Sexual segregation in foraging of greater kudu (*Tragelaphus strepsiceros*) in a heterogeneous savanna, in Chobe National Park, Botswana

Jason N. Kandume

Høgskolen i **Hedmark**

Master Thesis
at Faculty of Applied Ecology and Agricultural Sciences

HEDMARK UNIVERSITY COLLEGE

11 May 2012

ABSTRACT

Sexual segregation is common in ungulates and is generally related to differences in body size. Often males are larger than females, and the sexes live in separate groups outside the breeding season. I tested the season of sexual segregation in foraging of greater kudu (*Tragelaphus strepsiceros*) along the Chobe riverfront in relation to environmental heterogeneity on different scales. The study was conducted during the wet season from January to April 2010. The data were analyzed using Detrended Correspondence Analysis (DCA) in CANOCO for ordination and Analysis of variance (ANOVA in R program). Correspondence analyses results revealed that there was a clear separation of kudu females and males in nutrient rich habitats on alluvial and mixed soil while there was no clear pattern of segregation in the poor habitats on sandy soil.

Statistical analyses results revealed that feeding patches for both females and males differed from control plots in food quality. For females there were significant differences in preference index between trees available and trees browsed. In males there was no significant difference between trees available and trees browsed. In females habitat use seemed to be influenced by predation risk.

……………………   ……………………   ………….

Jason N. Kandume   Place   Date

TABLE OF CONTENTS

1. INTRODUCTION

Sexual segregation is an animal behavior where the sexes live separate and use different habitats and/or resources outside the breeding season (Stokke & du Toit 2000). This phenomenon has been widely observed among many ungulates (Miquelle et al. 1992; Ruckstuhl & Neuhaus 2000; Mysterud 2000; Stokke & du Toit 2000; Barboza & Bowyer 2000; Loe et al. 2006).

Sexual segregation appears to be positively related to sexual size dimorphism in ungulates, where sexes have considerably different body size in that males are usually larger than females (Stokke & du Toit 2002; Ginnett & Demment 1997; Jarman 1974; Mysterud 2000). These differences could result in differences in the type of diet selected, feeding behavior and habitat use that in turn, could have implications for the animals' interactions with other species and responses to habitat heterogeneity. A first hypothesis and the most quoted hypothesis that may explain sexual segregation is based on the Jarman-Bell principle states that there is a relationship between body size and choice of food in herbivores (Bell 1971; Demment & van Soest 1985; Jarman 1974). The metabolic requirement in herbivore scales with metabolic body mass (i.e. the body weight of the animal raised to the power of 0.75) (Demment & van Soest 1985). Large animals depend more on quantity while small animals depend more on quality (Jarman-Bell principle). This also applies to different sexes in species with sexual dimorphism, where males and females may be expected to differ in decision making at some scale (Jarman 1974; Senft et al. 1987).

However, the food intake capacity depends on the volume of the digestive tract which is related to the weight of the animal. There is a relationship between the weight and size of an animal and the food quality it can subsist on. Larger animals need to eat more but they don't need to extract as much nutrients from food they had eaten, the small animal can eat very little because it need extract more nutrients and energy from food they had eaten. Therefore, large animals can subsist on lower quality food than small animals because small animals have a higher metabolism rate.

A second hypothesis that has been proposed for explaining sexual segregation in herbivores is through scramble-competition (Clutton-Brock et al. 1987). Here females and males share the same resources. This type of competition could lead to segregation. Although females can sustain themselves on little high quality food, the food left might be too little or too poor for males. Therefore the males may be forced to move to other habitat in order to

find more resources. In addition, males may be forced to browse largely above the reach of females if the females have consumed the best food at a lower level.

A third hypothesis of sexual segregation in herbivores is based on differences in predation sensitivity (Stokke & du Toit 2000). Males are less prone to predation, so the male strategy is to select habitats with high food availability in order to maximize food intake and improve body condition and growth. Females, on the other hand, choose habitats that are predator free, because they are more at risk for predation especially if they have offspring.

A fourth hypothesis proposed to explain segregation in herbivores is by social segregation (Stokke & du Toit 2000). The males avoid the females in order to reduce energy costs of competition for females. The females avoid the company of males to avoid harassment from males.

Foraging in large herbivores involves decisions of where to find food and what to eat. According to Senft et al. (1987), such decisions are made in a hierarchy of scales including selection on landscape, plant community, patch, feeding station, plant species, and plant scale down to the single bite. A decision on one scale could restrict the options on the next scale. The decision on a large scale restricts what choices remain on a fine scale. Animals are often driven by abiotic factors on large scale (Senft et al. 1987). On an intermediate scale the animal's decisions are driven by quantity of food while on a finer scale it is driven by quality of food.

I studied the sexual segregation of greater kudu (*Tragelaphus strepsiceros*) in a heterogeneous savanna in the Chobe National Park, Botswana, relating it to habitat types and food quality and quantity.

Objective:

To find a reason for sexual segregation in foraging of greater kudu and assess the differences in food and habitat use between male and female kudu along the Chobe riverfront in relation to environmental heterogeneity at different scales.

Hypotheses:

1) On landscape scale, female kudu will forage mainly in the nutrient rich shrublands on alluvial or mixed soils, whereas males in addition will use the nutrient poor woodlands on sandy soils.

2) On a feeding patch scale, the difference in food quality between feeding patches and the matrix vegetation will be larger in females than in males.

3) On a feeding patch scale, the difference in food quantity between feeding patches and control plots will be larger in males than in females

4) Within a feeding patch, females will browse more selectively among trees than males.

2. STUDY AREA

The study was conducted in Chobe National Park in north-eastern Botswana, (approximately 17º50'S, 24º43'E), with an area of ca. 11 000 km². It is bordered by Zimbabwe to the east and the Chobe River and the Caprivi Strip of Namibia to the north. The present study focused on the area between the Chobe River and the tarmac road between Kasane and Ngoma Bridge, ca 350 km^2 (Figure 1). The region is relatively flat and the soil type in this area is nutrient poor with Kalahari sandy soil and nutrient rich alluvial soil in the floodplains and in the adjacent shrublands (Aarrestad et al. 2010; Rutina et al. 2005). The area has three main habitat types consisting of shrublands on alluvial soil, woodland on sandy soil and flood plains on alluvial soil. The habitat with alluvial soil has low plant biomass of relatively high nutritive quality while habitats with sandy soil are dominated by plants offering larger biomass of lower nutritive quality. More details about habitat types are shown below in the map of the study area (Figure 1).

The elevation is about 1000 meters above sea level (Uyapo & Jeff 2001). The climate is characterized as semi-arid with short, dry winters and moist, hot summers and with high levels of solar radiation. Rain falls mainly in the summer between October and May with mean annual precipitation of 685 mm (Stokke 1999). There is a mean daily maximum temperature of 39ºC and mean daily minimum temperature of 14ºC in October, the hottest month. July is the coldest month with a mean maximum temperature of 30ºC and a mean minimum temperature 4ºC (Aarrestad et al. 2010).

I chose this area because it is a heterogeneous environment and contains a large free roaming population of greater kudu. Moreover, the absence of fences in the park and the kudus' tolerance to human presence allow for good observations without greatly disturbing the animals` daily life. Kudu males weigh about 250 kg, females about 150 kg. Females and juveniles form small herds of six to fourteen individuals while males may be solitary or form small bachelor groups (Skinner & Chimimba 2005).

Chobe National Park has a rich suite of mammal species. The park is well-known for its spectacular number of elephants (*Loxodonta africana*). There are also other animals such as of lions (*Panthera leo*), leopard (*Panthera pardus*), giraffe (*Giraffa camelopardalis)* etc in the park (Table 1).

Table 1; Some other mammal species that are found in Chobe National Park (Skinner & Chimimba 2005 and Estes 1991).

