DIET SELECTION AND FORAGING EFFICIENCY OF NGUNI GOATS IN THE BUSHVELD OF GAUTENG, SOUTH AFRICA

By
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PREFACE

DECLARATION

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Prof. Scogings P. F.

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DEDICATION

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SUMMARY

Diet selection and foraging efficiency are primary driving behavioural processes in mammalian herbivore plant interaction. They determine the quality of production and also impact on vegetation, necessitating managerial inputs that will sustain productivity and conserve or improve on its plant species composition.

In view of a better understanding of browse/browser interaction in subtropical arid savannah, Nguni goats were adopted as our model browser considering their socioeconomic importance to local, regional and global economy.

The primary objective of this research was to determine the seasonal and plant species trend of diet selection indexed by intake and foraging efficiency indexed by intake rate. The secondary objective was to investigate how plant morphological variables such as spinescence, shoot morphology such as long shoots as opposed to short shoots, and broad as against fine leaves, phenological variables such as evergreen versus deciduous species, and plant chemical components including: crude protein, neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, cellulose, acid detergent lignin and condensed tannins relate and possibly explain the observed patterns.

Six browse plants, *Acacia nilotica*, *Acacia robusta*, *Ehretia rigida*, *Euclea crispa*, *Rhus lancea* and *Ziziphus mucronata* were used in the first experiment to determine short term intake during the dry and rainy seasons In the second experiment, 10 browse plants: *Acacia nilotica, Acacia robusta, Combretum epiculatum, Dicrostachys cinerea, Ehretia rigida*, *Euclea crispa*, *Gymnosporia buxifolia*, *Rhus lancea* and *Ziziphus mucronata* were used to determine short term intake rate in the dry, early rainy and late rainy seasons.

Diet selection was significantly affected by species ($F_{5,60}$= 31.87 ; p< 0.05) and the interaction between seasons and species ($F_{5,60}$= 2.52; p= 0.039). Intake was not significantly higher in the rainy relative to the dry season, 3.94 ± 0.42^a gDM compared to 3.57 ± 0.42^a gDM. *Rhus lancea* and *A. robusta* were the most preferred species in both seasons, while *Z. mucronata* was more preferred in the dry season than *E. crispa* but in the rainy season it was the opposite. *Dichrostachys cinerea* and *A. nilotica* were the least

preferred in both seasons, but with improved intake of *D. cinerea* in the rainy season, whereas that of *A. nilotica* declined significantly.

Intake of plant species with long shoots, which were also broad leafed, was significantly higher than that of old short shoot species (t= -3.99; df= 65.80; p= 0.0002). Similarly, intake of evergreen species was significantly higher than that of deciduous species (t= 5.22; df= 34.02; p< 0.0001).

Cellulose in the rainy season positively correlated with intake (r= 0.85; n= 6; p= 0.031), bite number cropped (r= 0.98; n= 6; p= 0.001) and browsing time (r= 0.93; n= 6; p= 0.007). In the dry season there was no correlation of any plant chemical components with intake except cellulose that correlated with the intake variable of bite size (r= 0.87; n= 6; p= 0.023). The following regression equation was generated from the correlation to model intake: Intake= 0.68 + BS (3.07), (R^2= 0.71; p< 0.05), where BS= bite size.

Intake rate varied amongst species (p< 0.05), as well as seasons (p< 0.05). Instantaneous intake rate in the dry season were highest for *A. caffra* and *G. buxifolia*, followed by *C. apiculatum*, *R. lancea*, *E. crispa*, *A. robusta* and *Z. mucronata*. The bottom tier comprised of *E. rigida*, *D. cinerea* and *A. nilotica.* At the onset of the rainy season, *A. robusta*, *A. caffra* and *R. lancea* had the highest instantaneous intake rate, followed by *C. apiculatum, E. crispa* and *Z. mucronata*. The lowest instantaneous intake rates were derived from *D. cinerea*, *E. rigida*, *G. buxifolia* and *A. nilotica*. At late rainy season, A. *robusta, A. caffra, C. apiculatum, E. crispa* and *R. lancea* yielded the highest intake rate, followed by *D. cinerea*, *G. buxifolia* and *Z. mucronata* in the middle tier, and the least were derived from E. *rigida* and *A. nilotica*.

