses is calculated as the average values from leaves and twigs. The scatter plots display a visual representation of the correlation between preference indexes of plant species in the diet of the black rhinoceros and N, P, NDF, digestibility, tannin and phynolic content of the plant species.

In BKT non of the quality parameters (N, P, digestibility) are significantly positively correlated with the preference indexes of the selected plant species. The percentage NDF is negatively correlated with the preference indexes but R^2 values are relatively close to 0 and indicate weak correlation .

The SPMs are negatively correlated with preference indexes. R^2 values are close to 0 and indicate weak correlation, however it might be an indication that high levels of secondary plant metabolites are associated with low(er) preference indexes.



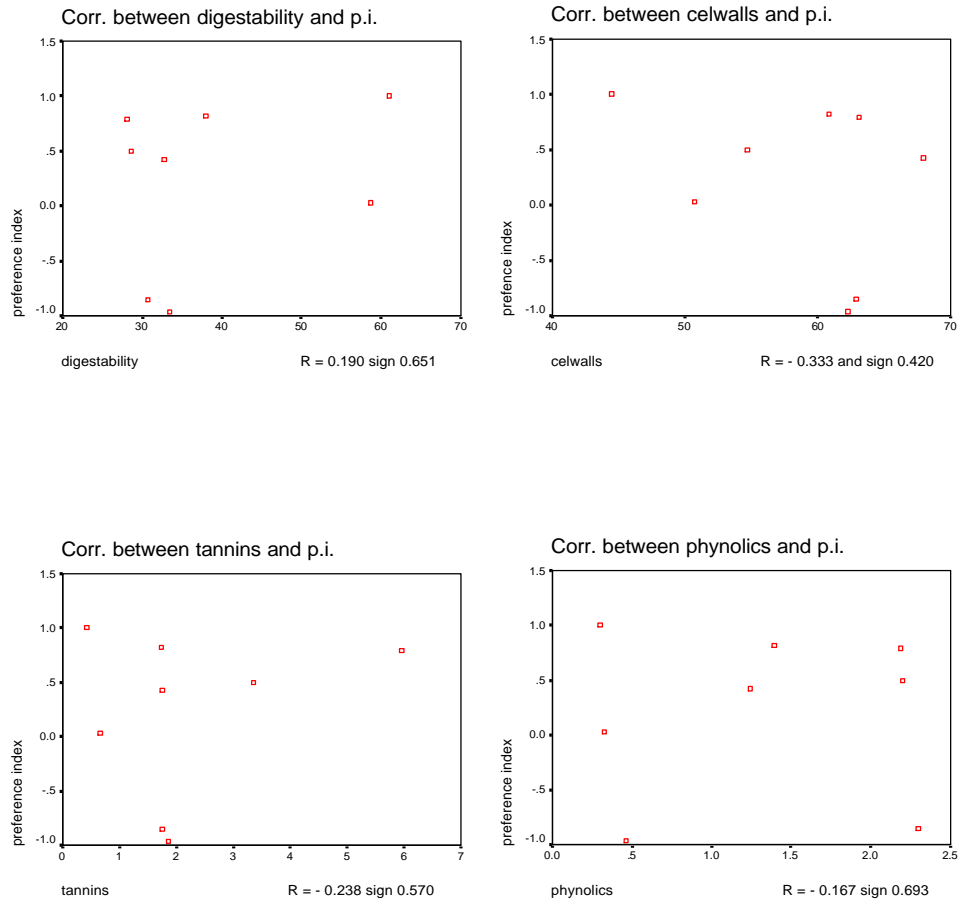
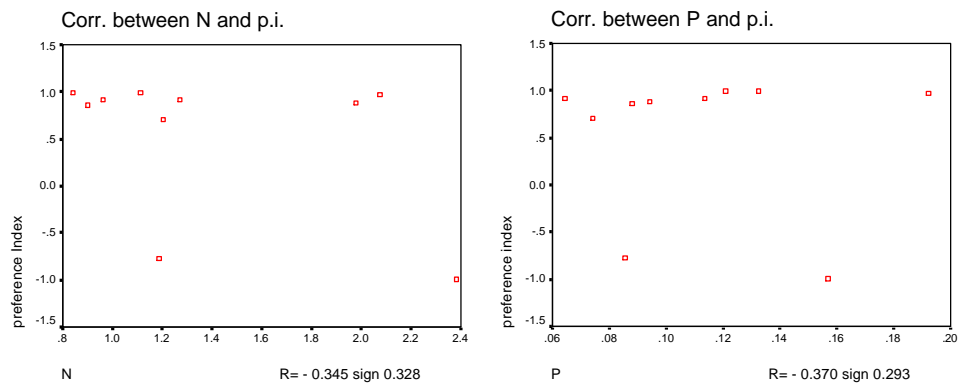


