Competition between black rhinoceros (*Diceros bicornis*) and greater kudu (*Tragelaphus strepsiceros*) in the Great Fish River Reserve, South Africa

Influence of black rhinoceros presence on the diet, density, bite size and feeding height of the greater kudu

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Table of contents

Abstract

This study focuses on possible competition between two browser species: the black rhinoceros (*Diceros bicornis*) and the greater kudu (*Tragelaphus strepsiceros*). In order to study the potential for competition, two research sites were selected, one in the Great Fish River Reserve (Reserve) where rhinos occur, and one in a part of the reserve that is not yet accessible to rhinos (the Annex area). We studied diet choice, diet quality, density, bite size and feeding height of kudus. Diet choice of kudus was studied by faecal analysis. Different statistical methods were used to compare the kudu diet between the Annex and the Reserve. Principal Components Analysis suggested a slight difference in diet composition. Two other methods (the Bray-Curtis and the Kulcynzski's Similarity Index) however, found no significant differences between the kudu's diet in the two areas. Foliage material of 13 plant species (five from the Annex; eight from the Reserve) was collected to analyze whether the quality of the forage species differed between these two areas. The plants were analyzed for crude protein (N), phosphor (P), phenol and condensed tannins content. No significant differences in quality were found between the forage species collected in the Annex and the Reserve. In order to determine the kudu density, line transect counts were carried out. On these transects two different faecal counting techniques were used: the standing crop method and the clearance method. DISTANCE software was used to determine the kudu dung density in both areas. The calculated dung densities show large differences between the two areas, with highest dung density in the Annex. Twig diameter and height measurements were collected from five important forage species. Larger bite sizes were taken in the Reserve, but bites were taken from a higher plant height in the Annex. Incontrovertible evidence that competition between rhinos and kudus does in fact occur in the Great Fish River Reserve is still lacking. However, some results in this study indicate the existence of competition. A shift in diet was expected, but no significant differences were found. These results suggest that, if competition between kudus and rhinos occurs, this has not effected the diet composition of kudus to a large extent. Kudus may deal with the competition issue by rhinos by first increasing bite size, or moving to an area that is not accessible for rhinos, before altering their diet composition. This also offers an explanation for the observed higher kudu density in the Annex.

1 Introduction

1.1 Theoretical framework

South African grass and woodland systems are characterized by a high diversity of large herbivores. Different species co-occur, sometimes even living in mixed herds and often using the same resources, of which the most important ones in ungulate ecology are habitat and diet (Putman, 1996). When large herds of different species of herbivores co-occur in an area, it raises the question whether these multispecies assemblages can coexist without conflict and if so, how they manage to live together without showing signs of competition.

1.1.1 Competition

A simple description of a niche was given by Hutchinson (1957) who stated that a niche is the sum of all environmental factors acting on the organism. Later, this definition was expanded by the discrimination between a fundamental niche and a realized niche. The first was defined as the environmental factors acting on the organism but without negative effects on the species survival and reproduction. The latter was defined as a part of the fundamental niche but the species is restricted due to interspecific interactions (Hutchinson, 1957 in Van Wieren & Van Langevelde, 2007).

The niche of an herbivore is composed of several environmental factors of which diet and habitat are the most important (Van Wieren & Van Langevelde, 2007).

When niches of species overlap, there is potential for competition. When different species are involved, the competition is called interspecific. Interspecific competition can be defined as a process by which two (or more) species compete for resources (often food or space) when resources are not sufficient to sustain the species due to the effects or presence of another species (Wiens (1989) in Prins *et al.*, 2000). Competition can be exerted by direct interaction of the species by for example aggressive behaviour towards the other species. This is called interference competition (Prins *et al.*, 2000). This study is more likely to focus on exploitation competition, where one species exerts a negative effect on the other species by limiting the resources for the other species (Prins *et al.*, 2000). Sometimes competition leads to displacement of one species from its prime habitat or its prime diet, forcing it to feed in a lower quality area or accept diets of lower quality. This is called scramble competition (Makhabu, 2005; Prins *et al.*, 2000). When niches of species completely overlap, one species is bound to completely eliminate the other, a process that is called competitive exclusion (Makhabu, 2005).

Competition between two species can have negative effects on both species (symmetric) or only one species is negatively affected whereas the other species has no negative effects (Prins *et al.*, 2000).

1.1.2 Coexistence

When species are completely separated in diet and habitat use, their niches do not overlap and they can coexist (van Wieren & van Langevelde, 2007; Putman, 1996; Makhabu, 2005). When the niches of two species overlap, there can be potential for competitive interaction. However, despite overlap in (fundamental) niches, coexistence between species is still possible providing that the potential resources do not overlap completely (Putman, 1996). As long as the overlap is incomplete, there remains a part of the resource array that a species alone may exploit. The species can 'withdraw' from the overlap interval and use this resource array where it does not undergo negative (competition) effects. This resource array that is not utilized by other species is called the exclusive niche of the species. Specializing on exclusive niches by behavioural adaptations (for instance a change in diet choice), or habitat segregation (change of habitat to one where there are no or less other species present to share the resources with), can minimize competition between species (Prins *et al.*, 2006).

Resource partitioning is another criterion for different species to coexist. Resource partitioning is the process by which species, living in the same community use resources such as food and space differentially (Makhabu, 2005). Coexistence is only possible when there is partitioning of resources and exclusive use of resources is allowed (Van Wieren & Van Langevelde, 2007).

1.1.3 Conditions for competition

There are three conditions that have to be met for competition to occur. First, the niches of different species have to overlap. But even when there is overlap, competition is not likely to occur when resources are sufficiently abundant to sustain both species. Therefore, a second requirement is that the resources are limited (Prins *et al*., 2000). This is usually the case in the dry season. When food becomes scarce, one species may turn to less profitable food sources and reduce competition (Makhabu, 2005). Normally, the resource overlap between species is expected to be low when the resources are scarce. When resources are abundant (wet season) resource overlap is expected to be high because then, both species have enough food even when their resources overlap (Putman, 1996).

A third condition that has to be met for competition to occur is the joint exploitation of the resources, and interference interactions related to the resource must negatively affect the performance of either or both species (Wiens (1989) in Prins *et al.,* 2000).

1.1.4 Niche Theory

When resources become limited, according to the niche theory, species will increase foraging on their exclusive niche and avoid the part of the niche that overlaps (Putman, 1996). This would indicate that competition for resources (food) results in a diet composition of fewer plant species (with a higher relative abundance of these species included in the diet).

1.1.5 Optimal Foraging Theory

According to the optimal foraging theory, natural selection favours individuals that select food items that convey maximal net benefit. If organisms maximize their net rate of energy or mass intake, the theory states that the optimal diet exhibits three predictions. First, individuals should choose to select or reject a particular food item based on the absolute abundance of other food items that convey a greater benefit. Food items of low value should be rejected if food items of higher value are available, even if the low value food items are abundant. A second prediction of the theory is that individuals perceive and consume available foods in rank order of preference. When high rank food items are abundant, there is no need to include low rank food items in the diet and these should be discarded. In infinite abundances, only high rank food items are included in the diet. The third prediction of the theory is that food items should be either rejected or selected; there is no partial consumption (Pyke *et al.* (1977) in Lacher *et al.*, 1981).

1.2 Diet quality

The quality of the herbivore diet is for a large part determined by the chemical composition of the forage species (Cooper *et al.*, 1988). Herbivores are assumed to select food sources with high amounts of nutrients (proteins and various mineral elements) and low amounts of secondary metabolites that can function as toxins or reduce the digestibility of nutrients.

Nutritional components that are important for herbivores in choosing a diet are crude proteins, condensed tannins and phenol content (Owen-Smith (1993) in Hooimeijer *et al.,* 2005). In addition, fibre content (including cellulose, hemicelluloses and lignin) is an important factor in determining the quality of an herbivore diet since these have a negative effect on the digestibility (Cooper *et al.*, 1988). The nutritional value of forage species however, varies between different plant species and different parts of the plant (Owen-Smith, 1979). Furthermore, seasonal changes do also affect the nutritional value (and therefore quality) of the forage species (Owen-Smith, 1979).

1.2.1 Crude proteins

Nitrogen content is positively related to the digestibility (Prins *et al.,* 2000). The nitrogen content of vegetation fluctuates over the year. The crude protein concentration in feeds gives an indication for the nitrogen content in the feed. An intake with a higher crude protein content has a positive effect on the condition of kudus (Hooimeijer *et al*., 2005).

1.2.2 Condensed tannins

Tannins are secondary metabolites produced by plants. Tannins are high molecular weight polyphenols that are capable of binding proteins. The ability of tannins to bind proteins makes them an effective plant defence- molecule because of their negative effects on protein digestion (Cooper & Owen-Smith, 1985). There are two different classes of tannins with different biological functions. These are hydrolyzable tannins and condensed tannins (Zucker (1983) in Cooper & Owen-Smith, 1985). Primarily condensed tannins play a role in the unpalatability of species of woody plants to browsing ruminants. The function of condensed tannins consists of inhibiting fermentation of the cell wall components by symbiotic microflora in the digestive tract. This results in a lower nutritional value of plant species that have high concentrations of these tannins, hence these species tend to be rejected by these herbivores. Results by Cooper & Owen-Smith (1985) suggests that plant species containing leaf concentrations of condensed tannins in excess of 5% (relative to the Sorghum standard) being most rejected as food while in the mature leaf phase. The greater kudu has been observed to reject plant species with high tannin content as their diet consists for a large part of woody plants (Cooper & Owen-Smith, 1985).

1.2.3 Phenol content

Phenols (sometimes called phenolics) are important chemical compounds for plant defence against herbivory. Phenols are capable of precipitating plant proteins and gastro-internal enzymes. Thereby, they are reducing protein availability and cell wall digestion (Robbins *et al.*, 1987).

1.3 Bite size & feeding height

1.3.1 Bite size

For browsing herbivores, selecting a certain bite size is of high importance since it can determine their nutrient intake rate per unit time and hence their fitness. Often, browsers make a trade-off between forage intake and nutritional quality. According to the research of

Wilson & Kerley (2003), browsers increase their bite size where browse density and quality decline.

The nutritional quality of a bite depends partly on its size (Hjeljord *et al*. (1982), Hanley (1997) in Wilson & Kerley, 2003). The nutritional quality of a twig varies with its diameter (Palo *et al*. (1992) in Wilson & Kerley, 2003). Larger diameter twigs have higher fibre content, and therefore are of lower quality. Larger bites result in a forage intake that consists of relatively more twig material and less high quality leaves. Furthermore, larger bites result in a forage intake that is lower in protein, soluble ash, energy, condensed tannins and digestibility (Wilson & Kerley, 2003).

1.3.2 Feeding height

Vertical zonation of browse quality in tree canopies was found by Woolnough & du Toit (2001). When examining the giraffe biomass browse units at different heights in comparison with other browsing species (kudu, impala and steenbok), they found higher leaf biomass browse units at high canopy levels (1.5 and 2.5 m) than at a low 0.5 m level, indicating a bite size advantage for larger browsers over smaller browsers. Smaller species browsing at low heights are predicted to force the larger browsers to feed at higher feeding sites (Woolnough & du Toit, 2001).

1.4 Problem statement

This study was performed in the Great Fish River Reserve (GFRR). The thicket vegetation in this area is classified as a distinct biome, the GFRR being one of the principal places it occurs (Knight & Cowling, 2006). It is important to ensure conservation of the thicket biome.

In particular, this study is focused on possible competition between two browser species: black rhinoceros (*Diceros bicornis*) and greater kudu (*Tragelaphus strepsiceros*). Since both species are browsing herbivores it is likely that, in addition to overlap in space, their diets too overlap. Such overlap of resources can be an indication that competition may occur when resources are limiting. If there is indeed an ongoing competition between these two species, this may have severe negative effects on the kudu population as well as on the rhino population.

In order to study the potential for competition, the feeding choice and density of the kudu are studied in the GFRR and in a part of the reserve that is not yet accessible to rhinos. It is hoped that this latter area will one day be fully fenced and opened up to use by rhinos. This study will contribute baseline data for this area.

1.5 Research objectives, questions and hypotheses

1.5.1 Diet composition

The goal of this part of the research is to determine if there is an alteration in the diet of the kudu when it shares a habitat with rhinos. When the diet of the kudu is different in co-occurrence with rhinos, this can indicate that the latter species exerts an effect on kudus.

The first question of this research is therefore:

- Is the diet of the kudu in a rhino-included area different than the diet of a kudu in a rhino-excluded area?

Sub questions that need to be answered are:

1. Is there a difference in plant species and number of different plant species in the diet of kudu in a rhino-included area compared to these factors in a rhino-excluded area?
2. Is there a difference in the relative abundance of these plant species in the diet of greater kudu in a rhino-included area compared to these factors in a rhino-excluded area?

Hypotheses:

- Kudus are expected to forage differently in areas where rhinos are present than in areas where rhinos are absent. Based on the optimal foraging theory, which suggests that species that are affected by competition for food are known to include more different plant species in their diet (Pyke *et al.* (1977) in Lacher *et al.*, 1981), the diet of kudu is expected to be composed of more plant species in a rhino-included area than the diet of kudu in a rhino-excluded area.
- The relative abundance of the different plant species included in the diet is expected to be lower in the diet of kudu in a rhino-included area than in a rhino-excluded area. According to the optimal foraging theory, kudus are expected to include more plant species in their diet when in competition with other animal species. However, the relative contribution of these plant species decreases.

1.5.2 Diet quality

If there are differences in the diet of kudu in a rhino-included area compared to the diet of kudu in a rhino-excluded area, it is possible that differences therein are the result of differences in quality of the forage material.

The second question of this research is therefore:

- Is there a difference in the quality of the diet of kudu in a rhino-included area compared to the diet of kudu in a rhino-excluded area?

Hypothesis

- The quality of the kudu diet is expected to be highest in a rhino-excluded area since the resources need not be shared with rhinos.

1.5.3 Density analysis

The goal of this part of the research is to determine the density of kudu in relation to rhino presence. If there is a striking difference in the kudu density in areas where this species co-occurs with rhinos compared to areas where rhinos are not present, this may indicate that the presence of rhino has an effect on kudus.

The third question of this research is:

- Is there a difference in kudu density between rhino-included and rhino-excluded areas?

Hypothesis:

- The kudu density is expected to be higher in areas where no rhinos are present than in areas where rhinos are included. This because of avoidance of negative effects exerted by rhinos on kudu population sizes.