Family	Scientific name	English name	Male (kg)	Females (kg)	Feeding type	Feeding strategy
Bovidae	*Aepyceros melampus*	Impala	55	41	Herbivore	Mix
Bovidae	*Syncerus caffer*	Buffalo	750-820	680-750	Herbivore	Grazer
Canidae	*Lycaon pictus*	African wild dog	25.5-34.5	19-26.5	Carnivore	
Elephantidae	*Loxodonta africana*	Elephant	4.700-6.048	2.160–3.232	Herbivore	Mix
Equidae	*Equus quagga*	Zebra	290-340	290-325	Herbivore	Grazer
Felidae	*Acinonyx jubatus*	Cheetah	43-54	35-37	Carnivore	
Felidae	*Panthera pardus*	Leopard	44.6	25	Carnivore	
Felidae	*Panthera leo*	Lion	225	152	Carnivore	
Giraffidae	*Giraffa camelopardalis*	Giraffe	1100	700	Herbivore	Browser
Hippopotamidae	*Hippopotamus amphibius*	Hippopotamus	1546	1385	Herbivore	Grazer
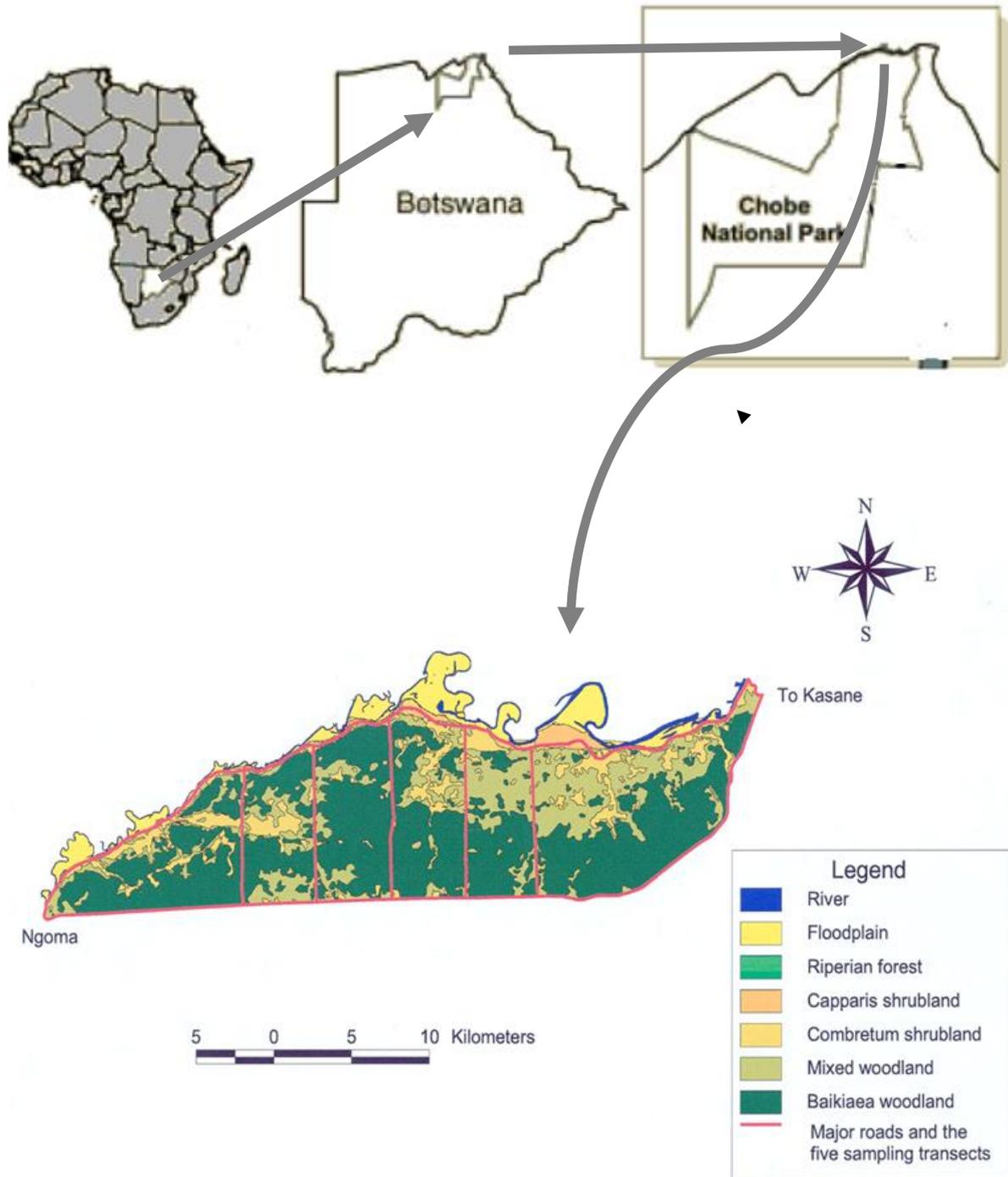
Figure 1: Map showing study area at a continental, regional and local scale respectively (in Africa Botswana, Chobe National Park. The upper two Maps in gray color are modified from Kalwij, et al. 2009 while the lower map is taken from Skarpe et al. 2004 (both with permission).

2.1.   Soil types

I worked with habitats on two distinct soil types, alluvial and sandy soil, within the study area. The types varied with distance from the river. The alluvial soil is typically found on the floodplains and on raised plains above the riverbank (Aarrestad et al. 2010). Alluvial soil is fine textured with lack of free drainage, and a good moisture condition. Alluvial deposits comprise of calcic gleysol, fluvisol and calcic luvisol (Aarrestad et al. 2010). Habitat types, such as floodplains and shrublands, are most common with alluvial soil (Table 2).

The sandy soil found here falls under the classification of aeolian Kalahari sand. The soil is white, pink, and red in color. It is dominated by different tree species and deep rooted perennial forbs. Sand soil is nutrient poor, porous; *ferralic* arenosol comprised of sand and silt particles from a sand bed (Aarrestad et al. 2010; Dougill & Thomas, 2004; Wang et al. 2007). The surface layers of sandy soils have poor capacity to hold water because it drains away. The sandy soil structure is loose, deep and structure-less. The nutrient content in sandy soils is very low due to coarse particles and has a very slow decomposition of organic materials (Aarrestad et al. 2010; Mendelsohn & Obeid 2005 Table 2). Habitat types found in sand soil are mixed woodland and *Baikiaea* woodland (Aarrestad et al. 2010; Table 2).

Table 2: Content of calcium, phosphorus and organic matter and pH in four different habitats of alluvial and sandy soil in Chobe National Park (from Skarpe et al. 2004).

Soil type	Habitat	Calcium (cmol kg^{-1})	Phosphorus (ppm)	Organic matter (%)	pH
Alluvial	Floodplain	14,2	9,1	2,4	4,7
	Shrubland	3,8	13,1	0,7	6
Sandy	Mixed woodland	1,1	4,4	0,4	5,1
	Baikiaea woodland	1,1	2,2	0,4	5

2.2. Vegetation

This study area is part of Sudano-Zambezian bio-geographical region that belongs to the high plateau of southern Africa (Aarrestad et al. 2010). The vegetation in the area is characterized by savannas on Kalahari well-drained sand and alluvial soil. It forms a transition zone between the northern miombo woodland, the typical vegetation of Zimbabwe and Zambia, and the southern Kalahari savannas. The seasonally flooded floodplains are dominated by a strongly rhizomatous grazing tolerant perennial grass *Cynodon dactylon* and a grazing-resistant, sharp stiff grass *Vetiveria nigritana* (Skarpe et al. 2004). Shrublands are found on alluvial soils close to the river. *Capparis tomentosa* and *Combretum mossambicense* are dominant species in this habitat. The composition of species in the shrubland farther from the river becomes mixed with small and medium sized tree species e.g. *Canthium huillense, Canthium glaucum, Markhamia zanzibarica, Croton megalobotrys, Croton gratissimus, Strychnos potatorum* and *Combretum species*.

The woodlands on sandy soil are dominated by trees such as *Baikiaea plurijuga, Pterocarpus angolensis Croton megalobotrys, Croton gratissimus* and shrubs such as *Combretum* species. *Baphia massaiensis* and *Bauhinia petersiana* (Skarpe et al. 2004).

3. METHODS

Data on kudu foraging were collected from early January 2010 to late April 2010 during the rainy season. Kudu were located and observed from a 4x4 vehicle along roads and tracks. Observations were done during the day between 06h00 and 18h00 when animals were visible. Binoculars were used to observe browsing animals in the distance. Data were collected on habitat type used by feeding kudu, kudu social grouping (males or breeding groups) and kudu foraging. A driving schedule was followed to distribute data collection evenly across habitats (alluvial or sandy soil). Fire breaks and tourist roads were used as daily fixed driving routes. Care was taken to include a balanced number of observations of males and females on both habitat types. Equipment such as stop watch, measuring tape, measuring rod and Vernier caliper were used in the field during the study.