Acacia caffra, A. robusta, R. lancea, C. apiculatum and *E. crispa* featured amongst species with the higest intake rate in all three seasons, whereas *G. buxifolia* from which one of the highest intake rates was derived in the dry season declined to amongst those with the least in both early and late rainy seasons. *Ehretia rigida, D. cinerae* and *A. nilotica* were consistent in all three seasons as the least efficiently foraged Browses with long shoots were more efficiently foraged upon than those with short shoots (t= -3.2; df= 284.64; p< 0.002). Evergreen plant species yielded higher instantaneous intake rate relative to deciduous species (t= 2.02; df= 278.01; p< 0.044). Intake rate of spinescent relative to

spineless species was not significantly different but more bites were cropped from spinescent relative to spineless species (t= 2.80; df= 256.77; p= 0.006). Bite sizes were smaller for spinescent relative to spineless species (t= -3.30; df= 227.4; p= 0.001).

There were significant positive correlations of cellulose with intake rate (r= 0.7; n= 10; p= 0.023), and with condensed tannins (r= 0.7; n= 10; p= 0.022) in the dry season. Additionally, cellulose also had a positive correlation with bite size in the same season (r= 0.7; n= 10; p= 0.016). At early rainy season, there was no correlation of intake with any of the plant chemical components, whereas, NDF (r= 0.6; n= 10; p= 0.044), hemicellulose (r= 0.8; n= 10; p= 0.012) and condensed tannins (r= 0.7; n= 10; p= 0.032) all correlated positively with browsing time at early rainy season. The following regression equations were derived to model intake rate and some intake rate related variables: (1) intake rate= 0.433 + BSDM (0.081), R^2= 0.68, $p< 0.05$ and BSDM= bite size dry matter; (2) Bite rate= 0.503 –BSDM (0.147), R^2= 0.597, $p< 0.05$ and BSDM= bite size dry matter; (3) Bite size dry matter= 1.713 – BR (4.210), R^2= 0.597 ,$p< 0.05$ and BR= bite rate, and (4) Intake dry matter= 3.804 + BSDM (0.865), R^2= 0.607, $p< 0.05$ and BSDM= bite size dry matter.

Diet selection and foraging efficiency were both influenced more by shoot and leaf morphology than by spinescence. Plant chemistry on the other hand had diverse and inconsistent effect on diet selection and foraging efficiency trends.

The results therefore have important and far reaching implications for Nguni goat and goat production as a whole in the bush veld of Gauteng and related ecological zones.

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CHAPTER ONE

RESEARCH RATIONALE AND GENERAL BACKGROUND

1.1. Research rationale

Domestic herbivores especially goats on range and communal lands face constant fluctuation of quantity and quality of their diet resources (Ben Salem and Smith, 2008), owing to widely adopted extensive husbandry practices. This results from changes in precipitation, humidity, temperature, fertility and soil moisture content, posing a serious challenge to appreciable levels of animal maintenance and production throughout the year. Browse species are either evergreen or carry foliage long into the dry season than grasses (Lukhele and Van Ryssen, 2003), making them vital diet resources for herbivores.

Among domestic herbivores, goats exhibit the widest ecological distribution (Alexandre and Mandonnet, 2005), ranging from forest through shrub-lands to arid desert areas relative to sheep and cattle. The quantity and quality of diet is critical to animals in husbandry representing a huge portion of production cost in intensive systems, and can be considerably reduced in extensive systems, given a sound knowledge of herbivore-browse interaction. Extensive systems of husbandry are characterized by low input (Ben Salem and Smith, 2008), and a high possibility of low output depending on management. Goats have the unique ability to efficiently utilize browse, herbaceous biomass and crop residue (Dove, 2010), transforming them into animal products of high biological value (meat and milk).

A greater proportion of global goat population is reared extensively (Peacock and Sherman, 2009; Solaiman, 2010), on range and communal land by small holders who depend entirely on natural vegetation in the grass-tree ecosystems (Papachristou *et al*., 2003). In semi-arid, arid and sub-humid savannas of the tropics and sub-tropics during the dry season and periods of drought, goats depend almost entirely on browse (Dziba *et al*., 2003; Papachristou et al., 2005). During these lean seasons, goats lose condition, ovulation is delayed and in periods of acute scarcity, mortalities occur (Le Houèrou, 1980; Ben Salem and Smith, 2008).