1.5.4 Bite Size & feeding height

The goal of this part of the research is to determine whether the bite size and the feeding height of kudus in a rhino-included area are different than the bite size and the feeding height of kudus in a rhino-excluded area. Bite size is defined as the diameter of a twig at the point of browsing.

The fourth question of this research is:

- Is there a difference in bite size and feeding height of kudus in a rhino-included area compared to the bite size and feeding height of kudus in a rhino-excluded area?

Hypothesis:

- The bite size of plants and shrubs foraged on by kudus in a rhino-included area is expected to be larger than the bite size in a rhino-excluded area. Small diameter twigs are of higher quality (Wilson & Kerley, 2003). When kudu and rhino co-occur, less small diameter twigs are available for kudus, forcing this species to take twigs of a larger diameter (and thereby include forage of lower quality in their diet).

- An alternative hypothesis is that in a rhino-included area, kudus browse on higher branches. Shifting their diet to higher browsing heights can have an advantage over rhinos because it enables them to forage in an exclusive niche that cannot be reached by the rhinos, which can reach heights above 2 m, but prefers to browse below 1 m with a highest biomass off take between 31-60 cm (Hillman-Smith & Groves, 1994; Ganqa *et al*., 2005; Winkel, unpublished). The twig diameter can remain of the same size (and of the same quality) as in a rhino-excluded area.
- A third hypothesis is that in a rhino-included area, there are less fluctuations in feeding height than in a rhino-excluded area, since the lower branches, that are also used by rhinos, are expected to be avoided by kudus.

1.6 Species

1.6.1 Greater Kudu (*Tragelaphus strepsiceros*)

The greater kudu is a browsing antelope with an average body weight between 180-250 kg (Cooper & Owen-Smith, 1985; Wilson & Kerley, 2003) and a shoulder height between 1.3 m (females) and 1.4 m (males) (Makhabu, 2005) (Appendix I). They are gregarious although herds are usually very small (Skinner & Smithers (1990) in Perrin & Allen-Rowlandson, 1993) consisting of related adults and sub adults together with juvenile and yearling young of both sexes (Owen-Smith (1984) in Perrin & Allen-Rowlandson, 1993). Home ranges (defined as the area in which an individual animal was seen during the study) are reported to cover 4-12 km^2 with the ranges of neighbouring groups overlapping, although no quantative data are provided (Owen-Smith (1984) in Perrin & Allen-Rowlandson, 1993).

Kudu can choose a wide variety of vegetation types as their habitat as long as shrubs and bushes are present to prevail cover (Allen-Rowlandson, unpublished). Food items that can be found in these habitat types include leaves, new shoots and fruits of most of the woody plants and forbs that are within reach, plus some fraction of the grass material (Brynard & Pienaar (1960), Conybeare (1975) in Owen-Smith, 1979). All of these food items can be selected by kudu. Woody plants and forbs however are preferred over grass material, the latter being included in their diet only occasionally (Owen-Smith, 1979).

1.6.2 Black Rhinoceros (*Diceros bicornis minor L.*)

With a body mass of 850-1000 kg (Wilson & Kerley, 2003), the black rhinoceros is considered one of Africa's largest browsing herbivores (Appendix I). Estimated numbers of this species have shown a strong decline over the past years (Garnier *et al*., 2001) and the black rhinoceros was officially declared critically endangered (IUCN, 2007). Since then, several measures were taken to prevent the black rhino from going extinct such as anti-poaching efforts (Van Lieverloo & Schuiling, unpublished) and reintroduction (Brown *et al*., 2003).

Large herbivores such as rhinos have a large impact on their habitat, which is comprised of thicket bush land (Luske & Mertens, unpublished). They are known to include a large variety of plant species in their diet, however feeding selective for herbs and shrubs with low phenol and alkaloid contents (Muya & Oguge, 2000).

2 Material and methods

2.1 Study area

The Great Fish River Reserve (GFRR) is located between Grahamstown and Fort Beaufort in the Eastern Cape Province, South Africa. The GFRR is approximately 44,000 ha in size and is comprised of three adjoining reserves: the Andries Vosloo Kudu Reserve, the Sam Knott Nature Reserve and the Double Drift Game Reserve. The vegetation type of the GFRR is recognized as thicket biome. The thicket biome, characterized by evergreen shrubs, tall succulents, climbers and very little grass is regarded as a biodiversity 'hotspot' (Knight & Cowling, 2006). Short Euphorbia Thicket (SET) is one of the four major thicket types that are classified in southeast South Africa and is also known as Xeric Succulent Thicket (Knight & Cowling, 2006; Fabricius *et al.*, 2002) (Appendix I).

Our study area lies in the western sector of the Andries Vosloo Kudu Reserve part of the GFRR, seen in the lower left corner of figure 1. This area is approximately 3500 ha in size (Brad Fike pers. comm.) and located between 33º04' and 33º09'S and 26º37' and 26º49'E (Ganqa *et al.,* 2005). The western part of the Andries Vosloo Kudu Reserve (in the remainder of this study indicated as Reserve) contains most of the Short Euphorbia Thicket vegetation type on the GFRR but also contains extensive amounts of Medium Portulacaria Thicket (MPT) (Peter Lent, pers. comm).

West of the Andries Vosloo Kudu Reserve, a fenced area exists that one day will be part of the reserve, but is not yet accessible for most animal species. The area, which is approximately 482 ha in size (Brad Fike, pers. comm.) and lies between 33º05' and 33º07'S and 26º36' and 26º38'E, is known as the Killarney or Annex area, shown in figure 1 indicated by the broken line. The surface area of the Annex used in this research is approximately 400 ha, since a part of it was not used for reasons of accessibility.

The vegetation type in the Annex is described as Short Euphorbia Thicket in which *Euphorbia bothae* is the most common species. *Portulacaria afra* is largely missing from the area, probably due to heavy grazing by livestock in the past. (Peter Lent, pers. comm.). This research was conducted during the (South African) winter season (July, August, September), which is the season in which resources are least abundant (Fred de Boer, pers. comm.). The data of this research that was collected in the summer (wet) season, was collected during the months April and May.

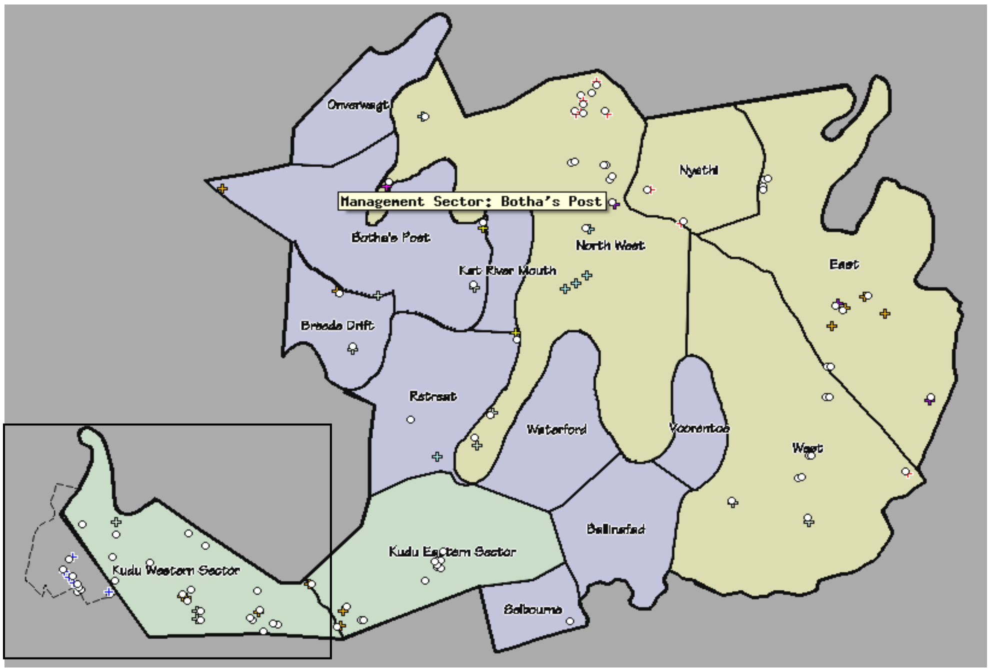

Figure 1 Map of the GFRR with in the lower left corner the Andries Vosloo Kudu Reserve (Reserve). The broken line indicates the Annex.

2.2 Study animals in the GFRR

The greater kudu is the browsing species that represents the highest biomass in the Reserve as well as in the Annex. They are capable of moving between the two areas by jumping over the fence, although most other species cannot move between these areas (Brad Fike, pers. comm). The density of kudu in the Reserve is roughly estimated to fluctuate around 0.07 ha^{-1}. This density is based on nine helicopter surveys that were conducted over the past 20 years. Helicopter surveys had not been conducted in the Annex (Brad Fike, pers. comm.).

Other browsing and mixed feeders present in the Reserve are: black rhino (*Diceros bicornis*), Cape eland (*Taurotragus oryx*), bushbuck (*Tragelaphus scriptus*), steinbuck (*Raphicerus ampestris) and* grey duiker (*Sylvicapra grimmia*) (Ganqa *et al*., 2005) of which only the latter three species are also present in the Annex but in relatively small numbers (Brad Fike, pers. comm).

Black rhinoceros is only present in the Reserve (not in the Annex), where it was first introduced in 1986. After their release, the population increased steadily (Brown *et al.*, 2003). In 2007, the GFRR has been estimated to contain a population of about 100 rhinos (Peter Lent, pers. comm.). In the remainder of this study, the rhino-included area will be indicated as the Reserve and the rhino-excluded area will be indicated as the Annex.

2.3 Diet analysis

In order to determine the diet of kudu, fresh dung was collected in both the Reserve and in the Annex (Appendix I). The pellets were collected in the morning and only fresh pellets (dropped that same morning) were taken. The collected pellets were kept in a freezer (-25 ºC) in separate plastic bags until further use.

Faecal samples were collected over a period of 12 weeks during the dry season. Each week, one sample was collected in the Reserve and one in the Annex. Each sample consisted of four subsamples. Each subsample consisted of approximately two pellets obtained from one pellet group. After every 3 week period, the collected samples were pooled, so that after 3 weeks, two pooled samples were available, one for the Annex and one for the Reserve. Hence, after 12 weeks, a total of four pooled samples from the Reserve and four pooled samples from the Annex were available for further analysis. The faecal analysis was carried out on these pooled samples. The faeces for the first pooled samples were collected in weeks 28, 29 and 30; the faeces for the second pooled samples were collected in weeks 31, 32 and 33; the faeces for the third pooled samples were collected in weeks 34, 35 and 36; the faeces for the fourth pooled samples were collected in weeks 38, 39 and 40.

In addition, one large pooled sample was collected in the Annex and one large pooled sample in the Reserve during the wet season. The faeces for these pooled samples were collected in weeks 16 and 19. These pooled samples were also analysed.

To determine the plant species composition of the samples, epidermis fragments of ingested plants were identified and quantified as described by De Jong *et al.* (2004). This method is based on the knowledge that the cuticle of plants cannot be digested by an animal's digestive system (Fitzgerald & Waddington, 1979). The cuticle carries a print of the underlying epidermis, which can be visible in the dung after digestion. Since the cuticle is often species specific, different plant species can be identified by factors such as hairs, glands, stomata form and size and cellular organization (Hooimeijer *et al.*, 2005).

The faecal samples were kept in glass jars and heated in water to 115 ºC under pressure (80 kPa) for approximately two hours and left to soak overnight (Tedelex pressure cooker 11 L 80 kPa). After cooling down, the samples were thoroughly mixed. A tablespoon of every sample was washed in a household blender with tap water (350 ml) for one minute and strained over a plankton sieve (0.01 mm). Ethanol (99.9%) was added until a concentration was reached of about 70%.

In order to conduct the epidermis analysis, the samples were transferred into a petri-dish and allowed to settle. The samples were analysed with a light microscope (Zeiss with 4x, 10x, 40x and 100x lenses). With a Pasteur pipette, ten random grab samples of the residue were taken and put as droplets on a glass slide (Rova-Mavi ± 76x26mm). The droplets were spread out evenly on the glass slide and covered with a cover slip (Menzel-Glazer 24x50 mm). On each slide, ten epidermis fragments were identified and measured in two transects (five fragments per transect). In order to measure the size of each fragment, a 1 mm^2 microscope grid of 0.01 mm^2 squares was inserted into the microscope eyepiece. Sizes were measured using a magnification of 100x.
In every sample, 100 fragments were identified. In order to identify the fragments, the fragment structure was compared to an existing reference collection of a wide spectrum of plant species present in the GFRR. This reference collection originates from a previous study performed by van Van Lieverloo & Schuiling (unpublished) and was extended with plant species from other areas (Hooimeijer *et al*., 2005). A complete list of the different plant species present in the reference collection is shown in Appendix II. Only fragments that were epidermis tissue were identified. Since the kudu is primarily a browser, fragments of grass species found in the sample were not determined to species level but classified under 'grasses'. Fragments that could be classified as epidermis were determined to species level as much as possible. When the exact species of a fragment could not be determined, but it was clear it was dicotyl tissue, this fragment was classified as 'dicot. epidermis'. When unclear whether the fragment was monocotyledonous or dicotyledonous, this fragment was classified as 'uncertain epidermis'.

The total area of the fragments of the plant species in every sample was calculated; the abundance of the plant species was calculated as a percentage of the total area of the fragments measured (De Jong *et al.,* 2004).

2.4 Quality analysis

Foliage material was collected of 13 plant species. Selection was based on the abundance of these species in both areas and the difference of the abundance of these species between the two areas. Five species were more commonly selected in the Reserve, eight were more commonly selected in the Annex (Table 1). Of these plant species, leave and twig material was collected at kudu browse height (Brad Fike pers. comm.) and analyzed for quality factors. The collected material was kept in paper bags for three weeks until transportation to Wageningen, the Netherlands. Approximately one month after collecting, the material was dried for approximately 48 hours at 70˚C in a stove in Wageningen, the Netherlands. The dried samples were thoroughly grinded and mixed in a Culatti grinder and analyzed for crude protein (N)- and phosphor (P)-concentration. In order to determine the total phenolics and condensed tannins, the dried samples were additionally grinded using a ball mill grinder (Retsch NM 2000, ISO 9001).