3.1. Kudu observation

When a kudu or kudu group were spotted, the vehicle was stopped and the browsing animals were observed and records were taken. Habitat type was visually classified as either shrubland on alluvial soil or woodland on Kalahari sand. In all kudu observations, I selected one mature animal, male or female, and observed its foraging. If the animal was far, binoculars were used. Males were observed only as single males or in pure male associations and females alone or in family groups with or without attending males. Time of browsing was recorded and the stop watch was started as soon as the kudu had its nose within ten cm from leaves biting, picking leaves, stripping branches and chewing. Time recording continued until the kudu stopped feeding, looked around, or walked away. The first tree that was observed as being browsed by the first targeted kudu within a plot was recorded as number one and the first kudu observed also as number one. If a kudu started browsing on another tree, it was recorded as a new observation (time reset) on a new line on the form. When the kudu moved out of sight but another individual was visible, it was selected for a new observation on the same site. During the observation I counted and recorded duration of the foraging, the number of twig bites, leaf picking and number of stripping actions on branches. Twig biting was defined as when a kudu was biting off the tip of a shoot, and stripping as when a kudu was stripping off leaves from the shoot, and leaf picking when a kudu use front of their mouth to pick leaves.

Height of browsing was given in relation to the animal as above head, head, neck, shoulder, chest and knee. Male kudu can reach higher on tree height than female kudu (Table 3).

Table 3: Browsing height estimated from that mean shoulder height is 121 centimeters female and 135 centimeters male kudus (Modified from Sklenar 2011).

| Browsing height	Estimated female height (cm)	Estimated male height (cm)	Estimated average height (cm)
Knee	45	50	50
Chest	85	100	90
Shoulder	121	135	130
Neck	150	160	150
Head	165	175	170

| Above head | 175 | 185 | 180 |

Figure 2; A group of male kudus (top picture) browsing on different plants, (below pictures) female kudus browsing on same plant.

3.2.   Plot design

With each observation of kudu, two plots were established immediately after the kudu observation to describe vegetation. These sampling plots I called kudu plots and control plots. Kudu plot was established from a point where individuals were observed browsing. The plot was defined as the area contained within a circle with a radius of 5.65 meters (100 m^2) with the tree recently browsed as the center point as described in Stokke (1999). A ─control plot" was established with the center 50 meters from the center of the kudu plot, perpendicular to the direction in which the kudu left the plot and to the right in relation to the direction of the

kudu movement (Figure 3). Obstacles such as roads were avoided by changing direction (left instead of right) in relation to kudu movement. I used kudu plots to represent feeding stations selected by the kudu and to document selection of browsed plants within the feeding station. The control plot was used to register the vegetation available for the kudu in this habitat. Thus, the kudu plot and control plot were used to show the differences between the available browse resource (control plot) and the selected feeding patches (kudu plot).
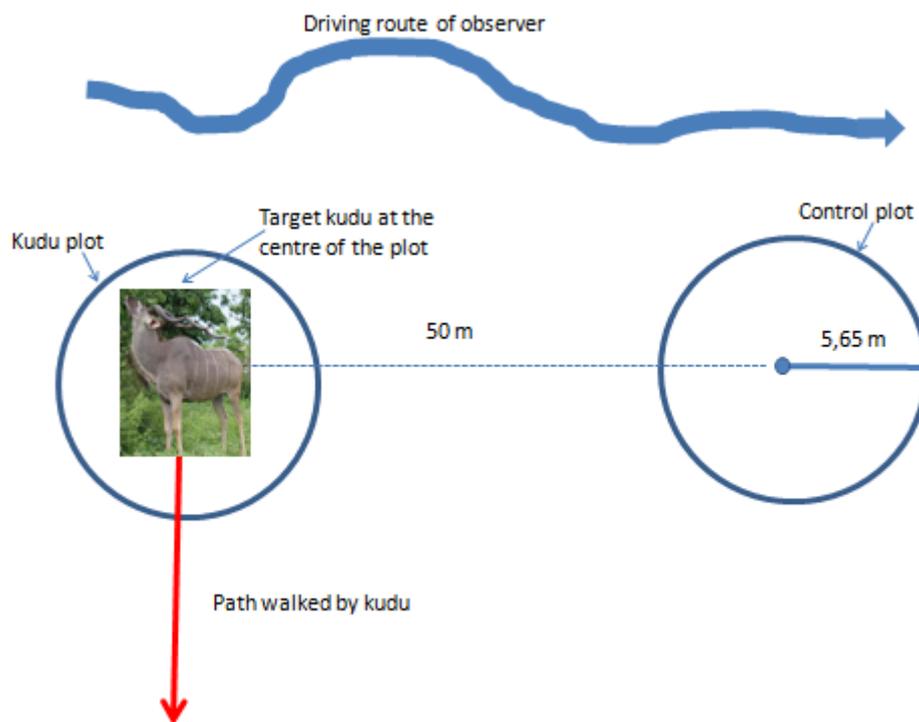
Figure 3: Method used to positioning the kudu plot and control plot in relation to the route by the observer and kudu browsing path. There are two plots, kudu plot and control plot with the same size. The control plot is placed with its centre 50 m perpendicular to the right of the path the kudu takes when leaving the kudu plot (the red arrow) Radius of the plots is 5.65m . This figure is not to scale (measurements given) and has been modified from Stokke (1999).

3.3 Vegetation measurements

Measurements were taken on all trees (browsed and not browsed) less than 0.5 m tall within the aforementioned plots. Tree height was defined as the height from the ground to the tip of highest living shoot. The stem height is the distance from the ground to the lowest green leaves and was measured to the nearest of 0.5 m up to 5 m using a telescopic measuring rod. I recorded the widest canopy diameter and the widest perpendicular canopy diameter on each tree of all species to an accuracy of 0.1 m using a tape measure. Ungulate twig bites from the current season were counted and a Vernier caliper was used to measure the bite diameters. The length of stripped sections of branches and twigs were measured using a ruler. The bite diameter and length of stripping were measured to an accuracy of 0.1 mm and 10 mm respectively, and the height of the bite or stripping above ground was measured to an accuracy of 0.1 m. I defined bite diameter as the diameter where the twig was bitten off. To distinguish between bites from the current season and older bites, color and position in relation to new shoots were used. Three twig bites were randomly selected and the diameter recorded. Bites above three meters above the ground were not included as they were beyond the reach of the kudu.

The same measurements of trees were done in control plots as in the kudu plots. Because of time constraints only density of the tree species was dealt with.

4. DATA ANALYSES

4.1. Ordinations

Data analyses were carried out using multivariate statistical analysis in CANOCO for Windows 4.5 (Lepš & Šmilauer 2003). This is a powerful statistical package originally designed to analyze plant sociology but it is now used in a variety of fields. I used it to analyze to what extent kudu browsing was related to the vegetation composition and soil nutrient condition. I used tree species density data and environmental data in ordination. Ordination is the method used to arrange species and samples in sequence along gradients. There are two types of ordination, direct and indirect gradient analysis. These are common ordination techniques in community ecology.

The methods of direct gradient analysis (also called the constrained or canonical ordination methods) are used to relate the species data through linear correlation of ordination axes with known environmental variables. In constrained ordination the variation in species composition are explained by supplied environmental variables. Indirect gradient analysis assumes that the structure in the response variable data depends on unknown, latent explanatory variables. The ordination axes represent these latent explanatory variables and can show the total variation in species data. The recorded environmental variables in indirect method are handled by placing them on top of the species data to give the best fit. Environmental variables are used to interpret the ordination in the diagram or figures.

Linear ordination assumes that the species response increases or decreases linearly with latent environment factors. Linear models can be selected when the length of gradient is less than ca 3 standard deviations. PCA or RDA option can be chosen under linear ordination method (Table 4). In unimodal model response expects that the species has an optimum on an environmental gradient when data has a large variation and long gradient in ordination. Detrending aims to remove any systematic relationship between the first and the second axes that causes the arc effect, by dividing the first axis in segments. Within each segment site, scores are adjusted by reducing their values with their average value on the second axis. When using Detrended Correspondence Analysis shows a length of gradient more than ca 3 standard deviations, then unimodal model can be selected (Lepš & Šmilauer 2003).

.