Fig 4-9, scatterplots showing correlation values between preference indexes, nutritional quality and plant secondary metabolites in Bushclump Karroid Thicket.

3.8.1 Correlation between preference indexes and chemical analyses of plant species in Tall Euphorbia Thicket

Correlation in TET shows similar results, with the difference that the correlation between N content and preference indexes is negative (with a low R^2 value) and NDF is not negatively correlated with preference indexes.



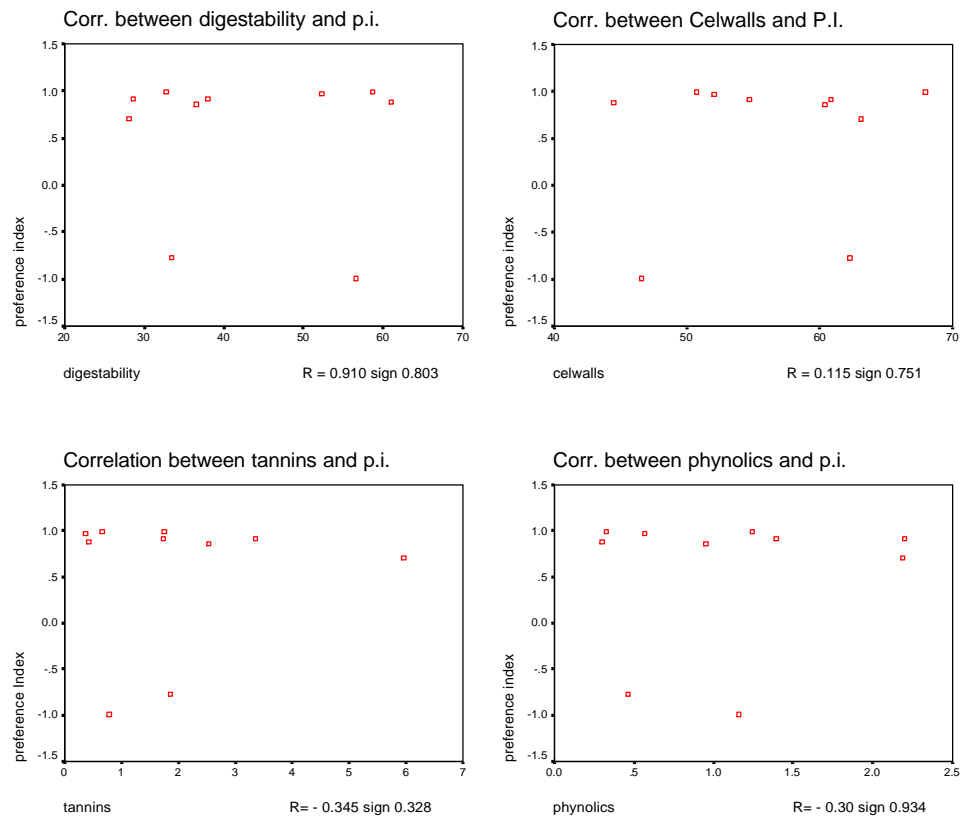


Figure 10-15, scatterplots showing correlation values between preference indexes, nutritional quality and plant secondary metabolites in Tall Euphorbia Thicket.