The elements N and P were measured after destruction with sulphuric acid (H_2SO_4), Se and salicylic acid. Measurements were performed using a Skalar San-plus autoanalyzer.

Total phenolics were measured using the Folin-Ciocalteu method (Waterman & Mole, 1994). Tannin concentrations were measured using the Proanthocyanidin method (Waterman & Mole, 1994).

Table 1 Abundance of 13 plant species in the diet in the Annex and in the Reserve.

Forage species	abundance in diet Annex (%)	abundance in diet Reserve (%)	area highest abundance in diet
Schotia afra	5.98	4.69	Annex
Euphorbia bothae	8.69	7.00	Annex
Ptearoxylon obliquum	3.45	0.81	Annex
Olea europeana spp africana	3.05	0.10	Annex
Maytenus capitata	7.79	4.29	Annex
Jasminum angulare	4.94	1.61	Annex
Ehretia rigida	1.23	0.09	Annex
Brachylaena ilicifolia	4.17	2.74	Annex
Portulacaria afra	3.50	7.32	Reserve
Pappea capensis	2.15	12.06	Reserve
Ozoroa mucronata	1.01	2.40	Reserve
Azima tetracantha	3.77	6.21	Reserve
Euclea undulata	4.00	6.01	Reserve

2.5 Density analysis

2.5.1 Line transects

In order to determine the kudu density, line transects were surveyed. On these transects two different faecal counting techniques were used: the standing crop method and the clearance method. These two faecal counting techniques are often used in census studies (Staines & Ratcliffe (1987) in Plumptre & Harris, 1995). The standing crop method involves transects that are surveyed only once and all dung present is counted. The clearance method involves counting dung on cleared transects after a certain period, after which the density of dung over this period can be estimated (Plumptre & Harris, 1995).

Kudu density was determined in these two ways in both the Reserve and the Annex. In both areas, a total transect length of 500 m was laid out. In the Annex, the total transect length was subdivided into five transect lines with lengths of 160, 100, 120, 60 and 60 m. In the Reserve the total transect length was subdivided in three transect lines with lengths of 200, 140 and 160 m. A picture of the study area in which the transect lines are situated is shown in Appendix III. These transects were used for the standing crop method first, after which the same transects were used with the clearance method one month later.

2.5.1.1 Standing crop method

Transects were randomly selected in Short Euphorbia Thicket. The transect lines were marked with a chain with a length of 20 m, that was removed in extension of the transect after the entire chain was surveyed. The transect lines were surveyed by two observers, that both observed the area to the left and the right of the line. Every pellet group of kudu dung that was visible from the transect line was recorded and removed. Removal of the dung was necessary to use the clearance method afterwards. Pellets were considered a group when they lay in a group of ten pellets or more of the same shape indicating that they were dropped by one individual animal at one time. Pellets that were not considered a group (nine or less) were only removed and not recorded. The shortest distance from the pellet group to the transect line was measured using a 10 m measuring tape (steel tape) and recorded. When pellets were dropped while the animal was walking, the dung was spread in a so called ‘trail’ in which case the shortest distance from the middle of the trail to the transect line was measured. Large bushes on the transect line were regarded as a ‘thickening’ of the transect line and the distance of the pellet groups to the bushes was measured instead. After each transect line, the GPS coordinates of the starting-point and the end-point of the line were recorded.

2.5.1.2 Clearance method

Approximately 28 days after having surveyed the transects, all eight transects were surveyed a second time in order to record all kudu faeces of one month. The same method as in the standing crop method was used, except that transects were not cleared.

2.5.2 Helicopter survey

Kudu individuals were also counted using a ‘Boma’ helicopter. The counts were performed in the Annex (400 ha) from 7.00 am -7.30 am and in the Reserve (700 ha) from 7.35 am -8.30 am, both on October 4, 2007 (Figure 2). The helicopter flew in parallel lines resulting in the coverage of strip-transects with a width of approximately 300 m. Flying speed was approximately 60 km/h at a height of approximately 25 m. Four observers in the helicopter searched for kudu and other large herbivore species. The two observers on the right hand site surveyed the right half of the transect line, the two observers on the left hand site surveyed the left half of the transect line. Only animals approximately 150 m or less from the helicopter were counted, to prevent double counting when flying the next transect. In addition to the number of animals observed, the sex of the kudus was recorded. One person recorded the counts.

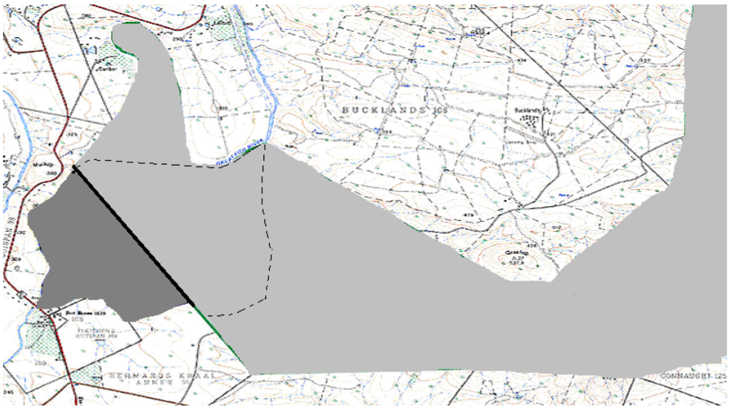

Figure 2 Area covered by helicopter survey. The dark area indicates the Annex. The lighter area indicates the 'Andries Vosloo Kudu Reserve' with, indicated by the dotted line, the area covered by the helicopter survey (the Reserve).

The helicopter survey yielded also counts of other species than kudu. The total metabolic weight of all large herbivores in both areas was calculated. This was done by using the metabolic weight ($W_{kg}^{0.75}$) for each species multiplied by the number of individuals of each species per area.

2.6 Bite size & feeding height

Twig diameter and height measurements were collected from the five plant species (*Rhus refracta, Azima tetracantha, Pappea capensis, Brachylaena ilicifolia, Euclea undulata*) that were most commonly selected as a food item by kudu resulting from the diet analysis. Branches of these species were then located in the Annex and in the Reserve and checked for kudu bites. The diameter at point of browsing was measured to the nearest 0.1 mm, using Vernier calipers (Wilson & Kerley, 2003). Bite heights were measured from the point of browsing to the ground using a tape measurer. One hundred bite marks and bite heights were measured of each of the five plant species. Fifty of the measurements were taken in the Annex, the other fifty in the Reserve.

2.7 Data analysis

2.7.1 Diet analysis

The diets of kudu in the Annex were compared to the diets of kudu in the Reserve using the Kulcynzski's Similarity Index (KSI) (De Jong *et al.*, 2004) and the Bray-Curtis measure of dissimilarity (Krebs, 1999). In the first method, all four dry period samples in the Annex were compared to the dry period samples in the Reserve, and the average over the dry period in the Annex was compared to the average of the dry period in the Reserve. Comparisons were made per plant species.

In the second method (Bray-Curtis), the composition of the kudu diet-samples in the Reserve was compared to the composition of the other kudu diet-samples of the Reserve that were collected on an other moment in time, and to the composition of the kudu diet-samples of the Annex, and vice versa.

The data was also tested for differences between coefficients of dissimilarity when comparing the wet season (wet/wet), the dry season (dry/dry) and when comparing wet season with dry season (wet/dry).

The Bray-Curtis coefficients of dissimilarity calculated when comparing the three area-comparisons (Reserve/Reserve, Reserve/Annex, Annex/Annex) and the two time-comparisons (dry/dry and wet/dry) were normally distributed (Kolmogorov-Smirnov) and an ANOVA was performed to test for differences between the three groups. The tests were performed using SPSS (version 15.0).

Multivariate analysis was performed using Canoco (version 4.51). First a Detrended Correspondence Analysis (DCA) was performed in order to determine that the species response was linear (length of gradient: < 4). Within a linear species response, environmental factors were not directly included, resulting in a Principal Components Analysis (PCA).

Canodraw was used to construct ordination diagrams. A biplot with samples and environmental factors, and a triplot with environmental factors were drawn.

2.7.2 Quality analysis

The polyphenol content, tannin content, percentages of N and P of the forage species collected in the Reserve were compared to that of the species collected in the Annex. When the data were normally distributed (Kolmogorov-Smirnov) and the variances were equal (Levene’s test), an independent sample t-test was used. When the data were not normally distributed, a Mann-Whitney U- test was used. When the data were normally distributed, but the variances were not homogenous, an independent sample t-test was used assuming unequal variances. All tests were performed using SPSS (version 15.0).

In addition, weighted averages were calculated for the four quality parameters: polyphenols content, tannins content and percentages of N and P. The content of these parameters in every separate plant species was multiplied with the abundance of these plant species in the area. The sum of the weighted averages per area was calculated and divided by the total abundance of the analyzed plant species in these areas.
Furthermore, the ratios of the abundances were calculated by dividing the abundance of the plant species in the Annex by the abundance in the Reserve. The ratios were plotted against the quality parameters.

2.7.3 Density analysis

DISTANCE 5.0 software was used to determine the kudu pellet group density in both areas (Thomas *et al.*, 2005). Microsoft Excel was used to summarize the perpendicular distances measured on each transect. A tab-limited text file of the Excel sheet was used to entry the data in DISTANCE. Separate analyses were carried out for the Annex data and the Reserve data by defining two different data filters. The first filter selected only transects laid out in the Annex, the second filter selected only transects in the Reserve. Truncation of the data was necessary to exclude extreme outliers from the analysis. Therefore both filters discarded the largest 10% of the distances (Ellis & Bernard, 2005).
DISTANCE offers different model definitions to analyze the data. Six model definitions used in a comparable kudu density study by Ellis & Bernard (2005), were used in this study: half normal cosine, half normal hermite polynomial, uniform cosine, uniform simple polynomial, hazard rate cosine and hazard rate simple polynomial. After analysis with these six models, the best model was chosen based on the criteria from Ellis and Bernard (2005): "*a combination of a low Akaike's information criterion (AIC), a low variance, and nonsignificant goodness-of-fit value (chi-square)*".
The data obtained by the standing crop method and the clearance method were analyzed separately by determining dung density. In addition, the dung density was determined over the samples collected in both the standing crop method and the clearance method combined.

2.7.4 Bite size & feeding height

The bite sizes and feeding heights in the Annex were compared to the bite sizes and feeding heights in the Reserve. This was done by a General Linear Model. Both plant species and area were used as fixed factors. The data were tested for equality of error variances (Levene's test) and the residuals were tested for normality (Kolmogorov-Smirnov). The data for bite size were transformed using a double square root. These tests were performed in SPSS, version 15.0.

In order to look at the fluctuations of the bite heights, the standard deviation of the bite heights in the Annex were calculated and compared to the standard deviation of the bite heights in the Reserve.

3 Results

3.1 Diet composition

Appendix IV shows the abundance of all forage species in the diet of kudus on the five different periods in the Annex and the Reserve. Also included are the average abundances of the plant species in the four periods of the dry season in both areas. During the months that this research was conducted (July, August, September), the total number of different species foraged on in the Annex (36) was similar to the total number of species foraged on in the Reserve (37) (Appendix IV).

Most forage species are included in the diet in the Reserve as well as in the Annex. When the average abundances of the dry period are taken into account, dicotyledonous forage species that are only included in the diet in the Reserve (unique species for the Reserve) are: *Grewia occidentalis, Jatropha capensis, Kalanchoe rotundifolia, Phyllanthus verrucosus* and *Phylobolus spp.* Unique dicotyledonous species for the Annex are*: Capparis sepiaria and Verbesina encelioides.* Unique monocotyledonous species for the Annex are *Asparagus spp.* and *Asparagus striatus,* whereas there are no unique monocotyledonous for the Reserve area.

Dicotyledonous forage species that are always included in the diet in both the Reserve and the Annex are: *Acanthaceae spp., Brachylaena ilicifolia, Carissa haematocarpa, Euclea undulata, Euphorbia bothae, Grewia robusta, Jasminum angulare, Maytenus capitata, Pappea capensis and Schotia afra.*

In the dry period, large differences appear to exist between the Reserve and the Annex in the abundance of *Pappea capensis* and *Portulacaria afra* that appear to be higher abundant in the diet in the Reserve than in the Annex and *Maytenus capitata* that appears to be higher abundant in the diet in the Annex than in the Reserve.

When comparing the abundances in the diet in the wet season with the dry season in the Reserve, differences are found in the species *Azima tetracantha,* which seems to be more abundant in the diet in the dry season than in the wet season. The species *Carissa haematocarpa* and *Schotia afra* however seem to be more abundant in the diet in the wet season. In the Annex, large differences are found in the species: *Euclea undulata, Jasminum angulare* and *Pappea capensis*, all three of which are more abundant in the diet in the wet season. The species: *Euphorbia bothae, Maytenus capitata, Portulacaria afra* and *Ptearoxylon obliquum* however appear to be more abundant in the diet in the dry season.

Calculations of the Kulcynzski's Similarity Index (KSI) yielded the results shown in appendix V. No significant differences were found between the kudu diet in the Annex and the Reserve in all four pooled samples in the dry period (1-4). Also the calculated average of all pooled samples in the dry period yielded no significant differences. Neither of the separate plant species was significantly different between the two areas.

The Bray-Curtis coefficients of similarity that were calculated when comparing the diet-samples of the Reserve and the diet samples of the Annex in both the dry season and the wet season are shown in a cross table (Appendix VI).

No significant differences were found between the Bray-Curtis coefficients of dissimilarity calculated when comparing the three groups Reserve to Annex (res-ann), Reserve to Reserve (res-res) and Annex to Annex (ann-ann) (ANOVA, $F_{2,25}$=0.039, P=0.962) (Figure 3).