There is, therefore, growing need to understand browse-browser interactions, considering the immense contribution of the former to the production of the later. Morand-Fehr (2005), acknowledged the huge influence of goat farmers over nutritional inputs as a result of management and explicitly, their ability to influence production quality.

This study seeks to understand, improve and enhance browse availability, utilization and year-round goat productivity; given that husbandry practices are mostly extensive.

1.2 General background

This section explores the distribution of savannahs and their primary agro-ecological use, socioeconomic relevance of goats to its inhabitants, generally adopted husbandry practices, morphological adaptations to forage, nutrient potential of browses, and associated chemical and physical deterrents.

1.2.1 Distribution of savannah ecosystem

Savannah biome comprises 12.5% of the earth's land area and is found in the drier tropical and subtropical regions (Grant and Scholes, 2006), 40% of South America, 60% of Australia and 65% of Africa (Higgins *et al*., 2007). The principal land use function of this ecological zone is livestock production and related agricultural activities (Higgins et al., 2007; Teague *et al*., 2009). The socio-economic importance of world savannas is immeasurably huge, with Africa and Asia accounting for 88% of global goat production (Alexandre and Mandonnet, 2005). It is a heterogeneous vegetation cover characterized by palatable and unpalatable grasses, forbs and a discontinuous tree/shrub over-storey (Grant and Scholes, 2006).

These savannas are being extensively modified by human activities, some of which include, extensive animal husbandry, crop cultivation, tree felling for fuel and timber, bush fires, road construction, recreation and environmental interactions (Marchant, 2007; Levick *et al*., 2009). Savannah ecosystems are facing enormous pressure from man in quest of arable land to grow food crops and construct habitat, pushing pastoral activities to the fringes and marginal communal lands. A wide-spread phenomenon in dwindling modified savannas is bush encroachment (Nyamukanza and Scogings, 2008). Grazing pressure degrades and reduces herbage growth while promoting over storey shrub and tree growth. Goats will serve as appropriate biological controllers of bush encroachment, given that, they browse on growing shrubs and trees.

1.2.2 Socioeconomic importance of goats

Goats are the first animals to be domesticated (Devendra and Solaiman, 2010), and have had a long standing relationship with man in religion, economy, nutrition and culture (Boyazoglu *et al*., 2005). Akingbade (2002) reported a wide acceptance of goats across religions and cultures in South Africa. Sheep and goats are referred to as small ruminants because of their size relative to those of cattle, camels, and buffalo. Small ruminant production is a vital socio-economic activity in the developing and resource poor economies of the world (Devendra and Solaiman, 2010).

Goats register an income contribution of 80% when compared to sheep and cattle with 40% and 45%, respectively, to the economies of countries with a low income base (Devendra, 2001; Mohrand-Fehr *et al*., 2005). They are generally valued for meat, milk, fibre and skins in developing countries (Devendra and Burns, 1983). Goats are relevant to small households because of their nutritional and financial contribution to the households and above all the minimal requirements for initial investment in the industry (Peacock, 2005). They yield small carcasses which can be marketed or consumed over a short period of time, and are highly productive (Lebbie, 2004). The financial contributions of goat rearing include insurance and security for short term liquidity, income generation to children and women who lack liquidity to embrace cattle rearing. Pastoral farmers with interest in cattle husbandry in Kenya have used goats as an initial stock to mobilize and deploy capital into the cattle industry (Peacock, 2005). Additionally goat droppings serve as a valuable source of manure to enhance nutrient cycling and improve soil fertility (Akingbade, 2002). In the traditional setting, they are slaughtered for cultural festivities and functions.

The goat industry is showing remarkable growth in Asia and Africa from 88% (Alexandre and Mandonnet, 2005) to 93% (FAOSTAT, 2007). South Africa has a total goat population of 6,3million, 40,437 of which are in Gauteng Province (National Dept of Agriculture, 2011). The province ranks as the lowest goat producer in the country and demands special attention to research and promotion of this vital economic activity.

In order to draw maximum economic and ecological benefit from goat rearing, their interaction with browse species and trees, need to be understood. Part of this interaction is the foraging behaviour of goats. Little is known about the foraging behaviour of goats in semi-arid savannas of South Africa.