The correlation between digestibility and SPMs are significant in both the vegetation types with $R^2 = -0.879$ $p < 0.01$ and $R^2 = -0.777$ $p < 0.01$ for tannins and phynolics in BKT. In TET $R^2 = -0.905$ $p < 0.01$ and $R^2 = -0.833$ $p < 0.01$ for tannins and phynolics. The correlation between cell wall constituents and digestibility in Bushclump Karroid Thicket has a R^2 value of -0.819 $p < 0.05$. In Tall Euphorbia Thicket the R^2 value is -0.852 $p < 0.01$.

4 Conclusion and discussion

4.1 Browseselection

Spatial distribution of available browse is depended on the available browse per plant species and plant density. The results of the Chi-square test regarding the distribution of the food items in the diet compared to the availability in browse volumes and plant

densities are significantly different and indicates that black rhinos in the Double Drift Game Reserve are selective in their foraging behavior.

Relative smaller X^2 values for the relationship between plant density and consumption might indicate that plant densities are of greater influence on diet choice than actual browse volumes. Herbivores have spatial memories and learn the location of food resources. They can remember the quantity and quality of the food items found at various sites (Bailly et al 1989a). Plant species respond to herbivory by increasing the release of SPMs. On the long term it can be beneficial to divide consumption on more individuals from the same plant species instead of large intake rates from one individual plant, because in this way concentrations of plant secondary metabolites remain lower.

The overall results indicate that forage selection patterns are not the result of high quality of the selected plant species, or by avoidance of high levels of SPMs. The results indicate weak correlations of SPMs with preference indexes, but none of them are significant.

A large number of studies have described black rhino diets (Goddard, 1968; Joubert et al, 1971; Mukinya, 1977; Kotze et al, 1993 and Oloo et al, 1994). In the Thicket vegetation of the Eastern Cape Province the diet choice of the black rhinoceros has been described by (Ausland et al 2002; Hall-Marten et al 1982 and Brown (2003).

Several of these studies on the diet composition of the black rhinoceros (Oloo et al 1994, 103 spp.), (Mukinya 1977, 70 spp.), (Goddard 1970, 102 spp.), (Goddard 1986, 191 spp.) indicate that black rhinos are browsers with a broad diet and have the tendency to focus on important plant species that form the bulk of their diet. This study described 54 plant species as part of the diet of the black rhinoceros. The number of described plant species in previous studies might be an indication that several potential food items remain undescribed, however the flattening end of the cumulative plant species curve indicates that the main profile of the diet has been adequately described and it appears that a relative small number of different plant species make up for more than 50 % of the diet in the different vegetation types. Whether the black rhinos select such a wide variety of plant species to supplement nutritional factors that are scarce amongst plant species, or avoid aversion (decrease of preference for food just eaten as a result of sensory input) as suggested by Provenca (1996) and Augner et al. (1997) is not known.

Important plant species in the diet in Bushclump Karroid Thicket and Tall Euphorbia Thicket, with the exception of *E. tetragonia* show moderate to high values of preference indexes and indicate that the black rhinos are well provided with adequate food items.

4.2 Chemical analyses of plant species

Depending on local conditions plant species vary in nutritional content. To prepare one sample, samples were taken from three plants in each vegetation type and correlation between preference indexes and chemical analyses might be influenced by sample collection.

The view on herbivore foraging as a trade off between toxin intake and nutrient regulation can be problematic, because it is not always clear to characterize specific PSMs as either toxins or nutrients (Bernays et al. 1987, Bernays 1991, Berenbaum 1996). Additionally it is also known that phytochemicals of similar biosynthetic classes do not necessarily have similar effects (Clausen et al. 1990). The difference between the present amount of PSMs and the actual biological effectiveness should be considered. Two biological effects of PSMs can be distinguished, a metabolic cost and a reduction of digestibility (energy, protein and minerals) availability. Another effect is the rapid deposition of barriers such as lignin (Bennet et al. 1994).