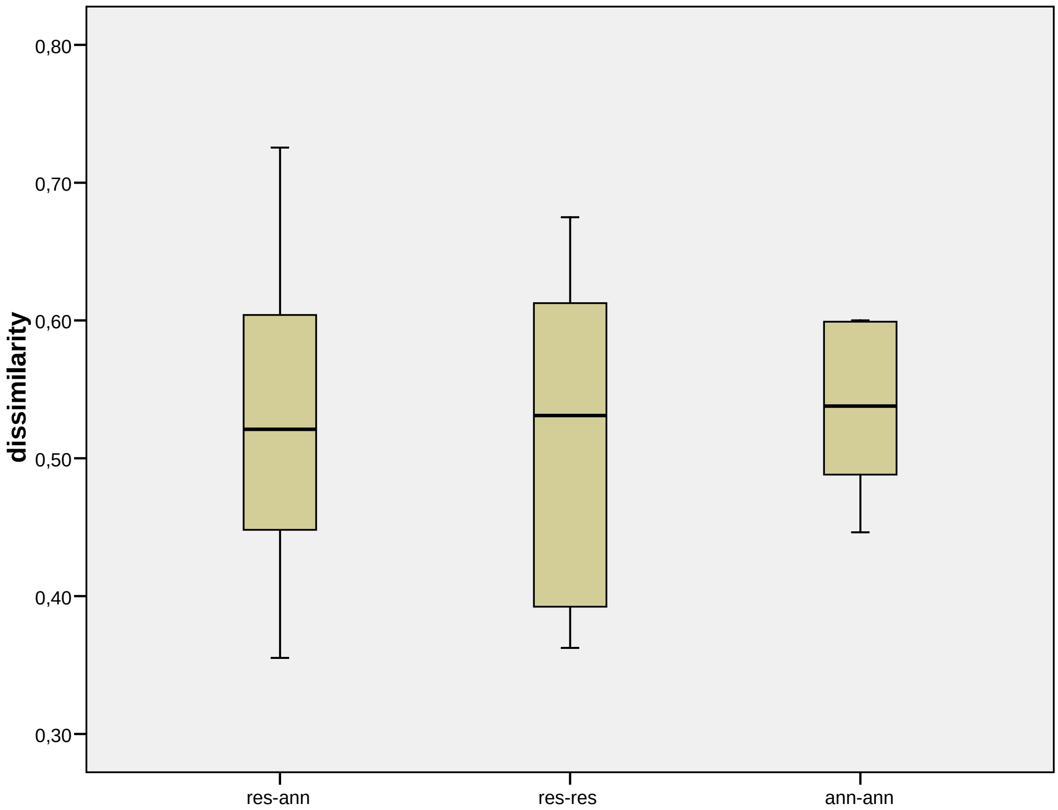

Figure 3 The box represents the interquartile range from first to third quartile and the smallest and largest non-outlier observations; the horizontal line in the box represents the median.
The left box represents the coefficients of comparison between the Reserve and the Annex (res-ann); the middle box represents the coefficients of comparison of the different samples within the Reserve (res-res); the right box represents the coefficients of comparison of the different samples within the Annex (ann-ann).

No significant differences were found between the Bray-Curtis coefficients of dissimilarity calculated when comparing the coefficients calculated within the dry season, within the wet season and between the dry and the wet season (ANOVA, $F_{1,42}$=0.624, P=0.434) (Figure 4).

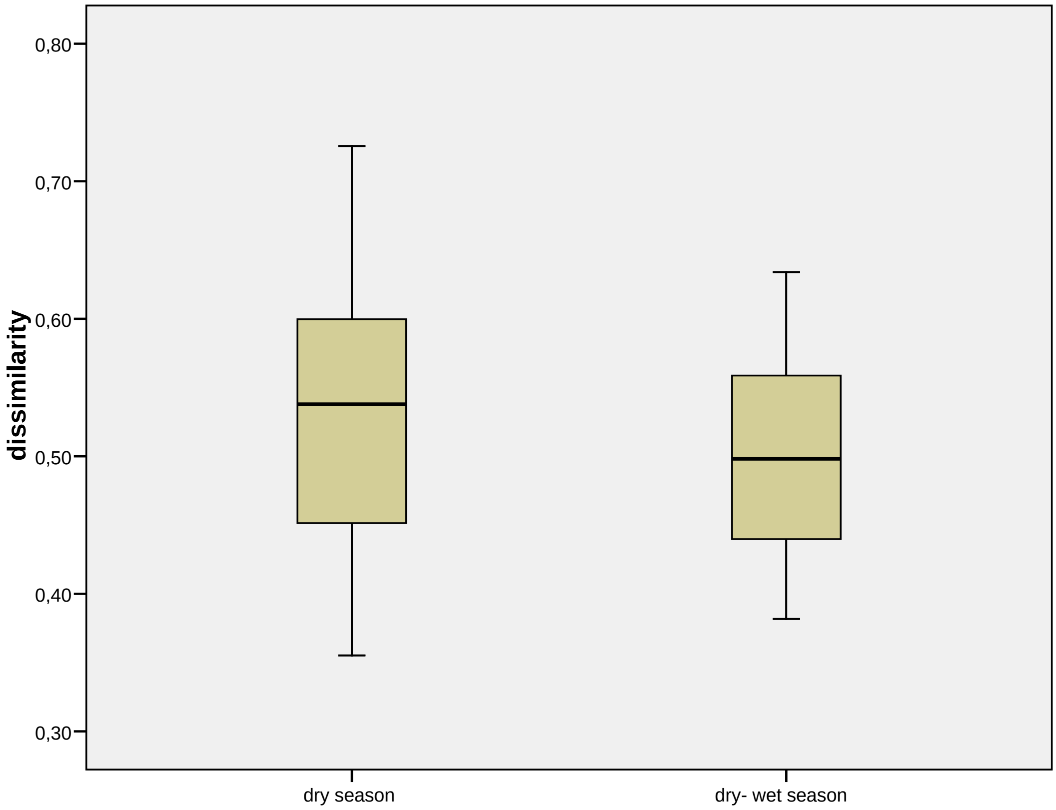

Figure 4 The box represents the interquartile range from first to third quartile and the smallest and largest non-outlier observations; the horizontal line in the box represents the median.
The left box represents the coefficients of comparison of the samples calculated within the dry season (dry season); the right box represents the coefficients of comparison calculated when comparing the dry season to the wet season (dry- wet season).

Multivariate analysis was done using a PCA. The analysis showed a difference in diet composition between the two areas (Figure 5).

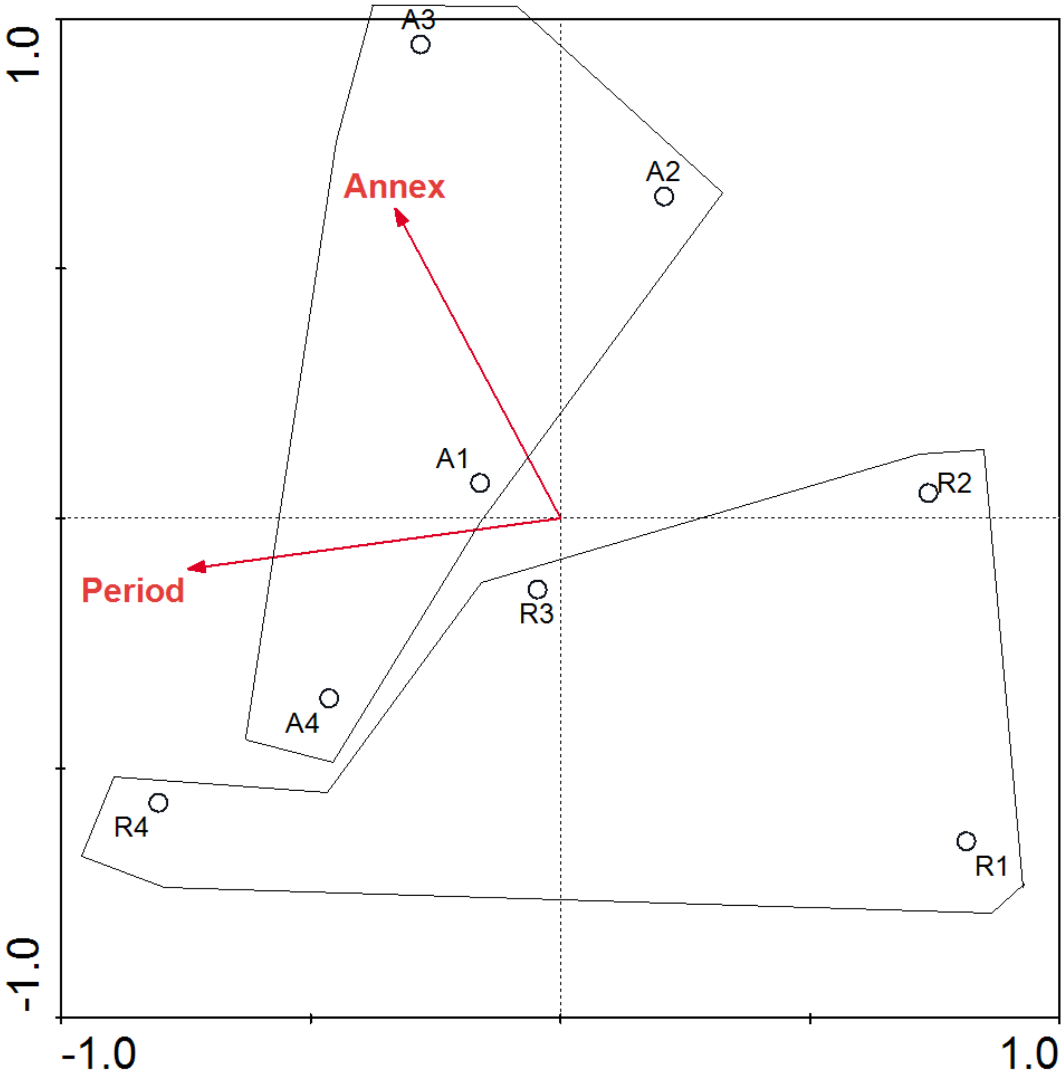

Figure 5 Biplot illustrating the results of Principal Component Analysis. Dots A1-A4 represent faecal samples collected in 3-weekly periods 1-4 in the Annex, dots R1-R4 represent faecal samples collected in these four 3-weekly periods in the Reserve. Samples collected in the same area are enclosed by a polygon. The environmental factors Annex and Period are represented by an arrow. The factor Annex represents the area, the Annex area is given in the biplot by an arrow, the Reserve area is opposite to this arrow.

Figure 6 shows a triplot in which the plant species are added. It shows which plant species are more abundant in the diet of kudus in the two different areas. In the Annex, *Jasminum angulare*, *Ptearoxylon obliquum*, *Acacia karroo*, *Capparis sepiaria*, *Ehretia rigida*, *Justitia protractra* and *Olea europaea spp africana* were more abundant in the kudu diet. In the Reserve, the plant species *Boscia spp*, *Asparagus densiflorus*, *Pappea capensis*, *Aloe tenusit*, *Portulacaria afra*, *Azima tetracantha* and grasses were more abundant.

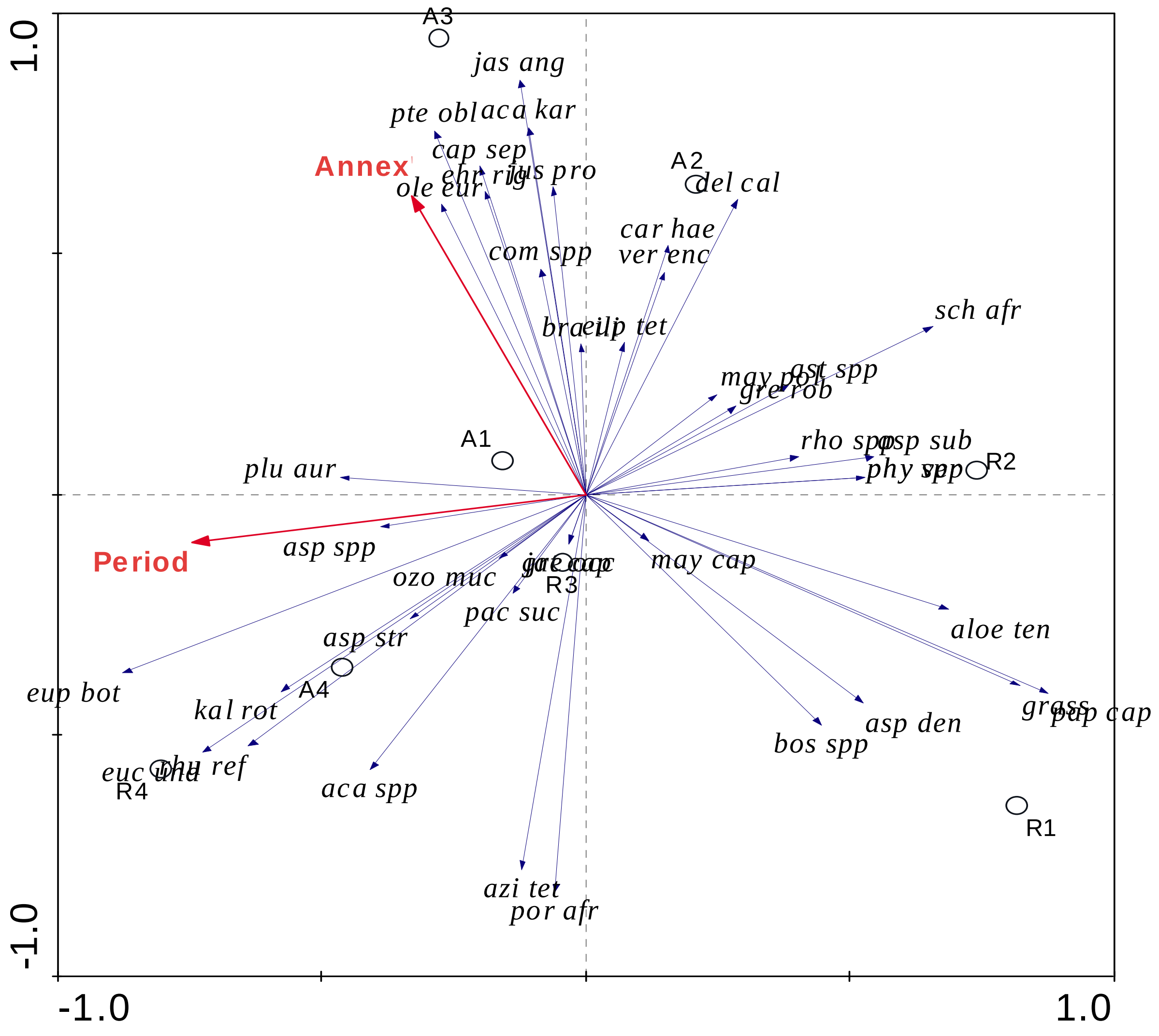

Figure 6 Triplot illustrating the results of Principal Component Analysis. Dots A1-A4 represent faecal samples collected in 3-weekly periods 1-4 in the Annex, dots R1-R4 represent faecal samples collected in these four 3-weekly periods in the Reserve. The environmental factors: Annex and period, and the different plant species are represented by arrows.