1.2.3 Goat husbandry

The two most common systems of goat husbandry are tethering and free ranging (Devendra and Burns, 1983), though they fit into all production systems, ranging from pastoral and agro-pastoral to small holder crop/livestock systems (Lebbie, 2004). In the context of South Africa, it is dominantly extensive on range and communal lands by small holders and emerging farmers (Bester *et al*., 2009).

1.2.4 Adaptational and foraging traits of goats

Goats are endowed with the dual ability to graze and browse (Skarpe *et al.,* 2007) thus making use of less nutritious as well as rich quality grass and browse forages (Lebbie, 2004; Solaiman and Owens, 2010). They consume 65-70% of browse, 20-25% of grass, and 5% of forbs (Solaiman, 2010), with seasonal variation in diet composition based on forage make-up. Goats are selective, agile and inquisitive (Devendra and Solaiman, 2010), resilient and tough (Peacock and Sherman, 2010), and are more at ease with variety of herbaceous and browse plants at their disposal (Devendra and Burns, 1983). This dynamic foraging behaviour of goats equips them to counter any fluctuation in diet resources (Alexandre and Mandonnet, 2005) and effect adjustments to accommodate change thus successfully inhabiting marginal arid lands.

Goat resilience has enabled them to perform well in arid areas and marginal lands relative to other ruminants (Lebbie, 2004; Lachica and Aguilera, 2005). Leaves, twigs and barks of young trees are a natural part of the goat’s diet in the wild because of their ability to adopt a bipedal stance (Dove, 2010). Bipedal foraging posture is characterized by standing on two hind legs while foraging, thereby increasing vertical foraging range and enhancing browsing. Sanon *et al*. (2008) studied the foraging height of goats, sheep and cattle,) and reported a foraging height of 2.42 times height at whether for goats compared to 1.58 and 1.57 times whether height for sheep and cattle, respectively. The goat head morphological make-up is different from that of sheep and cattle and is closely related to its foraging behaviour.

Morphologically, goats have a narrow muzzle that helps them to nibble and strip foliage between thorns in addition to a pointed tongue, jaws, mobile thin lips and a deep mouth (Solaiman and Owens, 2010). This adaptations contrast with those of grazers such as sheep and cattle with relatively broad muzzles and cornified tongue tip (Dove, 2010), allowing them to gather and cut herbage. The animal is versatile, dynamic, and unconventional (Peacock and Sherman, 2010), adapting its foraging pattern to changing vegetation composition and architecture: in the dry seasons or winter: they will eat bushes and trees, whereas in the rainy season, they will eat more nutritious grasses and legume herbage, and less browses (Skarpe *et al*., 2007; Dove, 2010). Goats therefore, consume large volumes of browse but vary their diet when feed resources are abundant.

They have the ability to distinguish bitter, sweet, and salty tastes (Dove, 2010); and will forage on a wide variety of plants that will not appeal to other ruminants (Solaiman and Owens, 2010). There is empirical evidence that goats can tolerate various toxins and plant secondary compounds (Papachristou *et al*., 2003; Dove, 2010; McDonald *et al*., 2011), common in browses and forbs. Plant secondary compounds beyond tolerable threshold become toxic. They include alkaloids, terpenes and hydrolysable tannins. Goats exhibit a selective behaviour when offered cut and carry forages, choosing the best available.

The wide range of goat diet can be attributed to plant growth stages and a dynamic spatial vegetation composition which has strong implications on individual plant nutrient composition, chemical and physical deterrents.

1.2.5 Nutrient status of browse

Browse is a major diet resource of goats in most ecological zones of the world, especially in environments with prolonged dry periods (Papachristou *et al*., 2005). It is rich in protein, fermentable carbohydrates, minerals, and vitamins, and must therefore be available in sufficient quantity to support the vital processes of maintenance, growth and reproduction. Browse vegetative parts such as shoots, leaves, and the new growth of trees and shrubs constitute goat nutrient sources (Solaiman, 2010). They contain a lower cell wall fibre (NDF), 30-50% relative to grasses but are highly lignified (Devendra and Burns, 1983). Lignin is indigestible and its presence in most browses reduces fibre and nutrient fermentation/digestion (McDonald *et al*., 2011) relative to that of unlignified grasses.