Table 4; The different models and types of gradient analysis in the program package CANOCO 4.5

	Indirect gradient analyisis	**Direct gradient analyisis**
Linear model	**(PCA)** Principle Component Analysis	**(RDA)** Redundancy Analysis
Unimodal model	**(CA)** Correspondence Analysis	**(CCA)** Canonical Correspondence Analyisis
Detrended unimodal	**(DCA)** Detrended Correspondence Analysis	**(DCCA)** Detrended Canonical Correspondence Analysis

I used Detrended Correspondence Analysis to decide whether I should use the ordination method based on linear model or unimodal model. The results from DCA showed, the length of gradient was 4.25, i.e., more than three standard deviations.

Thus, I selected unimodal model to run my species data using indirect gradient analysis in Correspondence Analysis because the length of gradient was 4.25 standard deviations. No transformation of the data was performed in Correspondence Analysis ordination, but down-weighting of rare species, an option in CANOCO, was selected to avoid them having an unduly large influence on the analysis (ter Braak & & Šmilauer 2002). Eigenvalues of the axes can be used to calculate the degree of variation explained.

Three true environmental variables were used in the study: alluvial soil, sandy soil and mixed soil. These are nominal variables and were assigned 1 if present or 0 if absent (Jongman et al. 1995). Four variables (kudu female plot, control female plot, kudu male plot and control male plot) were not truly environmental variables but were included to allow me to test whether they were significantly related to vegetation composition. I used forward selection in CCA analysis to test the environmental variables and relate kudu presence to vegetation. A Monte Carlo Permutation test was performed in CCA to test whether the environmental variables can explain the samples and species distribution in CCA. Default values within the program were used throughout the analysis. I used ordination method of my

data set to identify and describe the communities of tree species and relate them to environmental variables and relate kudu to vegetation. I considered a probability (p) value less than or equal to 0.05 as significant.

4.2.   Classification

Classification is a method of arranging sample units into groups according to similarity/dissimilarity. There are two types of classification methods namely agglomerative and divisive. Agglomerative methods start with individual samples and form groups with similar characteristics from the bottom up. Divisive is the method that starts with the whole group samples from the top, divides them into groups and continues dividing samples into subgroups until a desired level of division is reached. I used Two-Way Indicator Species Analysis (TWINSPAN) divisive method to form a hierarchical dichotomy.

The first division level in TWINSPAN splits the whole dataset into two groups. The second level TWINSPAN classification splits each of these groups into two subgroups etc. Applying TWINSPAN dendrogram, I used classes on the 1st and 2nd levels as a base to make my own clusters. Class 1 was divided in two clusters 1 and 2 according to kudu composition (Figure 6).

The clusters were arranged along CA axis 1 and 3 (Figure 4). I used axis 1 and 3 because they provided convenient interpretation of the graph. Four clusters were selected from ordination based on TWINSPAN classification.

4.3.   Vegetation quality on kudu plots and control plots

To explore differences in forage quality between kudu plots and control plots, I calculated selectivity indices of each browsed species in both female and male plots. I used a simple way of calculating selection index (B) of browsed tree species by $B_i=o_i/\pi_i$, o_i is the proportion of tree species $_i$ in the diet and π_i is the proportion of tree species $_i$ available (Savage 1931; from Manly et al. 1993).

Feeding site attractiveness values (FSAV) were used to determine the quality of vegetation in plots (Stokke, 1999). FSAV values for all plots were calculated according to the procedure outlined by Stokke (1999).

$$FSAV = \sum_{i=1}^{n} P_i \cdot B_i$$

Where P_i is the proportion of species $_i$ in the plot and B_i is the selection index for species $_i$. Differences between interdependent feeding patches and control plots for the males and female kudus were quantified with a pair-wise, 2-tailed t-tests and equal to 0.05 was used as significance value.

4.4. Food quantity in kudu plots and control plots

The food quantity analyses were performed using R™ (software version x 64 2.13.1). T-test in two ways ANOVA was used to test whether there were differences in number of trees and number of tree species between kudu female plots, control female plots, kudu male plots and control male plots. I assumed difference in number of trees and in number of tree species between feeding patches and control plots for the male and female kudu. The data were checked for normal distribution and equal variance prior to analysis.

I used the Dominance-diversity curves to show both tendency of tree species dominance and species diversity of individuals per plot between male feeding patches and control plots and female feeding patches and control plots.

4.5. Browsing selectivity among trees in male and female feeding patches

I used average selectivity index of browsed trees to compare with average selectivity index of available trees (browsed and non- browsed) within a plots to compare selectivity between males and females. I then used a t-test in two-way ANOVA to test the significant differences between male feeding patches and female feeding patches. The p-values were calculated and presented.

5. RESULTS

During the course of the study, data from a total of 300 plots were collected. A total of 248 animals were observed—167 kudu from alluvial soil, 69 kudu from sandy soil and 12 kudu from mixed soil (Table 5). Out of the 300 plots, there were 85 female kudu plots, 85 female control plots, 65 male kudu plots and 65 male kudu plots. A total of 2006 trees were recorded in the plots. All tree species recorded in the study are listed in alphabetical order by family name, scientific name, local name, abbreviated name and habitat type (Table 6).

Table 5; Total number of individual kudu observed in each habitat type in the entire study area.

	Alluvial soil	**Mixed soil**	**Sand soil**	**Total**
Females	107 (70 %)	7 (5 %)	39 (25 %)	**153** (100%)
Males	60 (63 %)	5 (5 %)	30 (32 %)	**95** (100%)

Table 6; Characteristics of all trees species in the studied area (van Wyk and van Wyk, 1997)

Latin name	English name	Family	Growth form	Abbr	deciduous/ evergreen	Soil type	Spine
Acacia erioloba	Camel Thorn	Fabaceae	Large/ medium tree	Aer	deciduous	Mix	yes
Acacia nigrescens	Knobthorn	Fabaceae	Large/ medium tree	Ani	deciduous	Alluvial	yes
Baphia massaiensis	Sand camwood	Fabaceae	Shrub or small tree	Bma	deciduous	Sand	no
Adansonia digitata	Baobab	Malvaceae	Tree	Adi	deciduous	Alluvial	no
Berchemia discolor	Bird plum	Rhamnaceae	Small to medium tree	Bdi	deciduous	Alluvial	no
Burkea africana	Wild seringa	Leguminosae	Medium tree	Baf	deciduous	Sand	no

Canthium glaucum	Pink-fruited rock elder	Fabaceae	Shrub or small tree	Cgl	deciduous	Alluvial	yes
Canthium huillense	Bush canthium	Fabaceae	Shrub or small tree	Chu	evergreen	Alluvial	no
Capparis tomentosa	Woolly caper-bush	Capparidaceae	Shrub or small tree	Cto	evergreen	Alluvial	yes
Colophospermum mopane	Mopane	Fabaceae	Shrub or medium tree	Cmo	deciduous	Alluvial	no
Combretum apiculatum	Red bush willow	Combretaceae	Small medium tree	Cap	deciduous	Alluvial	no
Combretum mossambicense	Knobbly combletum	Combretaceae	Shrub or small tree	Cmo	deciduous	Alluvial	yes
Croton gratissimus	Lavender fever berry	Euphorbiaceae	Shrub or small tree	Cgr	deciduous	Mix	no
Croton megalobotrys	Large fever berry	Euphorbiaceae	Small or medium tree	Cme	deciduous	Alluvial	no
Dichrostachys cinerea	Sickle bush	Fabaceae	Shrub or small tree	Dci	deciduous	Alluvial	yes
Erythroxylum zambesiacum	Zambezi coca tree	Euphorbiaceae	Shrub or tree	Eza	deciduous	Alluvial	no
Flueggea virosa	White berry-bush	Euphorbiaceae	Shrub or sometimes tree	Fvi	deciduous	Alluvial	yes
Friesodielsia obovata	Monkey fingers	Annonaceae	Shrub or small tree	Fob	deciduous	Sand	no
Gardenia volkensii	Bushveld gardenia	Rubiaceae	Small tree	Gvo	deciduous	Mix	no
Grewia flavescens	Donkey-berry	Tiliaceae	Shrub or small tree	Gfl	deciduous	Alluvial	no

Lonchocarous nelsii	Kalahari apple-leaf	Fabaceae	Small or tree	Lne	deciduous	Sand	no
Lonchocarpus capassa	Apple-Leaf	Fabaceae	Medium to large-sized	Lca	deciduous	Alluvial	no
Markhamia zanzibarica	Bell bean tree	Bignoniaceae	Small or sometimes tree	mza	deciduous	Mix	no
Strychnos potatorum	Grape strychnos	Loganiaceae	Small to medium tree	Spo	evergreen	Mix	no
Vangueria Infausta	Wild medlar	Rubiaceae	Shrub or small tree	Vin	deciduous	Mix	no