Correlation between preference indexes and phenolics might not be an accurate indication of potential avoidance of PSMs by black rhinoceros. Phenolics are described as a group of structurally diverse PSMs (Wong, 1973), and the potential avoidance of phenolics is caused by a range of chemical complexes of which the actual concentrations remain unknown and might differ per plant species. In this way phenolics are a non consistent parameter for each of the analysed plant species.

The literature describes somewhat contradictory results in which PSMs are described as anti feeding deterrents for herbivores as described by (Brayant et al. 1980; Cheeke, 1989; Bennet et al. 1994;). Owen-smith et al. (1988) found no clear correlation between condensed tannins and acceptability of plant species, but condensed tannin concentrations tended to be lower in more acceptable food items. Cooper et al. (1988) found no relation between measurements on total polyphenols, alkaloids, cyanogenic compounds, aromatic terpenoids and acceptability.

Black rhinoceros are able to utilise plant species that are unacceptable to many herbivores due to plant chemical and physical defence (Loutit et al. 1987). In general the diet of the black rhinoceros is moderate in protein, high in indigestible fiber (due to woody components) and contains PSMs (especially tannins). PSMs occur in many browse species and browsers are likely to ingest substantial amounts of PSMs. (Reed 1986). Owen-smith (1993) described a preference for tannin rich species and suggests that browsing animals developed physiological adaptations to neutralize these PSMs. This study described *E. tetragonia* and *E. triangularis* as important plant species in the diet. Both of these species contain a highly toxic substance (white latex), which is known to have negative clinical effects. *A. tetracantha* is another important plant species which has thorns that does not seem to effect the foraging behavior of the black rhinoceros. Two other important plant species in this study, *P. auriculata* and *E. undulata* contain the highest concentrations of tannins. Owen-smith (1993) described a preference for tannin rich species and suggests that browsing animals developed physiological adaptations to neutralize these PSMs.

4.3 Recommendations for future research

Despite its ecological importance from the viewpoint of both herbivore and plant evolution, Behmer et al (2002) described the absence of studies that explain and give a clear description of the interactive effects of PSMs and nutrients on herbivores foraging in environments with multiple food items that vary orthogonally in PSMs

and nutrient content. Future research is needed to describe and understand the interactions between browsers and forage availability.

Animals need a suite of vegetation components providing nutritional 'stepping stones' through various critical stages of the year (Owen-Smith et al. 1989). Despite the fact that the diet choice of the black rhinoceros has been described in the Great Fish River Reserve additional information is needed on the important plant species in the diet during critical periods.

The Double Drift Game Reserve presents a perfect opportunity for studying the impact of Black rhinoceros on Tall Euphorbia Thicket. Its low resilience makes it necessary to understand the impact of browsing on this vegetation type. Several parts of the reserve consist of almost pristine TET with little to no signs of Rhino activity (pers. obs. 2003). These parts of TET can be compared with TET where heavy browsing is known to occur since the introduction of the black rhinoceros or parts of the pristine TET can be fenced off by enclosures in the future to investigate differences in structure and species composition, caused by the foraging activities of the black rhinoceros.

Literature

Acocks, J.P.H. 1953. Veld types of South Africa. Memoirs of the botanical survey of South Africa 57.

Augner, M., Provenca, F.D. and Villalba. 1998. A rule of thumb in mammalian herbivores. *Animal behaviour*, 56: 337-345

Baily, D.W., Rittenhouse, R.H. and Richards, R.W. 1989a. Characteristics of spatial memory in cattle. *Applied Animal Behaviour Science* 23: 331-340.

Behmer, S.T., Simpson S.T. and Raubenheimer, D. 2002. Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology*, 83(9): 2489-2501.

Bernays, E.A. 1991. Relation ship between deterence and toxicity of plant secondary compounds to the polyphagus grasshoper *Schistocera americana*. *Journal of Chemical Ecology* 17: 2519-2526.

Berenbaum, M.R. 1996. Turnabout is fair play: secondary roles for primary compounds. *Journal of Chemical Ecology* 21: 925-940.