Efficient utilization of browse is constrained by the prevalence of plant secondary metabolites (PSM) such as tannins, terpenes, alkaloids and lignin (Papanastasis et al., 2008; McDonald *et al*., 2011). These chemical substances are described as plant secondary compounds, because their role in plant primary metabolic activity is apparently unknown. They have various structures and concentrations both within and among the compound class and plant species (Rogosic *et al*., 2008). Structural variation and concentration of

PSM in browse species will impose different mechanisms of action and scope of effects on browsing ruminants. Nutrient content of browse species vary as much as their related PSM. Browse has a wide variation of intra and inter-specific nutrient contents (Kaitho, 1997). A complete browse based diet with an energy value 4.72MJ ME Kg^{-1} DM can support goat maintenance and production (Kaitho, 1997), affirming its potential as sole diet resource for goats in the absence of herbage. Some protein rich browses have the potential of being used as supplement in poor quality roughage diets and thus ameliorate roughage utility (Ben Salem and Smith, 2008). Leguminous livestock fodder has crude protein (CP) of 10% and more in the leaves, pods and fruits and of necessity in the dry season when plant nitrogen content is low (Kaitho, 1997).

Utilization of browse forages by herbivores is strongly influenced by physical traits such as possession of spines, thorns, and hairs (Papachristou *et al.*, 2003), and associated digestibility reducing chemical compounds such as condensed tannins. The diet composition is dependent on edible browse/herbage ratio, access to browse biomass, and season, but fundamentally goats are regarded as mixed feeders: they graze and browse concurrently. Browse exhibits intraspecific and interspecific variation in nutrient composition within a set landscape within seasons and between years (Solaiman, 2010), rendering it difficult to state any particular value per se.

1.2.6 Plant secondary metabolites (PSM) and toxins

Most browses contain high levels of anti-nutritional factors, some of which include phenolics, lignin, silica, terpene-based organic compounds, tannins and alkaloids (Dove, 2010). These anti-nutritional factors do not play any role in plant primary metabolism.

Plant secondary metabolites play various roles against herbivory by ungulates, insects and pathogens (Solaiman and Owens, 2010). Evaluation of the significance of plant secondary metabolites on foraging behaviour of goats is important considering the crucial role of browse in communal goat husbandry. Of interest to this study are the condensed tannins because of their wide occurrence in browses (Muir, 2011).

Condensed tannins are polyphenolic compounds of high molecular weight that either exert a positive or negative influence on animal performance depending on their concentration in forage (Dove, 2010). They reduce the nutritive value of plants by forming indigestible insoluble complexes with proteins and carbohydrate when present at concentration of 5%

or more dry matter and are excreted unutilized (Solaiman and Owen, 2010). At concentrations lower than 5% in the rumen, they bind loosely with proteins, increasing protein supply to the glandular abomasum and small intestine where enzymatic digestion assimilation takes place. Lower levels of condensed tannins thus improve and enhance protein utility or protein use efficiency. Reversibility of protein-tannin complex bond is dependent on low pH and therefore break down of condensed tannins/protein complex is enhanced in the abomasum, where it is made available for enzymatic digestion in the small intestine. Additionally, tannins have anthelmintic properties in fighting nematodes in small ruminants (Muir, 2011).

1.3 Aims

The primary aim of this research was to study plant physical and chemical properties that influence intake and intake rate of browses within and among seasons in the Bushveld of South Africa.

Whereas the specific aims were:

1. To determine intake of confined goats fed 6 morphologically representative browse species in combination in a diet selection experiment in the dry and rainy seasons,
2. To investigate the maximum achievable intake rate of 10 morphologically representative browse species fed to confined goats individually in a foraging efficiency experiment in the dry, early rainy and late rainy seasons,
3. To relate the physical properties of (1) spinescence, (2) phenology and (3) leaf and shoot morphology, and the chemical components of (1) protein, (2) fibre and (3) condensed tannins to diet selection and foraging efficiency respectively

CHAPTER TWO

LITERATURE REVIEW

The focus of this chapter is to review literature on the utilization of woody plant species in relation to their nutritional, anti-nutritional, and morphological traits by goats in forest, shrublands and savannah ecosystems of the tropics and sub-tropics. These traits are perceived to influence herbivory by mammalian herbivores. The objective of this study is two-fold: acquire greater insight of browse/browser interaction in order to optimize the use of woody species in savannahs as vital forage resources; conserve and enhance vegetation species composition; and generate the ability to predict potential goat production outcome in related agro-ecological zones. The knowledge gained will be very useful in sound range forage resource management and improved mammalian herbivore production. Emphasis will be laid on the following theories:

- Optimal foraging theory(subject function maximization);
- Complementation hypothesis; and
- Mixing and dilution of toxins principle.