3.2 Diet quality

The forage species collected in the Reserve and the Annex did not show a significant difference in polyphenol content (independent samples t-test, t=0.084, df=11, P=0.934), tannin content (Mann-Whitney U, Z =-0.953, N=13, P=0.341), percentage N (independent samples t-test, t=1.075, df=9.735, P=0.308) and percentage P (independent samples t-test, t=0.981, df=11, P=0.348) (Appendix VII).

The weighted averages of the quality parameters (polyphenol content, tannin content, percentages of N and P) are given in table 2. No striking differences between the Annex and the Reserve were found.

Table 2 Weighted averages of quality parameters. The weighted averages are given for each diet quality parameter in the Annex and the Reserve.

	%P	%N	tannins (mg/g)	polyphenols (mg/g)
Annex	17.4902	120.7069	5.8356	0.6316
Reserve	16.4405	115.5985	5.7078	0.6311

The graphs of the ratios plotted against the quality parameters yielded no additional information.

3.3 Density analysis

3.3.1 Line transects

Density analysis by use of the standing crop method yielded a dung density of 1003 pellet groups ha^{-1} in the Annex (half normal cosine; CV=0.183). The same method yielded a dung density of 419 pellet groups ha^{-1} in the Reserve (uniform cosine; CV=0.257) (Table 3; Figure 7). Assuming that defecation rates are similar throughout the areas, the dung density represents the relative kudu densities.

The clearance method yielded a dung density of 298 pellet groups ha^{-1} in the Annex (uniform cosine; CV=0.207). In the Reserve, the clearance method yielded a dung density of 164 pellet groups ha^{-1} (uniform cosine; CV=0.204) (Table 3; Figure 7).

The two methods combined resulted in a dung density of 644 pellet groups ha^{-1} in the Annex (uniform cosine; CV= 0.203) and a dung density of 336 pellet groups ha^{-1} in the Reserve (half normal cosine; CV=0.251) (Table 3; Figure 7).

The calculated dung densities show large differences. However, the 95% confidence intervals are overlapping, suggesting no difference in dung density between the two areas.

Table 3 Dung densities determined in the Annex and the Reserve by two different methods: Standing crop and clearance (separately and combined), with the best fitting model, the 95% Confidence Interval (CI) and percentage Coefficient of Variation (%CV).

Location	Counting technique	Model	Dung density (pellet groups ha^{-1})	95% CI	% CV
Annex	Standing crop	half normal cosine	1003	619-1624	0.183
	Clearance	uniform cosine	298	174-511	0.207
	Standing crop and clearance	uniform cosine	644	410-1011	0.203
Reserve	Standing crop	uniform cosine	419	154-1137	0.257
	Clearance	uniform cosine	164	88-306	0.204
	Standing crop and clearance	half normal cosine	336	185-612	0.251

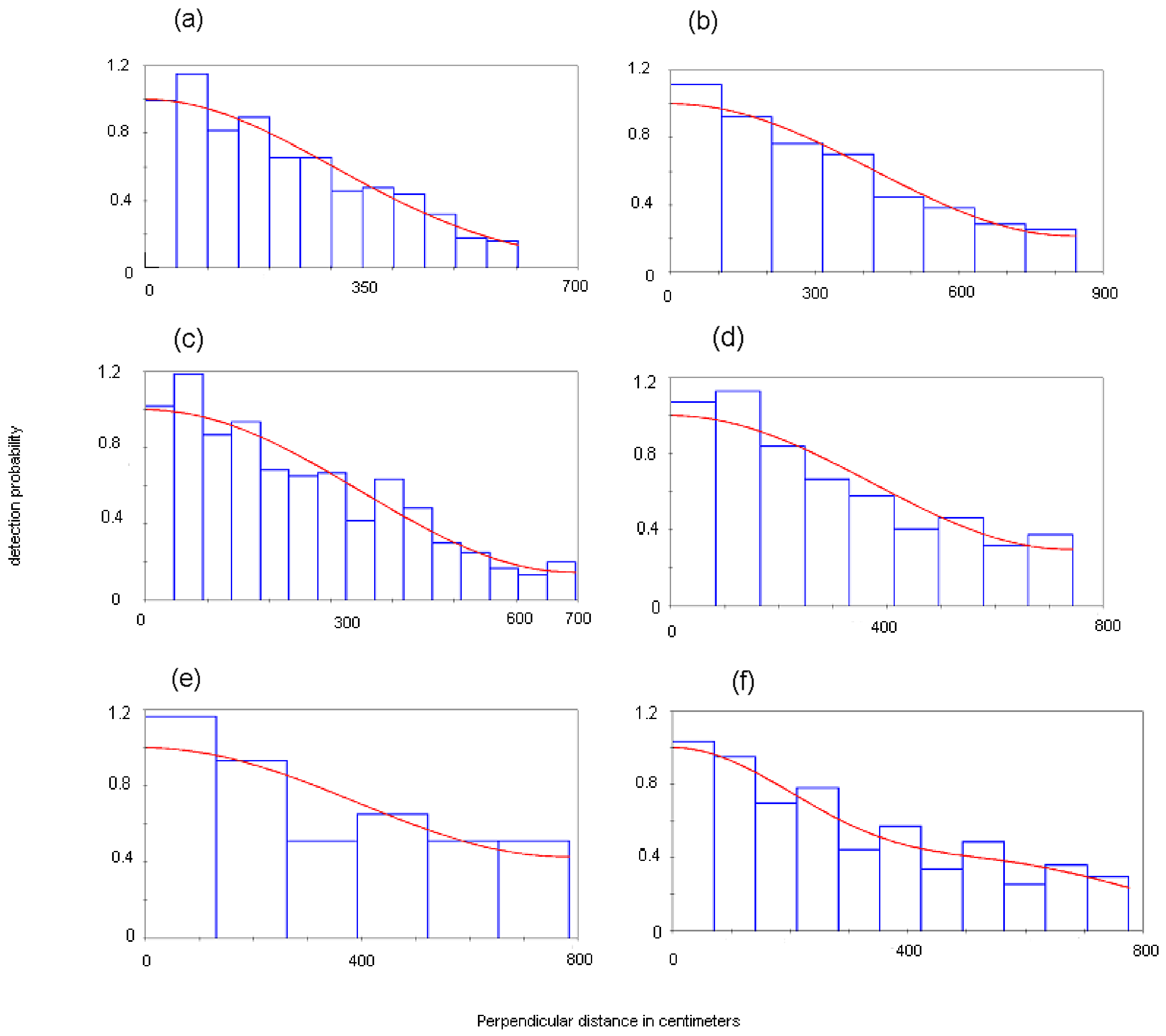

Figure 7 Histograms of perpendicular distances and fitted detection functions for (a) standing crop method in the Annex, (b) clearance method in the Annex, (c) standing crop and clearance method in the Annex, (d) standing crop method in the Reserve, (e) clearance method in the Reserve, (f) standing crop and clearance method in the Reserve.

3.3.2 Helicopter survey

A total of 100 kudu individuals were counted in the Annex. In the Reserve, a total of 77 kudu individuals were counted. This resulted in a kudu density of 0.25 kudus ha^{-1} in the Annex and 0.11 kudus ha^{-1} in the Reserve (Table 4).

Table 4 Results of the kudu counts from the helicopter survey.

	Annex	Reserve
total # kudu	100	77
# male	9	29
size area (ha)	400	700
density (kudu ha^{-1})	0.25	0.11

The total metabolic weight in the Annex was 16.2 kg ha^{-1} compared to 14.7 kg ha^{-1} in the Reserve (Table 5). The browsers in the Annex have a total metabolic weight of 14.27 kg ha^{-1} compared to the total metabolic weight of 11.43 kg ha^{-1} of the browsers in the Reserve (Table 6).

Table 5 Number of all species that were counted during the helicopter survey in the Annex and the Reserve (respectively N An and N Res), the number of animals per hectare in the Annex and the Reserve, the body mass of each species (from Prins & Olff, 1998; Coe *et al*, 1976; Haim *et al*., 1990 and Keymer, 1969), the biomass per species per area and the total biomass per area and the unit metabolic weight (MW) per species and the total MW per area.

Species	N An	N Res	N ha^{-1} An	N ha^{-1} Res	body mass (kg)	biomass (kg ha^{-1})		unit MW ($W_{kg}^{0.75}$)	total MW (kg ha^{-1})	
						Annex	Reserve		Annex	Reserve
black rhinoceros	0	13	0	0.019	816.0	0	15.154	152.7	0	2.84
buffalo	0	1	0	0.001	300.0	0	0.429	72.1	0	0.10
bushbuck	5	5	0.013	0.007	51.3	0.641	0.366	19.2	0.24	0.14
grey duiker	1	0	0.003	0	12.6	0.032	0	6.7	0.02	0
eland	0	16	0	0.023	471.3	0	10.773	101.2	0	2.31
hartebeest	0	43	0	0.061	134.0	0	8.231	39.4	0	2.42
kudu	100	77	0.250	0.110	213.0	53.250	23.430	55.8	13.94	6.13
ostrich	7	3	0.018	0.004	120.0	2.100	0.514	36.3	0.63	0.16
porcupine	1	0	0.003	0	11.4	0.029	0	6.2	0.02	0
steinbuck	5	1	0.013	0.001	11.1	0.139	0.016	6.1	0.08	0.01
warthog	20	17	0.050	0.024	73.5	3.675	1.785	25.1	1.26	0.61
total						59.9	60.7		16.2	14.7

Table 6 Total biomass and total metabolic weight (MW) of browsers, calculated for the Annex and for the Reserve, based on helicopter survey.

Species	biomass (kg ha^{-1})		total MW (kg ha^{-1})	
	Annex	Reserve	Annex	Reserve
black rhinoceros	0.00	15.15	0.00	2.84
bushbuck	0.64	0.37	0.24	0.14
grey duiker	0.03	0.00	0.02	0.00
eland	0.00	10.77	0.00	2.31
kudu	53.25	23.43	13.94	6.13
steinbuck	0.14	0.02	0.08	0.01
total	54.06	49.74	14.27	11.43

3.4 Bite size & feeding height

3.4.1 Bite size

A significant difference in bite size was found between the two areas (ANOVA, $F_{1,9}$= 10.921, P=0.001). Larger bite sizes were taken in the Reserve (mean Annex 1.1688; mean Reserve 1.2027).

3.4.2 Bite height

A significant difference in bite height was found between the two areas (ANOVA, $F_{1,9}$= 95.398, P<0.001). Higher bites were taken in the Annex (mean Annex 151.67; mean Reserve 129.87).

The standard deviation of the bite heights in the Annex (48.816) was smaller than the standard deviation of the bite heights in the Reserve (51.008).

4 Discussion

Potential for competition

For competition between different species to occur, certain conditions have to be met. First, the niches of the different species, such as habitat and diet, must overlap. Second, the resources have to be limited and third, there must be joint exploitation of these resources, and interactions related to the resource must negatively affect the performance of either or both species (Prins *et al.,* 2000; Putman, 1996).

The principal vegetation types in the research area are Medium Portulacaria Thicket and Short Euphorbia Thicket. Both rhinos and kudus are known to use these vegetation types (Brown *et al.*, 2003; personal observations). A large share of the plant species that are present in these vegetation types are included in the diet of kudus as well as in the diet of rhinos, as is shown in Appendix VIII. Species that are abundant in the diet of both animal species are *Grewia robusta, Euclea undulata, Euphorbia bothae* and *Azima tetracantha* (Ganqa *et al*., 2005; data from this study), however the quantity of some of these species in the diets show large differences. For instance, *Grewia robusta* and *Plumbago auriculata* are present in the rhino's diet in large quantities (Ganqa *et al*., 2005; Van Lieverloo & Schuiling, unpublished), whereas far lower quantities were found in the diet of kudus. Explanations for these differences are difficult to find, since this study was primarily focused on the diet of kudus and to a lesser extent on the diet of rhinos. A possible explanation can be found in the quality of these forage species. Unfortunately, the quality of *Grewia robusta* and *Plumbago auriculata* were not analysed in this research. An explanation for the different abundance of *Grewia robusta* in the diets can be that kudus may be more susceptible to the mechanical defences of this forage species than rhinos. In addition, the different research methods to investigate diet composition (backtracking, faeces analysis) can offer an explanation for the large differences in quantity found in some of the forage species.

Coe *et al*. (1976) found a linear relationship between mean annual rainfall and large herbivore biomass (Fig 8). This model provides a useful tool to estimate the maximum biomass density that could be expected for an intact indigenous large herbivore community, from meteorological data (Du Toit, 2002). However, the model is based on African savanna ecosystems, that are primarily occupied by grazing herbivores. This study was conducted in a thicket vegetation with a high amount of browsing herbivores. Therefore, the model might be less accurate in estimating the maximum herbivore biomass in this study area. Another drawback is that the accuracy of the model may be influenced to some extent by interactions between soil type and rainfall (Bell (1982), Bell (1986) in Du Toit, 2002). Biomasses for both the Reserve and the Annex were calculated from data obtained during the helicopter counts.

In table 7 calculations were made to determine the log10 large herbivore biomass and log10 rainfall. The biomass values for Annex and Reserve were almost similar (3.777 and 3.783 kg km^{-2}, respectively) and a mean value of 3.78 for the total study area was plotted in figure 8 (Coe *et al*., 1976). It is shown that the values for both study areas (Annex and Reserve) are situated above the mean prediction (solid lines), indicating that forage resources tend to be limited in both study areas.

Table 7 Calculated biomass in kg ha^{-1} and in kg km^{-2}, mean annual rainfall (Zucchini *et al*., 2003) and log10 of rainfall and biomass (kg km^{-2}).