.
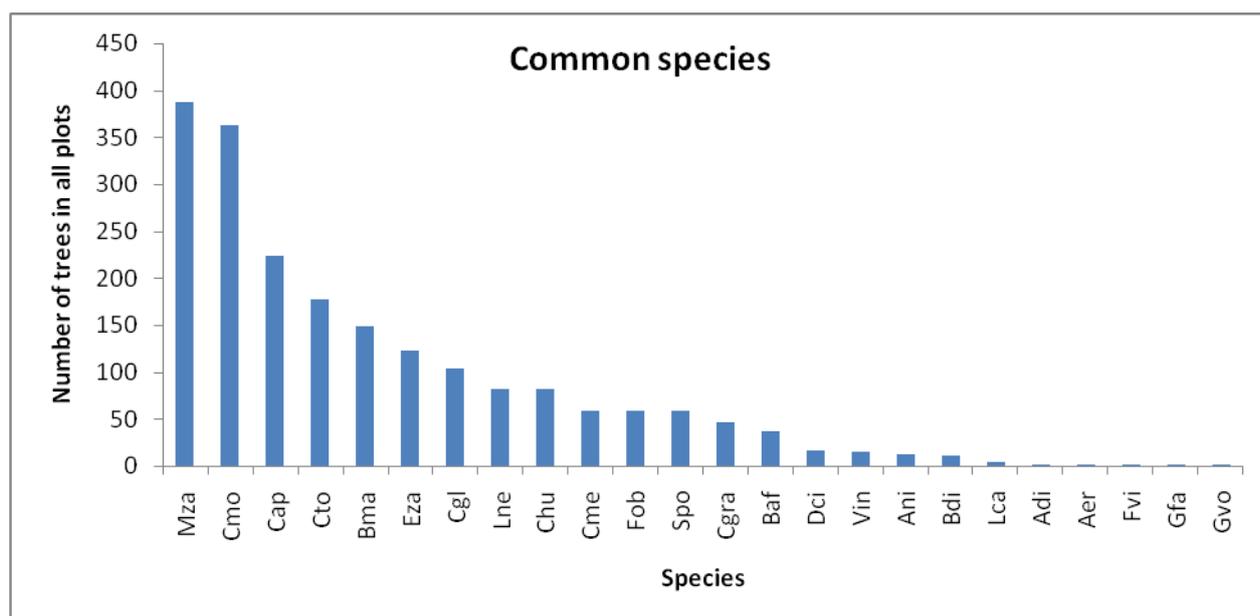
Figure 4: Number recorded of all tree species in all plots in the study. Abbreviations are shown in Table 6. Trees were arranged in descending order of occurrence.

## 5.1. Kudu selection of tree species composition and habitat type

Relationship between tree species composition and environmental variables

The test results from the forward selection and Monte Carlo Permutation tests in constrained ordination showed significant differences between sandy soil and alluvial soil in species while mixed soil showed no significant difference in species and sample distribution. In addition, there was a significant difference between control and kudu females in relation to vegetation. There were no significant differences between kudu males and control female (Table 7).

Table 7: Results of Monte Carlo Permutation tests of environmental variables and relationship between kudu plots, control plots and soil types, respectively, and vegetation composition from forward selection in CCA.

| Enviromental variables	F-value	P-value
Alluvial soil	16.41	0.002
Mixed soil	0.34	0.34
Sandy soil	21.73	0.002
Not truly environmental variables		
Control females	0.67	0.81
Kudu females	1.56	0.08
Control males	2.27	0.01
Kudu males	0.83	0.64

The CA ordination results show variations in species composition along two axes. The first axis is primarily a soil gradient. The vertical axis 3 displays a large variation, the cause of which is currently unknown. Alluvial and mixed soils are positively correlated to each other but negatively related to sand soil (Figure 5).
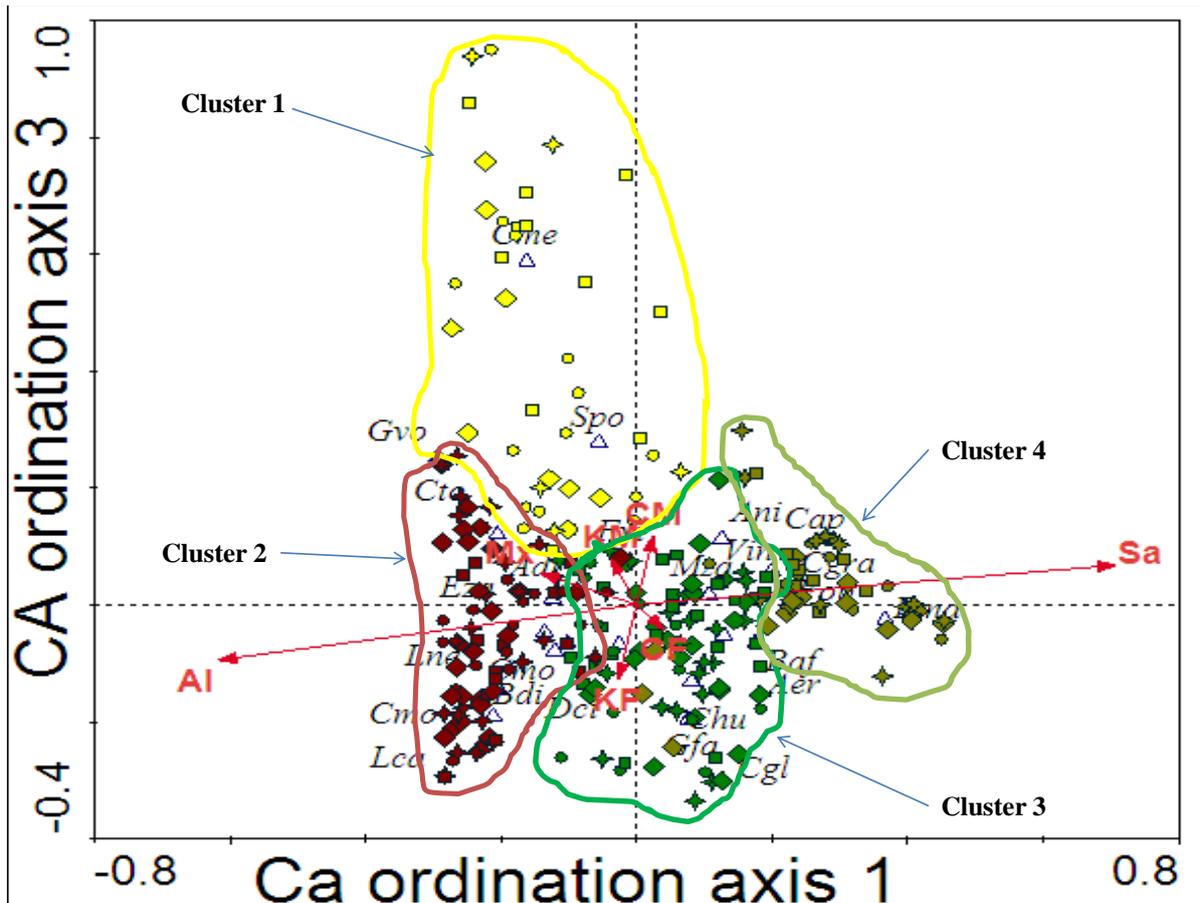
Fig. 5: Biplot from Correspondence Analysis (CA) showing species and environmental variables and Clusters. Circles represent kudu males plot, squares represent control males, diamonds represent kudu females and stars represent control females. Yellow represents class 1, brown represents class 2, and green represents class 3 and olive represent class 4. Triangles in the graph indicate tree species Abbreviations are as follows: Al= alluvial soil, SA=sand soil, Mx= mixed soil, KF=kudu female plots, CF=control female plots, KM=kudu male plots and CM=control male plots. The blue arrows indicate the cluster names from one to four. The names of tree species in the figure are in (Table 6).