These will give us a sound theoretical background to the research conducted at Roodeplaat animal improvement centre, South Africa on diet selection and foraging efficiency of Nguni goats in African savannas in the proceeding chapters. It will as well connect to potential foraging outcomes in similar and related savannah ecosystems.

2.1 Browse as forage

Browse is an essential diet resource for ruminants, providing forage year round (Assefa *et al.*, 2008).The deciduous species will also provide nourishment during critical periods when forage is in short supply (Papachristou *et al.*, 2005), in addition to advantages inherent in forage variety in diet. Goat husbandry increases with aridity (Landau *et al.*, 2000), given that 64% of sub-Saharan production takes place in semi arid and arid zones (Lebbie, 2004); highlighting the importance of browse as forage.

The increased use of browse is due to its ability to survive dry periods of the year when it makes up a significant portion of goat diet (Rogosic *et al.*, 2006; Ben Salem and Smith, 2008). During the dry season in the sahelian regions of Africa, goats spend 75% of their foraging time browsing with fruits, flowers, and pods of some trees constituting a greater portion of their diet (Ngwa *et al*., 2000).

Leguminous forage is rich in CP, minerals and vitamins supplying the much needed nutrients and enhancing the microbial degradation of poor quality herbaceous forages (Ngwa *et al*., 2000).Nutrient rich browses can therefore serve as supplements to enhance the degradation and digestion of poor quality forages (Kaitho, 1997). Browse will thus serves as an important alternative to herbage, especially when herbaceous biomass nutritive value has deteriorated markedly or is apparently absent (Codron *et al*., 2006). Otherwise, both herbaceous and browse forages are complementary, owing to the diversity of nutrient contents, fibre degradability and plant secondary compounds level. Browse nitrogen is partially bound to lignin and rendered unavailable for both ruminal microbial degradation and intestinal enzymatic breakdown (Fall-Toure and Michalet-Doreaux, 1995) mitigating protein richness of browse relative to herbaceous forage.

2.2 Goat-browse interaction

Focus will be on goats' response to browse and vegetation, and not the contrary. The use of woody plant species in savannas can be optimized given a comprehensive understanding of plant-herbivore interaction (Dziba, 2000). Browse is available in Roodeplaat throughout the year and of critical necessity during winter and dry summer when grass biomass is dry and of poor quality. Tree parts such as shoots, leaves, growing parts of shrubs, and forbs are goats preferred plant food components (Solaiman, 2010). In addition to the rich nutrient content, browses have various morphological and chemical anti-nutritional traits that deter herbivory and digestibility (Sanon *et al*., 2008).

The CP range of most browse species ranges between 12-30% whereas that of grasses is between 3-10% (Kaitho, 1997). Utilization of CP rich leguminous forage or browse fodder enhances degradation of poor quality grass herbage by herbivore (Kaitho, 1997). Browse species have diverse concentrations of PSM (Provenza *et al*., 2003; McAllister et al., 2005; Rogosic *et al*., 2008) and/or physical components (thorns and spines) that deter utility. Leaf biomass of browses has a rich cell content of protein, minerals, hydrolysable carbohydrates and vitamins, and a lower cell wall fibre content relative to that of grasses but is highly lignified (Gordon, 2002; Solaiman, 2010). Lignin is an indigestible polyphenolic structural component of browse (Codron *et al*., 2006; Papanastasis et al., 2008) attributing to it an anti-nutritional trait (Sanon *et al*.; 2008). Its close association with cellulose and hemicellulose of plant cell wall limits degradability (Gordon, 2003) of these components as well.

Major PSMs include tannins, terpenes, and alkaloids (Rogosic *et al*., 2008). They exert influences ranging from reduced browse nutrient value and animal productivity (Ben Salem *et al*., 2005), toxicity (Waghorn, 2008), abortion, and inefficient use of rangeland forage resources. Of significance to the study of foraging behaviour of goats are tannins and fibre (Sanon *et al*., 2008) owing to their wide occurrence in browses and impact on digestibility and nutrient availability.