Belovsky, G.E. 1997. Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evolutionary Ecology* 11: 641-672.

Bennet, R.N. and Roger, M. 1994. Tansley Review No. 72 Secondary metabolites in plant defence mechanisms. *New phyt.* 127: 617-633.

Birch, N.V., Avis, A.M. and Palmer, A.R. 1999. The effect of landuse on the vegetation communities along a topo moisture gradient in the mid Fish River valley, South Africa. *African journal of Range and Forage Science* 16(1): 1-8.

Boer De, W.F., Blijdenstein, A.F. and Longamane, F. 2002. Prey choice and habitat use of people exploiting intertidal resources. *Envorinmental Conservation* 29 (2): 238-252.

Brayant, J.P. and Kuropat, P.J. 1980. Selection of winter forage by subartic browsing vertebras. *Ann. Rev. Ecol. Syst.* 11: 261-285.

Brown, D.H., P.C. Lent, W.S.W. Trollope and A.R. Palmer. Browse selection of black rhinoceros *diceros bicornis* in two vegetation types of the eastern cape province in south africa with particular reference to *Euphorbiaceae*

Camp, K.G.T. and Hardy, M.B., 1999. Veld condition assessment. KwaZulu Natal Veld 2.4 18-31.

- Clausen, T.P., Provenca, F.D., Burritt, E.A., Reichardt, P.B. and Bryant, J.P. 1990. Ecological implications of Condensed Tannin Structure: a case study *Journal of Chemical Ecology*, Vol. 16, No. 8: 2381-2392.
- Evans, N.V., Avis, A.m. and Palmer, A.R. 1994. Changes to the vegetation of the mid Fish River valley, Eastern Cape, South Africa, in response to land use, as revealed by a direct gradient analyses. *African Journal of Range and Forage Science* 14(2): 68-74.
- Fabricius, C., Palmer, A.R. and Burger, M. 2002. Landscape diversity in a conservation area and communal rangeland in Xeric Succulent Thicket, South Africa. *Landscape Ecology* 17: 531-537.
- Goddard, J. 1968. Food preferences of two black rhinoceros populations. *East African Wildlife Journal* 6: 1-18.
- Gowda, J.H. 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos* 77: 279-284.
- Hall-Martin, A.J., Erasmus, T. and Botha, B.P. 1982. Seasonal variation of diet and faeces composition of black rhinoceros *Diceros bicornis* in the Addo Elephant National Park. *Koedoe* 25: 63-82.
- Helary F.H. Research proposal: comparison of the contribution of different habitat types to black rhinoceros (*Diceros bicornis*) nutritional status and reproductive potential.
- Joubert, E. and Eloff, F.C. 1971. Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* L. in south West Africa. *Madoqua* Ser. 1. No. 3, 5-53.
- Kotze, D.C. and Zacharias, P.J.K. 1993. Utilization of woody browse and habitat by the black rhino (*Diceros bicornis*) in Western Itala Game Reserve. *African Journal of Range & Forage Science* (1): 36-40.
- Loutit, B.D., Louw, G.N. and Seely, M.K. 1987. First approximation of food preferences and the chemical composition of the diet of the desert dwelling black rhinoceros, *Diceros bicornis* L. *Madoqua* 15(1): 35-54.
- Mabinya, L.V., Brand, J.M., Raats, J.G. and Trollope, W.S.W. 2002. Estimation of grazing by herbivores from analyses of dung. *African Journal of Range and Forage science* 19: 175-176
- MacArthur, R.H. and Pianka, E.R. 1966. An optimal use of a patchy environment. *The american naturalist* 100: 603-609
- Milliken, T. Martin, E.B. and Nowell, K. 1991. Rhinohorn trade controls in East Africa. *Traffic Bulletin*, 12: 17-21
- Moore, D.S. and McCabe, G.P. 1999. Introduction to the practice of statistics. Von Hoffman Press, Inc.