Area	biomass (kg ha^{-1})	biomass (kg km^{-2})	log10(biomass(kg km^{-2}))	mean rainfall (mm yr^{-1})	log10(rainfall)
Annex	59.88	5988	3.777	556.9	2.746
Reserve	60.70	6070	3.783	556.9	2.746

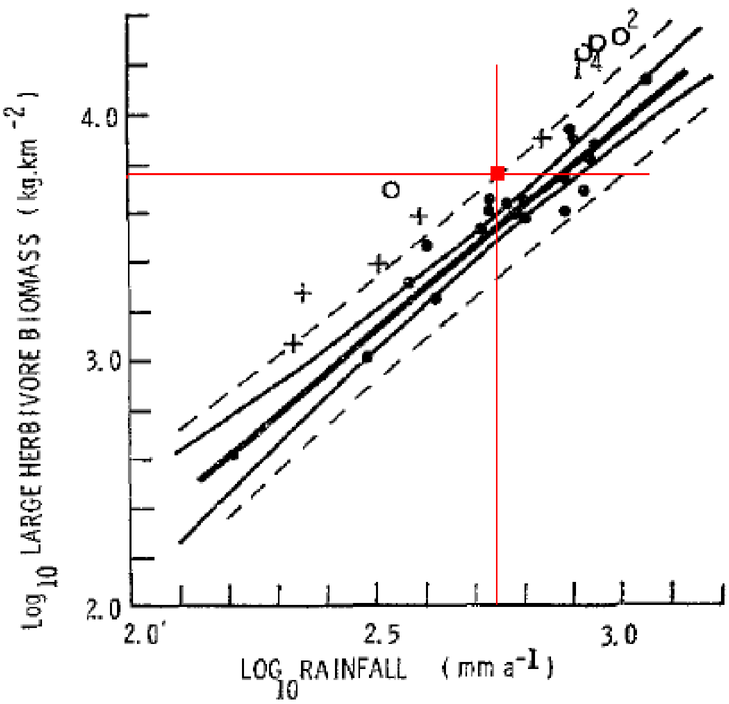

Fig 8 "*Carrying capacity in African wildlife areas in terms of large herbivore standing crop biomass and mean annual precipitation. The mean and individual prediction lines are shown by full and broken lines, respectively.*" (adapted from Coe *et al*., 1976; pg 349, fig 4). The biomass of the study area (log_{10} biomass of 3.78 kg km^{-2}) is represented by the red square.

With the first two prerequisites met, it can be concluded that there is indeed a potential for competition in the GFRR. Since no long-term data are available, it is assumed that the interactions related to the resource negatively affect the performance of one or both species.

Evidence competition

The Principal Components Analysis suggested a difference in diet composition between the Annex and the Reserve. However, this method is mainly descriptive (James & McCulloch, 1990). In this research, it suggested a slight difference in diet composition. SPSS was used to test the significance of these differences. The differences found in diet composition when comparing the three groups Reserve to Annex, Reserve to Reserve and Annex to Annex (Bray-Curtis dissimilarity) were not significant. This suggests that there is no shift in the kudu diet in an area where it has to share its resources with rhinos. The Kulcynzski's Similarity Index- method supports this conclusion since no significant differences were shown in the kudu diet between the two areas. These results suggest that, if there would in fact be competition between the two species, this has no effect on the diet composition of kudus and changing their diet is not a way kudus overcome the effects of competition with rhinos. Several studies showed that animals that are experiencing competition by other species, change their diet to overcome the effects thereof. For example Gordon & Illius (1989) found a difference in resource use of grazing animals (red deer, cattle and ponies) between seasons. During the summer period when resources were abundant, the three species congregated on the vegetation communities with high biomass and high quality of resources. During the scarce winter period however, the separate species had a relatively large exclusive resource use. This suggests that exploitative competition for the high quality food led to resource partitioning in the scarce winter season (Gordon & Illius, 1989). Diet shifts were expected in this study, but a significant diet shift was not found. An explanation for the fact that such a diet shift was not found in this study, could be that kudus first move to another area. If so, there can still be competition, but kudus may deal with the competition issue by spatial avoidance before shifting their diet. Similar results were found in a study performed by Voeten (1999), who found that, when resources became more scarce, the overlap in habitat decreased between zebra-wildebeest and cattle-wildebeest, whereas overlap in diet did not. Hence, the species still select similar diets but avoid each other by foraging in different habitats (Voeten, 1999).

The calculated dung densities show large differences between the two areas. Three different calculation methods yielded dung densities that were almost twice as high in the Annex compared to the Reserve. Although one has to take into account that the 95% confidence intervals are overlapping, suggesting the difference in dung density between the two areas is not significant. Results from the helicopter counts however, also supported the hypothesis that kudu density was higher in the Annex. The stocking rate for kudus in the Great Fish River Reserve has been estimated at 6-9 individuals km^{-2} (Ganqa & Scogings, 2007). In this study, kudu densities were calculated of 11 individuals km^{-2} in the Reserve and 25 individuals km^{-2} in the Annex. High densities of kudus have been recorded in areas where succulent semi-evergreen thicket predominates (Allen-Rowlandson (1980) in Owen-Smith, 2002) and kudu densities in these areas can exceed 10 individuals km^{-2}. Still, compared to these standards, the kudu density in the Annex seems extremely high. An explanation for the higher kudu density observed in the Annex could be that rhinos exert an effect on kudus forcing kudus to move to the Annex where an exclusive area is available without the presence of rhinos. This would suggest that there is indeed competition between rhinos and kudus when these species co-occur and kudus diminish the competition effects by moving to the exclusive area. However, when calculating the metabolic weight of all browsers in both areas, a metabolic weight of 14.27 kg ha^{-1} was found in the Annex and a metabolic weight of 11.43 kg ha^{-1} was found in the Reserve. The biomass is large for both areas (figure 8), indicating that not only the Reserve, but also the Annex might be reaching the maximal capacity of sustaining the amount of herbivores. In fact, the total biomass of the browsers in the Annex is even higher than in the Reserve leading to the assumption that competition pressure would be even higher in the Annex. Kudus make up by far the largest part of the total herbivore biomass in the Annex (86%). If competition occurs in this area, which is likely considering the higher competition pressure, it will be intraspecific (within one species) rather than interspecific. These observations raise the question why kudus prefer to select an area where competition pressure is likely to be higher. A possible explanation could be that kudus suffer from aggressive behaviour by rhinos (interference competition) rather than competition for food, although few studies about this topic area available. When resources become scarce, kudus and rhinos may aggregate near the resources that are still available. The rhinos may benefit from their larger size, since they receive lower costs from interference interactions (Valeix *et al.* 2007) and force kudus to move to their exclusive area (the Annex). Interference competition is not uncommon in herbivore assemblages. Elephants have also been known to cause a temporal shift in visiting time of antelope species at waterholes (Valeix *et al.* 2007). Aggressive behaviour of rhinos towards kudus however was not observed in this study. Very few studies have focused on interference competition and when the black rhinoceros is concerned, no data are available about aggressive behaviour towards other herbivores.

Before we can conclude that the differences in dung (and kudu) density are due to competition with rhinos, we must rule out other possibilities and other factors that may differ between the two areas, such as differences in vegetation composition. The Annex and the Reserve are adjacent areas but the vegetation in these areas is not entirely similar. The Reserve contains mostly the Short Euphorbia Thicket vegetation type but also extensive

areas with Medium Portulacaria Thicket, whereas in the Annex, *Portulacaria afra* is largely missing (Peter Lent pers. comm.). The differences in vegetation type may play a role in making an area more attractive for kudus. First, there is the matter of different forage quality between the areas, that can make one area more attractive than the other. However, no significant differences were found in diet quality (polyphenol content, tannin content, percentages of N and percentage P) of those plant species that were collected in the Annex and in the Reserve. This suggests that the quality of the plant species that are more abundant in the kudu diet in the Annex were not different from the quality of the plant species that were more abundant in the kudu diet in the Reserve. There seems to be no special benefit for animals to forage in either one of the areas as far as forage quality is concerned.
Another reason for kudus to select a particular vegetation type can be because the forage in this vegetation type is more accessible, or because the forage species have a higher cover. A higher cover can be beneficial for food consumption and also offers places to hide. In order to be certain that the differences in kudu densities are due to competition, both study areas should be similar. Therefore, the vegetation composition of both areas has to be studied.

Bite sizes were expected to be larger in a rhino-included area. A significant difference in bite size was indeed found between the two areas with, as expected, larger bite sizes taken in the Reserve. It is likely that, as a result of rhino foraging, fewer high quality small diameter twigs are available for kudu so they are forced to take larger bites, resulting in low quality bites. This can be regarded as a sign of resource partitioning (Wilson & Kerley, 2003) which would indicate that competition does occur and increasing bite size is a way for kudus to compensate for any negative effects. However, no other studies were found that show a direct relation between bite size and competition.

Bite heights measured in the Annex were significantly higher than the bite heights measured in the Reserve. This is in contradiction with the hypothesis that predicted higher bites in the Reserve as a result of competition with rhinos. It is difficult to find an explanation for these results. Maybe too few trees and species were measured and the bite heights that were measured were strongly dependent on the height of the tree or bush measured. Trees were selected randomly in both the Annex and the Reserve. By selecting only two or three trees of a certain species in one area, the sample size may not have been adequate and height of the trees or bush measured may have confounded the results.

The problem in measuring competition among large herbivores lies in the fact that conducting experiments or manipulating populations is logistically difficult (Mishra *et al*., 2004). Furthermore, interactions between species in natural communities are usually extremely complex (Putman, 1996) and results of competition measurements are hard to interpret. Establishing competition is in fact occurring in an area has therefore been difficult (Prins *et al.* 2006; Putman, 1996).

This research gives little incontrovertible evidence that competition between rhinos and kudus does in fact occur in the Great Fish River Reserve, although some of the results do indicate the existence of competition and should not be dismissed.

Kudus were expected to include different plant species in their diet in an area shared with rhinos. Such a diet shift however, could not be proven statistically. This however should not exclude the possibility of competition. A plausible explanation for the lack of diet shift could be that kudus move away from the area that is shared with rhinos, to the area that is not accessible for rhinos, before altering their diet composition. This allows them to keep feeding on their favorable plant species, avoiding interference with rhinos. Spatial avoidance is not uncommon in herbivore assemblages (Voeten, 1999).

This hypothesis also offers an explanation for the differences found in kudu densities between the Annex and the Reserve. The kudu density in the Annex was approximately twice as high as in the Reserve. This could be an indication of competition between rhinos and kudus in the Reserve as a result of which the kudus move to their exclusive niche (the Annex).

This study did found that kudus take larger bite sizes in the Reserve. Enlarging bite size and including less quality forage material in their diet, could be regarded as a reaction of herbivores to escape competition. The findings, in which kudus enlarge their bite size, when co-occurring with rhinos, make room for the possibility that enlarging their bite size in an area accessible to rhinos is a way to compensate for competition. Very little is known about bite size increase as a reaction of competition, since no studies have addressed this subject. Since larger bite sizes were found and no shift in diet, these findings suggest that enlarging bite size is preferred to shifting their diet.

Although a change in bite size to reduce competition is not found in the literature, moving to their exclusive niche to avoid the effects of competition with other species is proven to be common in herbivore interactions. However, the possibility of intra-specific competition in the Annex remains and moving away from the rhino included area can only increase the effects thereof.

Shifting their diet could be used as a last resort when other possibilities to avoid competition (moving to an exclusive area and enlarging their bite sizes) are not sufficient to overcome the effects of competition. Whether shifting their diet is in fact used as such a last resort remains a hypothesis that should be further investigated and more research on this particular topic is needed.

5 Recommendations for future research

To conclude that the difference in kudu density is due to rhino presence only, the vegetation in the Annex must be surveyed and statistically compared and declared similar to the vegetation present in the Reserve.

Since in this study all transects were laid out in SET, a recommendation for future research is to equally divide transects over the different vegetation types. Vegetation types that occur more frequently in the study area should be surveyed more than vegetation types that occur less frequently. Surveys should be designed in such a way that there will be an equal coverage probability throughout the region. Both high- and low-density areas in the study area should be surveyed (Marques *et al*., 2001).

It would be interesting to see in what particular order kudus cope with possible competition. Do they spatially avoid competition by rhinos or change bite size before changing the diet, as this research suggests? Research on this topic would give interesting insights in the overall process of competition.

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Appendix I: Images

Greater Kudu (photo by authors)

Black rhinoceros (photo by authors)

Short Euphorbia Thicket (photo by authors)

Kudu dung pellet group (photo by authors)

Appendix II: Plant species used in the reference collection

Acanthaceae

- *Justitia protractra*

Anacardiaceae

- *Ozoroa mucronata*
- *Rhus longispina*
- *Rhus refractra*

Apocynaceae

- *Carissa haematocarpa*
- *Pachypodium succulentum*

Asteraceae

- *spp*
- *Brachylaena ilicifolia*
- *Verbesina encelioides*

Bignoniaceae

- *Rhigozum obovatum*

Borgaginaceae

- *Ehretia rigida*

Cactaceae

- *Opuntia ficus-indica*

Caesalpinaceae

- *Schotia afra*

Capparidaceae

- *Boscia spp*
- *Cadaba aphylla*
- *Capparis sepiaria*

Celastraceae

- *Maytenus capitata*
- *Maytenus polyacantha*

Combretaceae

- *Combretum spp*

Crassulaceae

- *Kalanchoe rotundifolia*

Ebenaceae

- *Euclea undulata*

Euphorbiaceae

- *Euphorbia bothae*
- *Euphorbia tetragona* or *triangularis*

- *Jatropha capensis*
- *Phyllanthus verrucosus*

Fabaceae

- *Rhynchosia totta*
- *Tephrosia purpurea*

Lamiaceae

- *Leucas capensis*

Liliaceae

- *Aloe tenusit*
- *Asparagus densiflorus*
- *Asparagus spp*
- *Asparagus africanus*
- *Asparagus crassicladus*
- *Asparagus setaceus*
- *Asparagus striatus*
- *Asparagus suaveolens*
- *Asparagus subulatus*