5.1.2. Classification of plots

Three classes were selected from the TWINSPAN dendrogram (figure 6). The TWINSPAN first cluster was not well separated along the first CA axis but indicated a separation between male and female plots along CA ordination axis 3 (Fig. 5.).
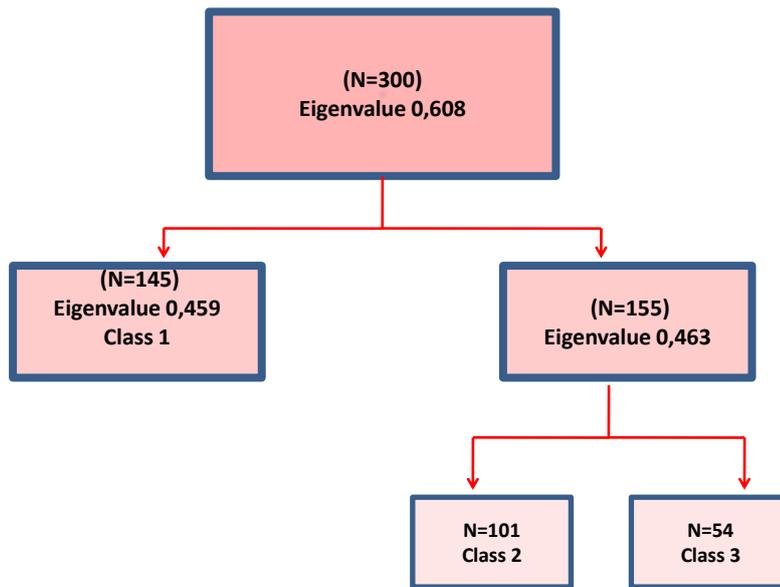
Fig. 6; Cluster samples grouped by two way indicator species analysis (TWINSPAN).

Cluster 1

Cluster 1 is dominated by tree species with the highest density such as *Capparis tomentosa*, *Croton megalobotrys*, *Markhamia zanzibarica*, *Strychnos potatorum* and *Erythroxylum zambesiaca* (from highest to lowest order of appearance). The most frequent tree species occurring in almost all plots in this cluster are *Capparis tomentosa*, *Croton megalobotrys*, *Strychnos potatorum* and *Markhamia zanzibarica*. This cluster is not related to any soil type (figure 5). There are 35 male, 27 female plots out of a total of 62 plots in this cluster. The majority of this cluster is situated near the riverside. There are 56 % of male plots and 44 % of female plots in this cluster.

Cluster 2

This cluster is dominated by high density of *Combretum mossambicense*, *Capparis tomentosa*, *Erythroxylum zambesiacum*, *Lonchocarous nelsii* and *Markhamia zanzibarica* in ranked order. The primary tree species that occurs in most of the plots in this cluster are *Capparis tomentosa*, *Combretum mossambicense*, *Erythroxylum zambesiacum*, and *Markhamia zanzibarica*. This cluster has positive correlation with alluvial soil and partly with mixed soil. It is negatively correlated to sandy soil (Figure 4). There is a dominance of female plots (61 female, 37 males out of 98 plots in this cluster). Most of the cluster grows some

distance away from the Chobe River in mixed soil type. There are 62% of female plots and 38 % male plots in this cluster.

Cluster 3

The species with highest density occurring in this plot are *Markhamia zanzibarica*, *Canthium glaucum*, *Combretum apiculatum*, *Combretum mossambicense*, *Canthium huillense*, *Erythroxylum zambesiacum*, *Lonchocarous nelsii*, and *Burkea africana* respectively. The most frequent trees species that occurs in almost all plots in this cluster are *Markhamia zanzibarica*, *Combretum apiculatum*, *Canthium huillense*, *Combretum apiculatum Canthium glaucum*, *Combretum mossambicense* and *Lonchocarous nelsii*. This cluster is slightly positively related to sand soil. There are 47 male plots out of 89 plots which means there is 48% of female plots and 52 % male plots in this cluster.

Cluster 4

This cluster is dominated by a high density of *Baphia massaiensis*, *Combretum apiculatum*, *Markhamia zanzibarica*, *Friesodielsia obovata*, *Croton gratissimus* and *Burkea africana*. The most common tree species that occurs in almost all plots are *Combretum apiculatum*, *Baphia massaiensis*, *Markhamia zanzibarica*, *Friesodielsia obovata* and *Croton gratissimus*. This cluster has a positive relation with sand soil but is negatively related to alluvial soil. There are 31 female plots out 51 plots meaning that 60% are female plots and 40 % male plots in this cluster.

5.2.   Selectivity index

Male and female selectivity index of each species were similar but not exactly the same (Table 8a and b).

Table 8; Selectivity indices for each tree species browsed by males. Tree species acronyms are defined in Table 6.a)

Tree species	Proportion of available	Proportion in diet	Sel. index by males
Cto	11,59	30,12	2,6
Ani	0,48	1,2	2,49
Spo	4,83	12,05	2,49
Chu	4,59	10,84	2,36
Eza	7,97	14,46	1,81
Bma	3,86	3,61	0,94
Cmo	13,53	10,84	0,8
Fob	1,93	1,2	0,62
Lne	4,59	2,41	0,53
Mza	21,98	10,84	0,49
Cgl	5,31	2,41	0,45

b) Selectivity index for each tree species that are being browsed by females. Tree species acronyms are defined in Table 6.

Tree species	Proportion available	proportion in diet	Sel. index by females
Chu	4,18	13,04	3,12
Cto	9,65	27,83	2,88
Bdi	0,72	1,74	2,41
Eza	5,91	13,04	2,21
Spo	3,03	6,09	2,01
Cgl	5,76	6,09	1,06
Mza	13,69	13,91	1,02
Cme	1,73	1,74	1,01
Fob	4,76	4,35	0,91
Baf	1,59	0,87	0,55
Cmo	23,05	7,83	0,34
Lne	2,59	0,87	0,34
Bma	11,53	2,61	0,23

5.3. Vegetation quality in kudu plots and control plots

Female kudu feeding plots did not differ in feeding site attractiveness values (FSAV) from the control plots, whereas male kudu plots and male control plots showed a tendency to differ in FSAV (Table 9b). There were significant differences in FSAV between female and male kudu feeding plots (Table 9c).

Table 9; The ANOVA summary of feeding site attractiveness values (FSAV) between control plots and kudu plots a) females, b) males and c) between male and female feeding plots.

a)

Variables (females)	Mean	95% Cl Lower	Upper	Df	T-value	P-value
Control	116,84	100,03	133,66	163	13,72	0,50
Kudu	124,95	108,03	141,87	163	14,58	

b):

Variables (males)	Mean	95% Cl Lower	Upper	Df	T-value	P-value
Control	93,83	78,60	109,05	130,00	12,19	0,06
Kudu	114,15	99,15	129,14	130,00	15,06	

c):

Variables	Mean	95% Cl Lower	Upper	Df	T-value	P-value
Females	120,96	110,04	131,88	295	21,80	0,30
Males	104,23	92,02	116,43	295	16,80	

5.4. Food quantity in kudu plots and control plots

There were more trees in female kudu plots than in female control plots (Table 10). There was no difference in number of trees between male kudu plots and male control plots, and there were higher numbers of trees in female kudu plots than in male kudu plots (Table 10).

Although female kudu plots did not differ in number of tree species compared to male kudu plots, there were significant differences between feeding patches and controls for both females and males. Female and male feeding patches have a higher number of species compared to their respective control plots (Table 11).

Table 10; ANOVA summary of number of trees in all plots.

Number of Trees

| Variables	Mean	Sd	df	P-value	T-value	Assumption
Control females	6,32	3,77	83	0,01	1,99	Equal variances
Kudu females	8,26	5,27				
Control males	5,56	3,29	65	0,22	1,10	Equal variances
Kudu males	6,27	3,30				
Kudu females	8,26	5,27	141	0,01	2,00	Unequal variances
Kudu males	6,27	3,30				

Table 11: ANOVA summary of number of species in all plots. I compared plots between female control plots with female kudu plots, male control plots with male kudu plots, and female kudu plots with male kudu plots.