- Mukinya, J.G. 1977. Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. *East African Wildlife Journal* 17: 125-138
- Molyneux, R.J. and Ralphs, M.H. 1992. Plant toxins and palatability to herbivores. *Journal of Range Management* 45: 13-18.
- Oloo, T.W., Brett, R.B. and Young, T.P. 1994. Seasonal variation in the feeding ecology of black rhinoceros (*Diceros bicornis* L.) in Laikipia, Kenya. *African Journal of Ecology* 32: 142-157.
- Owen-Smith, R.N. Megaherbivores. The influence of very large body size on ecology. Cambridge University Press 1988.
- Owen-Smith, N., and S.M. Cooper 1989. Nutritional ecology of a browsing ruminant, the Kudu, through the seasonal cycle. *Journal of zoology* 219(1): 29-43.
- Owen-Smith, N., 1993. Evaluating diet models for an African browsing ruminant, the Kudu: how constraining are the assumed constraints? *Evolutionary Ecology* 7 (5): 499-524.
- Palmer, A.R., Avis, A. 1994. The description, mapping and evaluation of recent change in the contemporary vegetation patterns. Mid-Fish River Zonal Study. Land and Agriculture Policy Centre, Pretoria.
- Pulliam, R.H. 1975. Diet optimization with nutrient constraints. *American naturalist* 109: 765-768.
- Reed, J.D. 1896. Relationship among the soluble phenolics and proanthocyanidins and fibre in East African browse species. *Journal of Range Management*. 39: 5-7
- Rosenthal J.P. and Kotanen P.M. 1994. Terrestrial plant tolerance to herbivory. *Tree* vol. 9, 145-148
- Rohner, C. and Ward, D. 1997. Chemical and mechanical defence against herbivory in two sympatric species of desert *Acacia*. *Journal of Vegetation Science* 8: 717-726
- Provenca, F.D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *Journal of animal science* 74: 2010-2020.
- Smith, R.L. 1990. *Ecology and Field biology*. 4th Edition. New York: Harper Collins
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging theory*. Princeton University Press. New Jersey, USA.
- Tatman, S.C., Stevens-Wood, B. and Smith, B.T. 2000. Ranging behavior and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. *African Journal of Ecology* 38: 163-172.

Trollope, W.S.W. and Webber, L.N. Assessment of veld condition of bush based on height for estimating browsing capacity for black rhino in the Great Fish River Reserve-preliminary procedure. Department Livestock and pasture science, UFH.

Appendix 1 diet composition species less than 2 percent contribution

Diet composition in Bushclump Savanna

plant species	bites	bites %	dryweight gr	dryweight %
<i>Phyllanthus verricosus</i>	3	9.090909	9.38436	0.426944
<i>Asparagus crassycladus</i>	5	15.15152	12.11225	0.55105
<i>Andromischus sphenophyllus</i>	2	6.060606	15.0764	0.685905
<i>Asparagus sauviolens</i>	6	18.18182	15.60114	0.709778
<i>Pappea capensis</i>	4	12.12121	18.18238	0.827212
<i>Delosperma calycinum</i>	4	12.12121	18.6912	0.850361
<i>Asparagus sp.</i>	4	12.12121	24.87368	1.131635
<i>Acacia karoo</i>	5	15.15152	26.54275	1.207569