Malvaceae

- *Abutilon sonneratianum*

Meliaceae

- *Ptearoxylon obliquum*

Mesembryanthemaceae

- *Phylobolus spp*
- *Delosperma calycinum*

Mimosaceae

- *Acacia karroo*

Oleaceae

- *Jasminum angulare*
- *Olea europaea spp africana*

Plumbaginaceae

- *Plumbago auriculata*

Portulaceae

- *Portulacaria afra*

Rubiaceae

- *Coddia rudis*

Salvadoraceae

- *Azima tetracantha*

Sapindaceae

- *Pappea capensis*

Solanaceae

- *Lycium ferocissimum*
- *Solanum coccineum*

Sterculiaceaea

- *Hermannia micranthus*

Tiliaceae

- *Grewia occidentalis*
- *Grewia robusta*
- *Grewia spp*

Verbenaceae

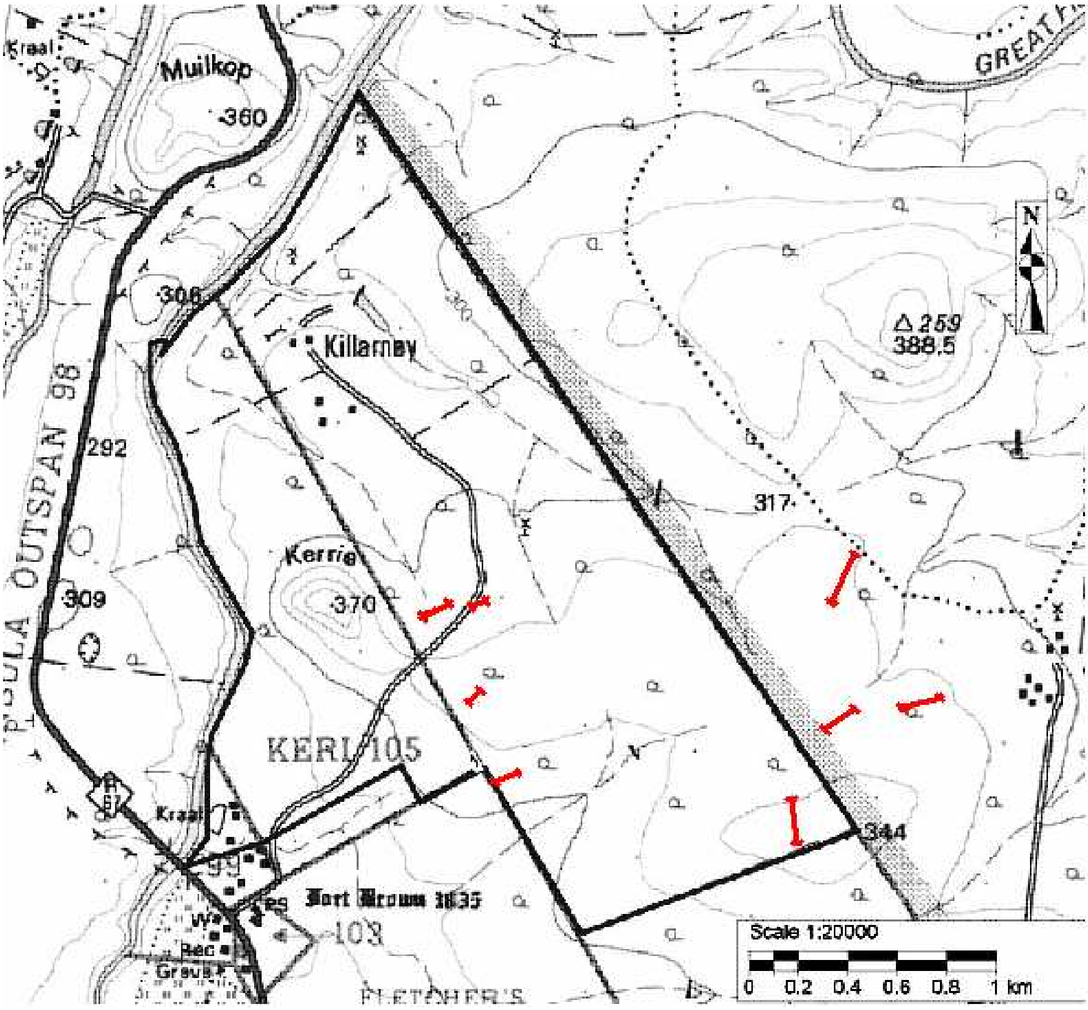
- *Lantana*

Vitaceae

- *Rhoicissus*

Appendix III: Distribution of line transects in study area

Line transects are indicated by red lines. The fence that separates the Annex from the Reserve is indicated with the thick dotted line. Five transects are situated in the Annex. Three line transects are situated in the Reserve.



Appendix IV: Diet Composition

The table shows the abundance of the plant species in the kudu diet over the different periods (1, 2, 3, 4, Average 1-4 and wet season) in the Reserve area (Res.) and the Annex area (An.). The numbers represent the percentages per forage species found in the faecal samples per period.

	Res. 1	An. 1	Res. 2	An. 2	Res. 3	An. 3	Res. 4	An. 4	Res. 1-4	An. 1-4	Res. Wet	An. Wet
Grasses and other graminoids												
grass (undetermined)	5.3	0.8	2.5	1.1	0.0	0.0	0.2	0.6	2.0	0.6	1.4	0.3
Non-graminoid monocots												
Aloe tenusit	2.1	0.0	0.6	1.1	0.9	0.4	0.5	0.0	1.0	0.4	0.0	0.0
Asparagus densiflorus	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.9	0.0
Asparagus spp.	0.0	0.0	0.0	0.0	0.0	0.4	0.0	1.4	0.0	0.5	0.0	1.8
Asparagus striatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.2	0.0	0.0
Asparagus subulatus	0.0	0.0	4.2	0.4	0.0	0.0	0.0	0.0	1.1	0.1	0.0	0.0
dicots												
Acacia karroo	0.0	0.3	0.6	0.4	0.0	3.7	0.0	0.0	0.2	1.1	0.0	0.0
Acanthaceae spp.	4.4	7.8	2.3	2.0	5.8	0.9	10.3	2.0	5.7	3.2	2.4	1.9
Asteraceae spp.	0.9	0.0	0.0	2.0	0.6	0.0	0.0	0.0	0.4	0.5	0.9	0.0
Azima tetracantha	9.3	5.0	0.8	0.0	9.2	1.3	5.5	8.8	6.2	3.8	0.0	1.0
Boscia spp.	2.8	0.0	0.6	0.9	0.0	0.4	1.2	0.6	1.2	0.5	0.5	0.0
Brachylaena ilicifolia	2.8	5.6	2.1	3.3	5.3	3.9	0.7	3.9	2.7	4.2	1.2	3.7
Cadaba aphylla	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Capparis sepiaria	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.4	0.0	0.0
Carissa haematocarpa	1.9	0.6	5.9	0.9	0.9	8.0	1.0	2.7	2.4	3.0	7.1	1.3
Combretum spp.	0.0	1.1	0.0	3.0	3.0	1.1	0.5	0.0	0.9	1.3	1.2	1.9
Delosperma calycinum	0.5	0.0	0.6	0.7	0.0	1.1	0.0	0.6	0.3	0.6	0.0	0.0
Ehretia rigida	0.4	1.7	0.0	0.0	0.0	3.2	0.0	0.0	0.1	1.2	0.7	0.0
Euclea undulata	3.7	2.2	1.3	3.0	5.3	3.2	13.7	7.6	6.0	4.0	10.4	17.4
Euphorbia bothae	1.4	7.0	0.8	1.7	5.3	7.5	20.2	18.6	7.0	8.7	11.3	4.6
Euphorbia triangularis or tetragona	0.4	1.4	1.5	5.9	0.4	0.0	2.2	0.0	1.1	1.8	1.7	0.2
Grewia occidentalis	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.1	0.0	1.9	0.0
Grewia robusta	3.2	1.4	2.8	1.7	3.6	3.9	1.5	2.4	2.8	2.3	3.5	2.6
Jasminum angulare	0.7	2.2	3.0	4.6	1.1	12.1	1.7	0.8	1.6	4.9	0.0	7.0
Jatropha capensis	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.4	0.0	0.0	0.8
Justitia protractra	0.4	1.4	0.6	3.1	5.1	4.1	0.0	0.6	1.5	2.3	3.1	0.3
Kalanchoe rotundifolia	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.3	0.0	0.0	0.0
Leucas capensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Maytenus capitata	7.7	7.8	2.5	8.9	6.2	2.8	0.7	11.6	4.3	7.8	5.2	2.1
Maytenus polycantha	0.0	0.0	0.4	0.7	1.1	0.0	0.0	0.0	0.4	0.2	0.0	0.0
Olea europeana spp africana	0.0	5.3	0.0	0.0	0.0	6.9	0.3	0.0	0.1	3.1	0.0	0.0
Ozoroa mucronata	1.4	0.8	2.5	0.0	2.6	2.6	3.1	0.6	2.4	1.0	1.7	0.0
Pachypodium succulentum	0.5	2.5	0.6	0.7	5.8	0.0	1.0	1.2	2.0	1.1	3.5	0.0
Pappea capensis	23.9	1.4	18.6	3.3	5.1	0.0	0.5	3.9	12.1	2.2	5.4	21.6
Phyllanthus verrucosus	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Phylobolus spp.	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Plumbago auriculata	0.0	0.3	0.4	0.6	0.0	0.4	0.5	1.2	0.2	0.6	1.2	0.0
Portulacaria afra	8.6	9.5	5.1	0.0	6.0	0.0	9.6	4.5	7.3	3.5	8.0	0.0
Ptearoxylon obliquum	0.0	1.1	1.7	2.2	0.0	8.4	1.5	2.0	0.8	3.4	0.7	0.8
Rhoicissus spp	1.4	3.6	1.5	1.7	0.9	0.0	0.0	0.0	0.9	1.3	0.0	1.3
Rhus refractra	0.0	0.0	0.8	0.4	1.1	0.0	3.6	3.9	1.4	1.1	0.9	0.0
Schotia afra	5.5	5.6	9.7	13.1	3.2	1.9	0.3	3.3	4.7	6.0	6.6	6.9
Verbesina encelioides	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
dicot. epidermis	7.4	14.2	22.0	30.4	13.9	16.4	12.3	12.9	13.9	18.5	14.9	16.1
uncertain epidermis	2.6	8.9	1.9	1.5	5.8	3.9	5.7	3.7	4.0	4.5	3.5	5.3
Categories eg.												
Grasses and other graminoids	5.3	0.8	2.5	1.1	0.0	0.0	0.2	0.6	2.0	0.6	1.4	0.3
Non-graminoid monocots	2.8	0.3	4.9	1.5	0.9	0.9	0.5	2.0	2.3	1.2	0.9	1.8
dicots	81.9	75.7	68.6	65.6	79.5	78.9	81.3	80.8	77.8	75.2	79.2	76.5
Rest	10.0	23.2	23.9	31.9	19.7	20.3	18.0	16.5	17.9	23.0	18.4	21.4
number grasses and other graminoids	1	1	1	1	0	0	1	1	1	1	1	1
number non-graminoid monocots	2	2	2	2	1	2	1	2	3	5	1	1
number dicots	21	22	26	24	23	21	22	20	33	30	22	19
total number of species	24	25	29	27	24	23	24	23	37	36	24	21

Appendix V: Kulcynzski's Similarity Index

Differences in diet composition calculated with Kulcynzski's Similarity Index (p.53). The percentages of each plant species found in the kudu diet are given for each period (1, 2, 3 and 4 and the average over these four periods, Reserve indicated by R and Annex indicated by A). The KSI (Kulcynzski's Similarity Index) values were calculated between the areas for every plant species and period. The critical values are given per period. All species with a KSI value higher than the critical value for 'diets similar', show significantly no difference in abundance between the Annex and Reserve and are indicated in bold. Species with a KSI value lower than the critical value for 'diets different', are significantly different between the areas. Such species however were not found.