Number of Species

Variables	Mean	Sd	df	P- value	T-value	Assumption
Control females	2,79	1,24	83	0,01	1,99	Equal variances
Kudu females	3,16	1,25				
Control males	2,64	1,08	65	0,02	2,00	Equal variances
Kudu males	3,01	0,95				
Kudu females	3,16	1,25	15	0,44	2,00	Unequal variances
Kudu males	3,02	0,95				

5.4.1 Dominance-diversity

Dominance-diversity curves showed a weak tendency to differ between plots for males and females. Because the curve shape is flat, these results indicate that kudu females and control females have highest species diversity. This means that there are more species of intermediate abundance, but they are not dominant. Kudu males and control males have a high dominance of tree species and lower species diversity.
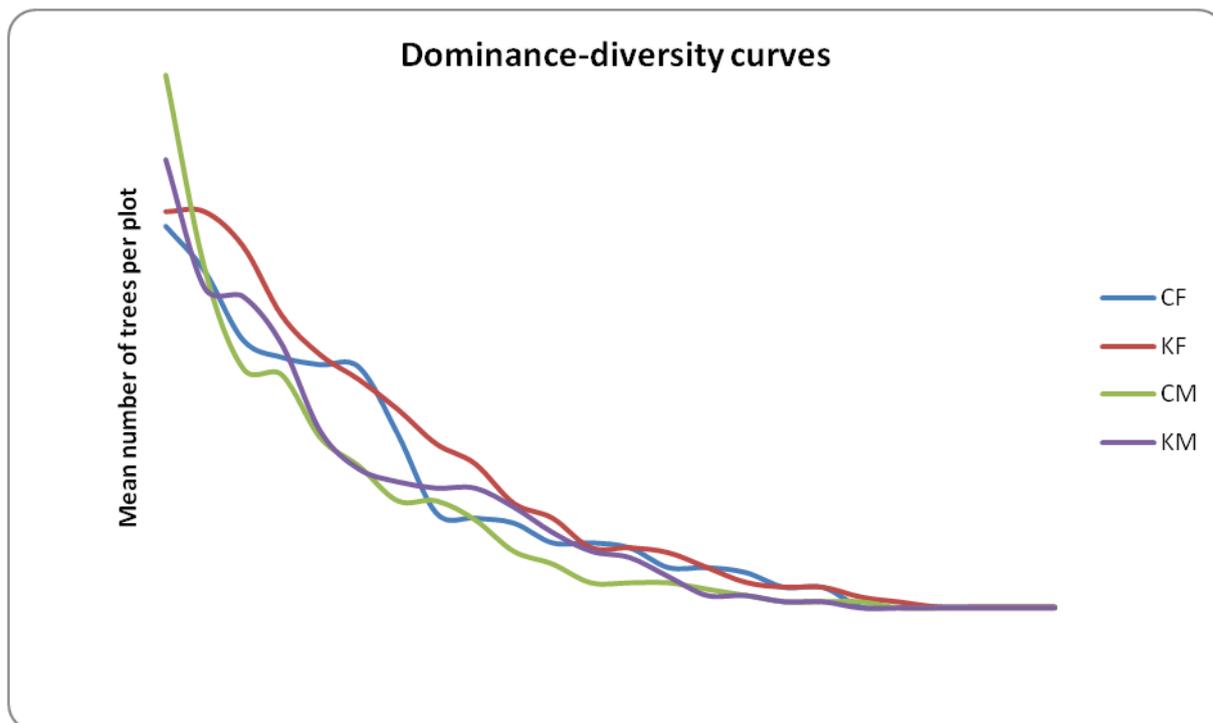
Figure 7; The dominance-diversity, number of individuals per plot of tree species shown as for CF= control females, KM= kudu females, KM= kudu males and CM= control males.

5.5.   Browsing selectivity among trees in male and female feeding patches

There are no significant differences between selectivity index of trees in feeding plots by males and females.

Table 12; ANOVA summary of average selectivity index for trees browsed between female and male feeding plots.

| Variables | Mean | 95% Cl | | Df | T-value | P-value |
		Lower	Upper			
Females (aver. Index)	17,38	3,84	30,92	22	2,66	0,70
Males (aver. Index)	13,86	-0,86	28,58	22	1,95	

There was a tendency (p=0.07) for female kudu to select high quality trees within the feeding patches according to selectivity index of each species. There was significant difference between the average quality of trees selected by female kudu and the average quality of all trees, selected and not selected, in plots (Table 13a).

There was no significant difference between average qualities of trees selected by male kudu from the average quality of trees in the plots (Table 13b).

Table 13a) ANOVA summary of average selectivity indices for all trees (selected and not selected trees within feeding patches) for females (a) and males (b).

Variables (females)	Mean	Df	P-value
Trees available	1,47	158	1.51E-08
Trees browsed	2,43	158	

b).

Variables (males)	Mean	Df	P-value
Trees available	1,4	128	1.92E-06
Trees browsed	2,13	128	

6.   DISCUSSION

6.1   Kudu selection of tree species composition and habitat type

My study found evidence of sexual segregation in greater kudu (*Tragelaphus strepsiceros*) in a heterogeneous savanna, in Chobe National Park, Botswana. As a first hypothesis, I tested that both sexes of kudu in Chobe National Park would forage in the vegetation on the rich alluvial soil close to the river, but the male would also use the vegetation on the poor Kalahari sand. Results differed from the hypothesis as the majority of both sexes were observed on nutrient rich alluvial soil while few individuals were found on vegetation on sandy soils. This implies that both sexes like the plant species in alluvial soil.

The Correspondence Analysis ordination separate habitats mainly used by males and females along axis 3. Males chose the habitat described as cluster 1, while females choose clusters 2 and 3. I hypotheses that males prefer the vegetation that close to the river while females prefer the vegetation that are distance from the river. It may be that females select habitat dominated by *Combretum mossambicense* and *Markhamia zanzibarica* because such vegetation is dense and therefore a good place for females and their offspring to hide from predators. I propose that *Combretum mossambicense* helps the kudu avoid being detected by predators, because the tree trunks are the same color as the kudu (personal observation). Males were mostly found in vegetation dominated by *Capparis tomentosa*. *Capparis tomentosa* is one of the trees species that contributes most in diet for many herbivores species both during wet and dry season (Makhabu 2005). This may be because the animals need the higher nutrient value of both the fruits and leaves especially during the rainy season. *Capparis tomentosa* is also an evergreen tree which could make it more attractive to herbivores particularly in the dry season.

Similarly, du Toit (1995) reported that female kudu are reluctant to use riverine habitat, because females are vulnerable to predators such as leopard (*Panthera pardus*) which favor this type of habitat. In Kruger National Park in South Africa he found the strongest segregation between sexes in the wet season, when males mainly used the riverine habitat, while females were mostly found in the border between hills and the riverine area. This is the same pattern as in my study.

33

6.2.   Vegetation quality in kudu plots and control plots

According to my second hypothesis, I expected feeding patches for both females and males to differ from the surrounding vegetation in quality.

Males and females selected almost the same tree species but in slightly different orders. According to the selectivity index, *Capparis tomentosa, Strychnos potatorum and Cathium huillense* were highly selected by both male and female kudu compared to other plant species in feeding patches. This suggests that those tree species were the most favored and palatable species for both sexes. These tree species may have higher nutrient concentration or less defenses against herbivores than other species. In addition, Kazonganga (2011) found that kudus preferred trees that have been impacted by elephants which were often the case with *Canthium huillense, Combretum mossambicense* and *Erythroxylum zambesiacum.* Makhabu (2005) reported that *Capparis temontosa* contributed 20.2% in diet composition of kudu and *Combretum mossambicense* contributed 42.1 % in diet composition during wet season

I found that female feeding patches and control plots had higher number of high quality trees than male feeding patches and control plots. There was no significant difference for food quality measured as feeding site attractiveness values between female feeding patches and control plots. Females need to be selective and require more nutritious food, males need to maximize rate of intake or eat more food and can subsist on lower quality food. Therefore, in this case, males should have chosen to have a higher density of trees in feeding patches than females.

In retrospect the distance of 50 meters that I used between female feeding and control patches was too short in relation to the scale of habitat selection and diet selection. I suggest, for further research, that the 50 meter distance between females feeding patches and control plots be increased for food quality analysis. I propose that female kudu select higher quality feeding patches on large scales unlike males which select on a small scale.

Furthermore, I found differences in food quality between feeding patches and control patches for males. This suggests that male kudu select in a smaller scale picked up by the 50 meter distance used between plots. However, the 50 meter distance seemed to be enough for males to make decision of where to find enough good quality food, particularly because male kudu feed singly and not in groups like females.

I found a significant difference in food quality in feeding patches between females and males. Females selected habitat of higher quality than males. This agrees with the Jarman-Bell

principle (Bell 1971; Jarman 1974) as stated in the introduction. Species with larger body size have the ability to tolerate a poorer quality diet, because of the allometric relationship between the metabolic rate and gut capacity (Demment & van Soest 1985). Therefore females should select for higher quality food and my results agree with this.

6.3. Food quantity in kudu plots and control plots

Female kudu feeding patches and control plots differed significantly in number of trees, and females selected feeding patches with higher density of trees than in the surrounding vegetation, as represented by control plots.