Diet composition in Bushclump Karroid Thicket

plant species	bites	bites %	dryweight	dryweight %
<i>Asparagus afrikana</i>	2	2.777778	1.601656	0.05041
<i>Carissa heamatoxylon</i>	1	1.388889	2.497405	0.078602
<i>Scutia myrtina</i>	1	1.388889	2.497405	0.078602
<i>Asparagus sibulates</i>	2	2.777778	3.683644	0.115938
<i>Lycium fercissimum</i>	2	2.777778	6.056123	0.190608
<i>Ruschia sp.</i>	2	2.777778	8.132749	0.255967
<i>Cappares sepiara</i>	1	1.388889	10.11337	0.318304
<i>Ehretia rigida</i>	2	2.777778	10.25424	0.322738
<i>Asparagus crassycladus</i>	3	4.166667	10.56524	0.332526
<i>Acacia karoo</i>	3	4.166667	14.95433	0.470667
<i>Pappea capensis</i>	3	4.166667	17.03096	0.536026
<i>Mestoklema sp.</i>	4	5.555556	19.7133	0.620449
<i>Rhus refracta</i>	4	5.555556	22.15115	0.697177
<i>Delospera calycinum</i>	8	11.11111	27.01323	0.850204
<i>Asparagus sauviolens</i>	8	11.11111	29.11675	0.916409
<i>Rhigozum obovatum</i>	4	5.555556	37.50976	1.180568
<i>Grewia occidentalis</i>	7	9.722222	48.95037	1.540645
<i>Schotia afra</i>	7	9.722222	58.44687	1.839534
<i>Phyllanthus verrucosus</i>	8	11.11111	58.74149	1.848807

Diet composition in non-identified vegetation types

plant species	bites	bites %	dryweight	dryweight %
<i>Asparagus striatis</i>	1	1.176471	0.415416	0.013193
<i>Delosperma calycinum</i>	3	3.529412	3.83181	0.121688
<i>Ptearexylon obiquuml</i>	4	4.705882	4.929893	0.156561
<i>Achyropsis leptostachya</i>	3	3.529412	5.575791	0.177073
<i>Asparagus sibulates</i>	8	9.411765	7.49149	0.23791
<i>Rhus refracta</i>	1	1.176471	7.546866	0.239669
<i>Jatropha capensis</i>	6	7.058824	8.589322	0.272775
<i>Pleurostyliia capensis</i>	4	4.705882	9.509286	0.30199
<i>Grewia occidentalis</i>	2	2.352941	10.81509	0.343459
<i>Asparagus crassiciadus</i>	6	7.058824	10.98065	0.348717
<i>Cassine crotia</i>	4	4.705882	11.33606	0.360004
<i>Maytenus heterophylla</i>	3	3.529412	12.58185	0.399567
<i>Asparagus afrikanar</i>	7	8.235294	13.95839	0.443282
<i>Schotia afra</i>	2	2.352941	14.80484	0.470163
<i>Asparagus sauviolens</i>	9	10.58824	17.61776	0.559494
<i>Capares sepiara</i>	1	1.176471	20.36417	0.646713
<i>Phyleboles sp.</i>	2	2.352941	21.19498	0.673097
<i>Jasmina angulara</i>	6	7.058824	27.70711	0.879906
<i>Maytenus capitata</i>	13	15.29412	52.43051	1.665057

Diet composotion Tall Euphorbia Thicket

plant species	bites	bites %	dryweight	dryweigh %
<i>Andromischus sphenophyllus</i>	1	0.862069	2.372479	0.031504
<i>Ptearexylon obliquum</i>	2	1.724138	2.501588	0.033219
<i>Diospylos scabrida</i>	2	1.724138	4.047384	0.053745
<i>Asparagus crassiciadus</i>	3	2.586207	4.159069	0.055228
<i>Phyleboles sp.</i>	3	2.586207	5.280393	0.070118
<i>Ehretia rigida</i>	1	0.862069	5.296162	0.070328
<i>Phyllantus verrucosus</i>	4	3.448276	5.695809	0.075635
<i>Asparagus sauviolens</i>	2	1.724138	5.704444	0.075749
<i>Aloe ciliaris</i>	2	1.724138	6.946509	0.092243
<i>Zanthoxylum capense</i>	1	0.862069	7.13145	0.094699
<i>Leucas capensis</i>	2	1.724138	7.726879	0.102605
<i>Acalypha glabrata</i>	2	1.724138	9.318988	0.123747
<i>Gnidia sp.</i>	2	1.724138	15.56005	0.206622
<i>Asparagus sibulates</i>	2	1.724138	16.99078	0.225621
<i>Maytenus polycantha</i>	4	3.448276	24.58569	0.326473
<i>Saercoctema viminale</i>	5	4.310345	27.1915	0.361076
<i>Cappares sepiara</i>	5	4.310345	29.57932	0.392784
<i>Rhiguzum obovatum</i>	3	2.586207	29.99718	0.398333
<i>Asparagus sp.</i>	13	11.2069	33.13808	0.440041
<i>Maytenus peduncularis</i>	4	3.448276	33.64905	0.446826
<i>Pappea capensis</i>	10	8.62069	47.61072	0.632223
<i>Portulacariaafra</i>	1	0.862069	52.74006	0.700335
<i>Schotia afra</i>	10	8.62069	64.55328	0.857203
<i>Grewia robusta</i>	32	27.58621	132.5698	1.760395