	R1	A1	KSI 1	R2	A2	KSI 2	R3	A3	KSI 3	R4	A4	KSI 4	R1-4	A1-4	KSI1-4
grass (undetermined)	5.3	0.8	**27.4**	2.5	1.1	**60.8**	0.0	0.0		0.2	0.6	**43.8**	2.0	0.6	**48.5**
Aloe tenusit	2.1	0.0	0.0	0.6	1.1	**72.8**	0.9	0.4	**67.0**	0.5	0.0	0.0	1.0	0.4	**54.5**
Asparagus africanus	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Asparagus crassicladus	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Asparagus densiflorus	0.7	0.3	**56.8**	0.0	0.0		0.0	0.0		0.0	0.0		0.2	0.1	**56.8**
Asparagus setaceus	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Asparagus spp.	0.0	0.0		0.0	0.0		0.0	0.4	**0.0**	0.0	1.4	0.0	0.0	0.5	0.0
Asparagus striatus	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.6	0.0	0.0	0.2	0.0
Asparagus suaveolens	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Asparagus subulatus	0.0	0.0		4.2	0.4	**16.1**	0.0	0.0		0.0	0.0		1.1	0.1	**16.1**
Acacia karroo	0.0	0.3	0.0	0.6	0.4	**73.6**	0.0	3.7	**0.0**	0.0	0.0		0.2	1.1	**25.7**
Acanthaceae spp.	4.4	7.8	**72.0**	2.3	2.0	**93.3**	5.8	0.9	**26.0**	10.3	2.0	**33.1**	5.7	3.2	**71.8**
Abutilon sonneratianum	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Asteraceae spp.	0.9	0.0	0.0	0.0	2.0	0.0	0.6	0.0	**0.0**	0.0	0.0		0.4	0.5	**85.5**
Azima tetracantha	9.3	5.0	**70.0**	0.8	0.0	0.0	9.2	1.3	**24.7**	5.5	8.8	**77.0**	6.2	3.8	**75.6**
Boscia spp.	2.8	0.0	0.0	0.6	0.9	**81.4**	0.0	0.4	**0.0**	1.2	0.6	**67.5**	1.2	0.5	**59.5**
Brachylaena ilicifolia	2.8	5.6	**67.0**	2.1	3.3	**77.7**	5.3	3.9	**84.1**	0.7	3.9	**30.1**	2.7	4.2	**79.3**
Cadaba aphylla	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Capparis sepiaria	0.0	0.0		0.0	0.0		0.0	1.5	**0.0**	0.0	0.0		0.0	0.4	0.0
Carissa haematocarpa	1.9	0.6	**44.8**	5.9	0.9	**27.0**	0.9	8.0	**19.4**	1.0	2.7	**55.9**	2.4	3.0	**89.2**
Coddia rubis	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Combretum spp.	0.0	1.1	0.0	0.0	3.0	0.0	3.0	1.1	**53.0**	0.5	0.0	0.0	0.9	1.3	**80.9**
Delosperma calycinum	0.5	0.0	0.0	0.6	0.7	**92.4**	0.0	1.1	**0.0**	0.0	0.6	0.0	0.3	0.6	**64.8**
Ehretia rigida	0.4	1.7	**34.7**	0.0	0.0		0.0	3.2	**0.0**	0.0	0.0		0.1	1.2	13.4
Euclea undulata	3.7	2.2	**75.3**	1.3	3.0	**60.0**	5.3	3.2	**75.4**	13.7	7.6	**71.0**	6.0	4.0	**79.9**
Euphorbia bothae	1.4	7.0	**33.6**	0.8	1.7	**67.4**	5.3	7.5	**82.9**	20.2	18.6	**95.7**	7.0	8.7	**88.9**
Euphorbia triangularis or tetragona	0.4	1.4	**40.3**	1.5	5.9	**40.0**	0.4	0.0	**0.0**	2.2	0.0	0.0	1.1	1.8	**76.0**
Grewia spp.	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Grewia occidentalis	0.0	0.0		0.0	0.0		0.4	0.0	**0.0**	0.0	0.0		0.1	0.0	0.0
Grewia robusta	3.2	1.4	**61.2**	2.8	1.7	**75.4**	3.6	3.9	**96.7**	1.5	2.4	**77.3**	2.8	2.3	**91.7**
Hermannia micranthus	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Jasminum angulare	0.7	2.2	**47.9**	3.0	4.6	**78.1**	1.1	12.1	**16.3**	1.7	0.8	**64.5**	1.6	4.9	**49.3**
Jatropha capensis	0.0	0.0		0.0	0.0		1.5	0.0	**0.0**	0.0	0.0		0.4	0.0	0.0
Justitia protractra	0.4	1.4	**40.3**	0.6	3.1	**33.6**	5.1	4.1	**88.8**	0.0	0.6	0.0	1.5	2.3	**79.6**
Kalanchoe rotundifolia	0.0	0.0		0.0	0.0		0.0	0.0		1.4	0.0	0.0	0.3	0.0	0.0
Lantana	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Leucas capensis	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Lycium ferocissimum	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Maytenus capitata	7.7	7.8	**99.5**	2.5	8.9	**44.5**	6.2	2.8	**62.3**	0.7	11.6	**11.1**	4.3	7.8	**71.1**
Maytenus polycantha	0.0	0.0		0.4	0.7	**72.8**	1.1	0.0	**0.0**	0.0	0.0		0.4	0.2	**66.3**
Olea europeana spp africana	0.0	5.3	0.0	0.0	0.0		0.0	6.9	**0.0**	0.3	0.0	0.0	0.1	3.1	5.5
Opuntia ficus-indica	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Ozoroa mucronata	1.4	0.8	**74.6**	2.5	0.0	0.0	2.6	2.6	**99.6**	3.1	0.6	**33.1**	2.4	1.0	**59.2**
Pachypodium succulentum	0.5	2.5	**34.7**	0.6	0.7	**92.4**	5.8	0.0	**0.0**	1.0	1.2	**91.3**	2.0	1.1	**72.0**
Pappea capensis	23.9	1.4	**11.0**	18.6	3.3	**30.3**	5.1	0.0	**0.0**	0.5	3.9	**23.4**	12.1	2.2	**30.3**
Phyllanthus verrucosus	0.0	0.0		0.2	0.0	0.0	0.0	0.0		0.0	0.0		0.1	0.0	0.0
Phylobolus spp.	0.0	0.0		1.3	0.0	0.0	0.0	0.0		0.0	0.0		0.3	0.0	0.0
Plumbago auriculata	0.0	0.3	0.0	0.4	0.6	**86.5**	0.0	0.4	**0.0**	0.5	1.2	**59.2**	0.2	0.6	**54.7**
Portulacaria afra	8.6	9.5	**95.2**	5.1	0.0	0.0	6.0	0.0	**0.0**	9.6	4.5	**63.7**	7.3	3.5	**64.6**
Ptearoxylon obliquum	0.0	1.1	0.0	1.7	2.2	**86.5**	0.0	8.4	**0.0**	1.5	2.0	**86.1**	0.8	3.4	**38.0**
Rhigozum obovatum	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Rhoicissus spp	1.4	3.6	**55.9**	1.5	1.7	**94.2**	0.9	0.0	**0.0**	0.0	0.0		0.9	1.3	**82.8**
Rhus longispina	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Rhus refractra	0.0	0.0		0.8	0.4	**60.8**	1.1	0.0	**0.0**	3.6	3.9	**96.3**	1.4	1.1	**87.0**
Rhynchosia totta	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Schotia afra	5.5	5.6	**98.8**	9.7	13.1	**85.1**	3.2	1.9	**75.4**	0.3	3.3	**19.0**	4.7	6.0	**87.8**
Solanum coccineum	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Tephrosia purpurea	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Verbesina encelioides	0.0	0.0		0.0	0.6	0.0	0.0	0.0		0.0	0.0		0.0	0.1	0.0
KSI average			39.3			50.1			26.4			39.3			48.9
Stdev			33.7			35.6			36.5			35.2			33.6
1.73 x std			58.2			61.5			63.1			60.9			58.2
critical value diets similar			5.7			14.5			-10.1			4.1			15.3
critical value diets different			-18.9			-11.4			-36.7			-21.6			-9.3

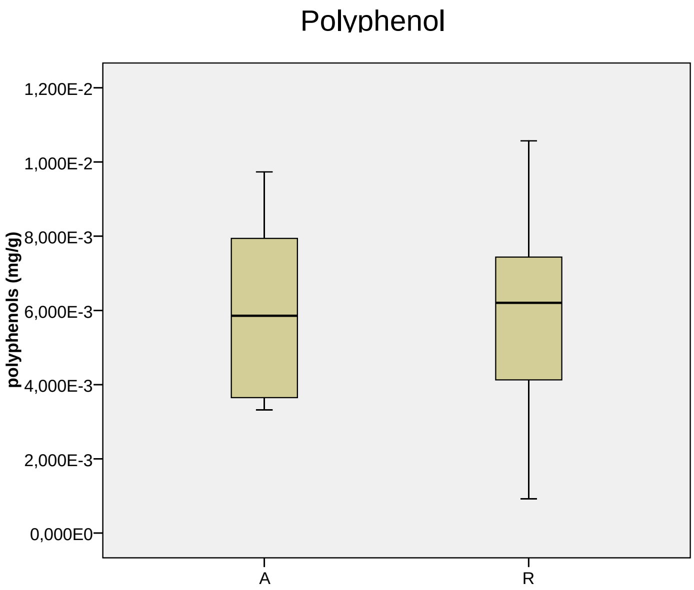
Appendix VI: Diet Dissimilarity

The cross table shows the Bray-Curtis coefficients of dissimilarity calculated between all samples collected in the dry season (1,2,3,4) and the wet season (wet) in the Annex (ANN) and the Reserve (RES).

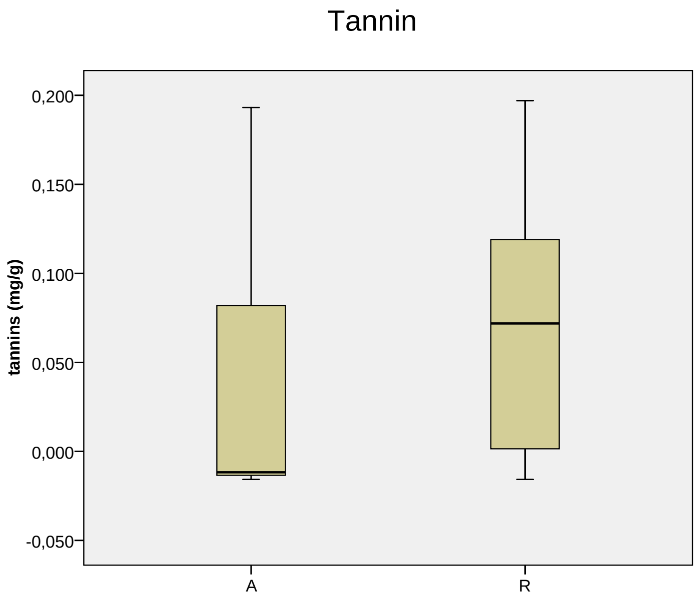
		ANN					RES				
		1	2	3	4	wet	1	2	3	4	wet
	1	x	0.49	0.54	0.45	0.61	0.44	0.56	0.36	0.46	0.43
	2	x	x	0.60	0.54	0.53	0.54	0.47	0.50	0.73	0.51
ANN	3	x	x	x	0.60	0.61	0.72	0.62	0.59	0.69	0.55
	4	x	x	x	x	0.56	0.46	0.58	0.38	0.37	0.39
	wet	x	x	x	x	x	0.45	0.43	0.55	0.63	0.52
	1						x	0.36	0.39	0.61	0.48
	2						x	x	0.55	0.67	0.47
RES	3						x	x	x	0.51	0.38
	4						x	x	x	x	0.45
	wet						x	x	x	x	x

Appendix VII: Diet Quality

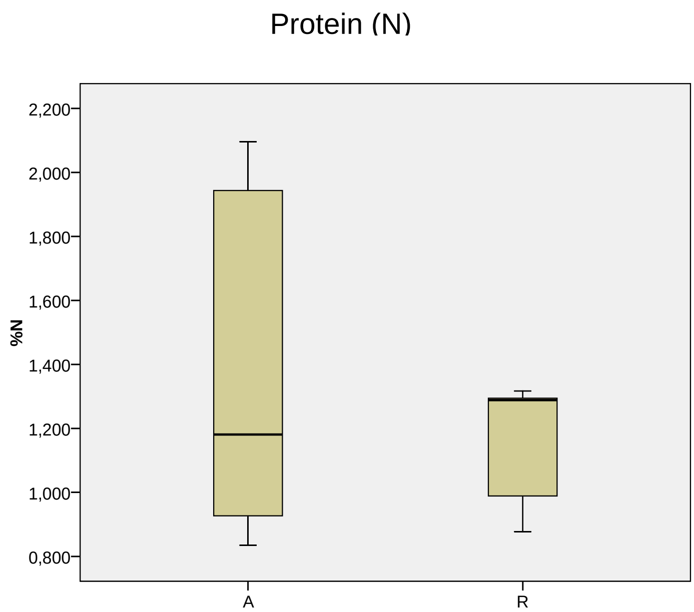
The boxes represent the interquartile range from first to third quartile and the smallest and largest non-outlier observations; the horizontal line in the boxes represents the median.



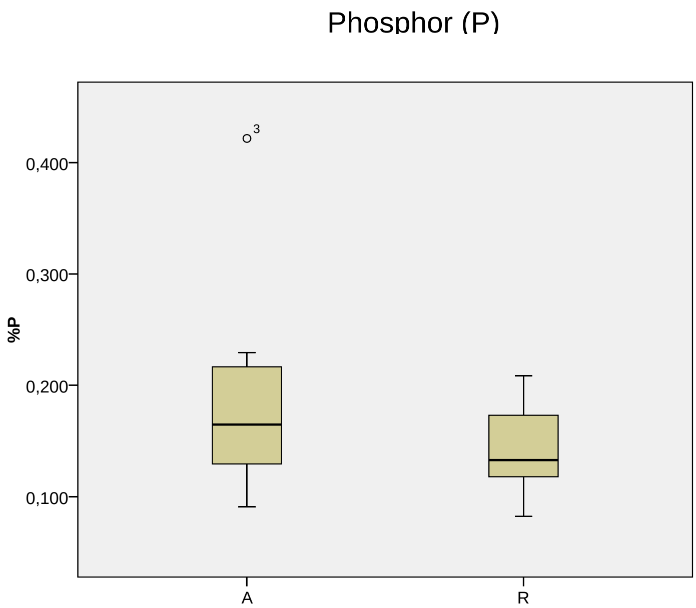
The left box represents the polyphenol content in mg/g in the Annex. The right box represents the polyphenol content in mg/g in the Reserve.



The left box represents the tannin content in mg/g in the Annex. The right box represents the tannin content in mg/g in the Reserve.



The left box represents the protein content (%N) in the Annex. The right box represents the protein content in the Reserve.



The left box represents the phosphor content (%P) in the Annex. The right box represents the phosphor content in the Reserve.

Appendix VIII: Diet comparison of kudus and rhinos

The table shows the abundance of plant species in the diet of kudus and rhinos. The numbers in the table represent the percentages of the dicotyledonous plant species that were found in the faecal analysis of kudus and backtrack analysis of rhinos. These analyses were performed in the winter season in SET (in the GFRR). The kudu results are adapted from this study, the black rhino results are adapted from Ganqa *et al*. (2005).

plant species (dicots)	kudus		rhinos
	Annex	Reserve	
Acacia karroo	1.1	0.2	1.1
Acanthaceae spp.	3.2	5.7	
Asteraceae spp.	0.5	0.4	
Azima tetracantha	3.8	6.2	8.5
Boscia spp.	0.5	1.2	
Brachylaena ilicifolia	4.2	2.7	
Carissa haematocarpa	3.0	2.4	1.1
Cassine crocea			0.3
Combretum spp.	1.3	0.9	
Delosperma calycinum	0.6	0.3	
Ehretia rigida	1.2	0.1	4.3
Euclea undulata	4.0	6.0	1.1
Euphorbia bothae	8.7	7.0	4.0
Euphorbia triangularis or tetragona	1.8	1.1	
Grewia occidentalis		0.1	1.1
Grewia robusta	2.3	2.8	16.2
Jasminum angulare	4.9	1.6	
Jatropha capensis		0.4	5.9
Justitia protractra	2.3	1.5	
Kalanchoe rotundifolia		0.3	
Maytenus capitata	7.8	4.3	
Maytenus heterophylla			3.7
Maytenus polycantha	0.2	0.4	1.6
Olea europeana spp africana	3.1	0.1	0.3
Opuntia ficus-indica			0.3
Ozoroa mucronata	1.0	2.4	0.3
Pachypodium succulentum	1.1	2.0	
Pappea capensis	2.2	12.1	0.3
Phyllanthus verrucosus		0.1	0.3
Phylobolus spp.		0.3	
Plumbago auriculata	0.6	0.2	25.5
Portulacaria afra	3.5	7.3	
Ptearoxylon obliquum	3.4	0.8	
Rhoicissus spp	1.3	0.9	
Rhus longispina			1.1
Rhus refractra	1.1	1.4	0.3
Schotia afra	6.0	4.7	0.5
Verbesina encelioides	0.1		

A Bray-Curtis dissimilarity of 0.77 was calculated between the diets of kudus and rhinos in the Reserve. A Bray-Curtis dissimilarity of 0.78 was calculated between the diets of kudus in the Annex and that of rhinos in the Reserve.