I also found that there were no significant differences between number of trees in male kudu feeding patches and control patches. This suggests that the male kudu used patches that had the same amount of food as the surrounding vegetation and seemed less selective than females at a small scale. I propose that the 50 meter distance was sufficient to analyze food quantity between female feeding patches and control plots but that it is not sufficient for food quantity analysis in males.

Female kudu had higher density of trees in feeding patches than had male kudu. This implies that females are more selective of areas that have higher density of trees than males. I also found that there were significant differences between the number of tree species in female kudu feeding plots and control plots. Feeding patches had higher number of species than control plots. This implies that females select feeding patches with a higher variety of plant species than control plots.

I also found that there were significant differences between the number of tree species in male kudu feeding plots and control plots. Feeding patches had a higher number of tree species than control patches. This suggests that male kudu select browsing patches that have higher variety of trees species. Finally, there was no significant difference between male and female kudu in number of plant species in feeding patches. This implies that both sexes select for high quality foraging habitat.

6.4. Browsing selectivity among trees within feeding patches

My last hypothesis, I tested that kudu female would be more selective within feeding patches than males. My results support this hypothesis. My results show that females have a significant difference in average selectivity index between trees available and trees browsed.

Female kudu selected trees with the highest selectivity index among trees available. This implies that females make decisions on what tree to browse within the feeding patches. According to what I have observed in the field, most of the female kudu I recorded were in groups. I observed that the leading female kudu of the group select the feeding patches that can provide enough food for the followers. I also noticed that individual female kudu mostly browsed on the same tree while it was rare to find individual male kudu feeding on the same tree.

Lastly, the analysis between trees available and trees browsed in males showed no significant difference. This implies that males are less selective within patches than females. Males were often observed feeding alone or in pairs but feeding on different trees unlike females who preferred to feed on the same tree.

7. CONCLUSIONS

In this thesis I evaluated the sexual segregation in the foraging behavior of greater kudu by assessing the differences in food and habitat use between male and female kudu in the wet season along the Chobe riverfront in relation to environmental heterogeneity on different scales. I expected sexual segregation to comply with the Jarman-Bell principle that larger animals are able to tolerate a lower quality diet than smaller ones. However, my results suggest that sexual segregation is not only based on food quality and quantity. In females, predation risk seems to be the main key of habitat selection while male results revealed that they selected for food quality and quantity.

8. ACKNOWLEDGMENTS

9. REFERENCES

Aarrestad P. A., Masunga G. S., Hytteborn H., Pitlagano M. L., Morokane W. & Skarpe C. 2010. Influence of soil, tree cover and large herbivores on field layer vegetation along a savanna landscape gradient in northern Botswana. Journal of Arid Environments. Volume 75: 290-297

Barboza P. S. & Bowyer R. T. 2000. Sexual segregation in dimorphic deer: a new Gastrocentric hypothesis. Journal of Mammalogy. Institute of Arctic Biology and Department of Biology and Wildlife. University of Alaska Fairbanks. Volume 81: 473-489.

Bell R. H. V. 1971. A grazing ecosystem in the Serengeti. Ecological Society of America 225: 86-93.

Coates Palgrave K. 1993. Trees of southern Africa. - Struik Publishers, Cape Town

Clutton-Brock T. T., Iason G. R. & Guinness F. E. 1987. Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). Journal of Zoology Volume 211, 275–289.

Cromsigt J. P. M, Prins H. T & Olff H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Diversity and Distribution. Blackwell Publishing Ltd. 513-522.

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

Dougill A. J. & Thomas A. D. 2004. Kalahari Sand Soils: Spatial Heterogeneity, Biological Soil Crusts and Land Degradation. Department of Environmental and Geographical Sciences. Volume 15: 233-242.

Du Toit J. T. 1995. Sexual segregation in kudu: sex differences in competitive ability, predation risk or nutritional needs? South African Journal of Wildlife Research. Volume 25: 127-132.

Du Toit T. & Stokke S. 2000. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. East African Wildlife Society, Journal of Ecology 40: 360-371.

Estes R. D. 1991. The behavior guide to African mammals: including hoofed mammals, carnivores, primates. Russel Friedman books, South Africa.

Ginnett F. T. Demment W. M. 1997. Sex differences in giraffe foraging behavior at two spatial scales. Oecologia 110: 291- 300.

Jarman P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour volume 48: 215-267.

Jongman R. H. G., ter Braak C. J. F. & van Tongeren O. F. R. 1995. Data analysis in community and landscape ecology. Cambridge University Press.

Kazonganga B. 2011. Sexual segregation in greater kudu (*Tragelaphus strepsiceros*) in a heterogeneous savanna, in Chobe National Park, Botswana. Master of Science thesis, Hedmark University College.

Kalwi J. M., De Boer W. F., Mucina L., Prins H. H. T., Skarpe C & Winterbach. **C.** 2009. Tree cover and biomass increase in a southern African savannah despite growing elephant population. Ecological Society of America. Ecological Applications. Volume 20: 222-233

Lepš J. & Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, New York.

Loe L. E., Irvine R. J., Bonenfant C., Stien A., Langvatn R., Albon S. D., Mysterud A. & Stenseth N. C., 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. Journal of Animal Ecology. Volume 75: 485–496.

Makhabu S. W. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. Journal of Tropical Ecology. 21: 641-649.

Manly B. F. J., McDonald L. L. & Thomas D. L. 1993. Resource selection by animals – statistical design for field studies. Chapman & Hall, London, pp 177

Mendelsohn J. & El Obeid S. 2005. Forest and woodlands of Namibia. Struik Publishers. Cape town. RSA.

Miquelle D. G., Peek M. J. & Ballenberghe V. V. 1992. Sexual segregation in Alaskan Moose. Wildlife Monographs, No. 122. Page 3-57.

Mysterud A. 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivore.Oecologi. Springer-Verlag. Pp 40–54.

Ruckstuhl E. K. & Neuhaus P. 2000. Sexual segregation ungulates: a comparative test of three hypotheses. Cambridge Philosophical Society. *77*: 77-96

Rutina L. P., Moe, S. R. & Swenson J. E. 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry season browse availability for impalas *Aepyceros melampus*. Wildlife.Biology. 11:207-213.

Skarpe C., Aarrestad P. A., Andreassen P., Dhillion S. S., Dimakatso T., Du Toit J. T., Halley D. J., Hytteborn H., Makhabu S., Mari M., Marokane W., Masunga G., Modise D., Moe S. R., Mojaphoko R., Mosugelo D., Motsumi S., Neo-Mahupeleng G., Ramotadima M., Rutina L., Sechele L., Sejoe T. B., Stokke S., Swenson J. E., Taolo C., Vandewalle M & Wegge P. 2004. The Return of the Giants: Ecological Effects of an Increasing Elephant Population. Ambio Volume 33: 276-282.

Savage R.E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fishery Investigations, Ministry of Agriculture, Food and Fisheries, Series 2. 12: 1-88

Skinner J. D. & Chimimba C. T. 2005. The mammals of the southern African subregion. Cambridge University Press, pp 814

Senft R. L., Coughenour M. B., Bailey D. W., Rittenhouse L. R., Sala O. E. & Swift D. M. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 3711: 789-799.

Sklenar M. 2011. Sexual segregation in kudus from Mokolodi. Master of Science thesis, Uppsala University

Stokke S. & du Toit J. T. 2000**.** Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. Ecography 23: 70-80

Stokke S. 1999. Sex differences in feeding patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. Canadian Journal of Zoology. 77: 1723-1732.

ter Brack C. J. F., & Šmilauer P. 2002. CANOCO reference manual and user's guide to Canoco for windows: Software for Canonical Community ordination (version 4). Micro-computer Power, Ithaca, NY, USA.

Uyapo J. & Jeff P. 2001. Large ungulate habitat preferences in Chobe National Park, Botswana. Journal Range of Management. Volume 55: 341-349

Van Wyk B. & Van Wyk P. 1997. Field Guide to Trees of Southern Africa. Struik, South Africa.

Wallgren M. 2001. Mammal communities in the Southern Kalahari – distribution and species composition. Master of Science Thesis. Committee of Tropical. Ecology, Minor Field Study 69. Uppsala University.

Wang L., Odorico P. D., Ringrose S., Coetzee S. & Macko S. A. 2007. Biogeochemistry of Kalahari sands. Journal of Arid Environments 71: 259–27.