Appendix 2, preference indexes for browsed plant species with a contribution of less than 2 % in Bushclump Karroid Thicket and Tall Euphorbia Thicket.

Plant species		% drweight	% bvolum	Preference index
<i>Asparagus afrikana</i>	0	0.05041		
<i>Carissa heamatoxylon</i>	1	0.078602	0.171486	0.371404
<i>Scutia myrtina</i>	1	0.078602	1.347779	0.889788
<i>Asparagus sibulates</i>	0	0.115938		
<i>Lycium fercissimum</i>	0	0.190608		
<i>Ruschia sp.</i>	0	0.255967		
<i>Capparis sepiara</i>	1	0.318304	0.402914	0.117316
<i>Ehretia rigida</i>	1	0.322738	17.32277	0.96342
<i>Asparagus crassycladus</i>	0	0.332526		
<i>Acacia karoo</i>	1	0.470667	6.045874	0.855547
<i>Pappea capensis</i>	1	0.536026	12.279	0.916344
<i>Mestoklema sp</i>	0	0.620449		
<i>Rhus refracta</i>	1	0.697177	8.885814	0.854497
<i>Delosperma calycinum</i>	0	0.850204		
<i>Asparagus sauviolens</i>	0	0.916409		
<i>Rhigozum obovatum</i>	0	1.180568		
<i>Grewia occidentalis</i>	1	1.540645	0.335811	-0.64208
<i>Schotia afra</i>	1	1.839534	3.19918	0.26984
<i>Phyllanthus verrucosus</i>	0	1.848807		

Plant species		% dryweight	% bvolum	Preference index
<i>Andromischus sphenophyllus</i>	0	0.031504		
<i>Ptearexylon obliquum</i>	1	0.033219	5.246431	0.987416
<i>Diospyros scabrida</i>	1	0.053745	0.007414	-0.75755
<i>Asparagus crassycladus</i>	1	0.055228	0.001408	-0.95029
<i>Phylobolus sp</i>	0	0.070118		
<i>Ehretia rigida</i>	1	0.070328	0.557845	0.776087
<i>Phyllanthus verrucosus</i>	1	0.075635	0.007847	-0.81201
<i>Asparagus sauviolens</i>	1	0.075749	0.010744	-0.75157
<i>Aloe ciliates</i>	0	0.092243		
<i>Zanthoxylum capense</i>	0	0.094699		
<i>Leucas capensis</i>	1	0.102605	0.001462	-0.97191
<i>Acalypha glabrata</i>	0	0.123747		
<i>Gnidia sp.</i>	0	0.206622		
<i>Asparagus sibulates</i>	0	0.225621		
<i>Maytenus polychanta</i>	0	0.326473		
<i>Saecostema viminale</i>	0	0.361076		
<i>Caperis sepiara</i>	1	0.392784	0.024754	-0.88143
<i>Rhigozum obovatum</i>	0	0.398333		
<i>Asparagus sp.</i>	0	0.440041		
<i>Maytenus peduncularis</i>	1	0.446826	6.264759	0.866849
<i>Pappea capensis</i>	1	0.632223	7.010346	0.834552
<i>Portulacaria afra</i>	1	0.700335	0.124786	-0.69753

<i>Schotia afra</i>	1	0.857203	1.003168	0.07846
<i>Grewia robusta</i>	1	1.760395	0.002876	-0.99674