2.3. Biochemical and physical anti-nutritional traits of browse

All plants have PSM (Provenza *et al*., 2003), which occur in variable concentrations.
Tannins are the most preponderant phytochemicals in browses of hot and warm climates (Waghorn, 2008) that affect acceptability, intake, and utilization, whereas spinescence which is characterized by the possession of thorns limits or reduces herbivory (Wilson and Kerley, 2003b).

2.3.1 Tannins

Tannins are some of the most recurrent and common antinutritional compounds in browse species (Assefa *et al*., 2008). They are a group of polyphenolic compounds of variable complexity (Rogosic et al., 2008; Waghorn, 2008) common in browse and legume forages. Tannins are divided into two general groups, hydrolysable tannins (gallotannins and ellagitannins) which are parent polyols esterified with gallic or hexadroxydiphenic acid, and condensed tannins (proanthocyanidins) which are linear or branched polymers of flavanoid units (Makkar, 2003) with inter-flavanoid carbon bonds.

2.3.2 Hydrolysable tannins

Hydrolysable tannins (HT) are made of gallic acid or ellagallic acid which are the building blocks and a hexose core onto which they are esterified (Haslam, 1989). Inter-gallic bonding can take place resulting to more complex polymeric forms. They are potentially toxic and degraded in the rumen (Waghorn, 2008), readily undergoing acid microbial-hydrolysis in the colon to sugar moieties and simple phenolic compounds (Mueller-Harvey, 2001).

Hydrolysis and degradation of HT in the rumen results in absorption and concentration of phenols in blood (Assefa *et al*., 2008), causing toxicity. Toxicity occurs, when the accumulation of phenols in the blood stream attains concentration level that the liver cannot detoxify (Waghorn, 2008). Thus, the effect of HT on protein and carbohydrates is not as profound nor is it significant as that of condensed tannins which are both deprivative and inhibitory to nutrient availability and metabolism.

2.3.3 Condensed tannins

Condensed tannins (CT) are flavanoid polymers of high molecular weight (500-3000) common in many browse forage species consumed by goats (Waghorn, 2008; Muir, 2011) and seldom in grasses (Waghorn, 2008). They exert both beneficial and deleterious effects to herbivore nutrition. Beneficial effects by increasing protein use efficiency (Nsahlai *et al*., 1998; Rogosic *et al*., 2008; Muir, 2011) and deleterious effects by reducing browse acceptability due to astringent and bitter sensation (Ben Salem *et al*., 2005),as well as the ability to bind and precipitate protein and other nutrients.

Forage plants with moderate levels of condensed tannins to goats have acceptability that is independent of their presence (Dove, 2010). Rumen pH is near neutral (pH 5.0-6.7) retaining the condensed tannin-protein bond for subsequent disintegration and digestion distally in the acidic abomasum and small intestine (McAllister *et al*., 2005). Complexing of protein by CT prevents formation of soluble protein foams which trap ammonia and provoke bloat in ruminants (McDonald *et al*., 2011). Bloat prevention by CT creates more space for forage intake.

Condensed tannins occur in higher concentrations in most evergreen forage browse than the deciduous ones (Muir, 2011; Hattas *et al*., 2011). Browse from dry infertile soils has a higher incidence of condensed tannins relative to that of the humid regions (Katjiua and Ward, 2006). Condensed tannin concentration increase in some browses from wet to dry season (Assefa *et al*., 2008). Goats and other browsing ungulates in semi arid and arid ecological zones must therefore develop some special mechanisms to tolerate/degrade tannins.

The presence of CT in the rumen environment elicits a reduction in proteolytic and fibrolytic microflora, slowing forage degradation (Muir, 2011). Protein binding by CT deprives rumen microflora from this essential nutrient that is required for flora/fauna protein synthesis and multiplication. Condensed tannins exert similar binding effect on carbohydrate deterring fermentation and decreasing volatile fatty acid and ammonia production (Ben Salem *et al.*, 2005). They bind dietary iron, copper, sulphur, and phosphorus decreasing mineral availability from forages thus negating ruminant nutrient metabolism (Muir, 2011). Condensed tannins in high concentration depress animal production and in severe cases result to death (Rogosic *et al.*, 2008)

The most critical deleterious effect of CT is the irreversible complexing and precipitation of protein by heavy molecules which are unattended to and subsequently excreted (Solaiman and Owens, 2010).

2.3.3.1 Adaptation of goats to condensed tannins

Goats tolerate and consume more tannin-rich browses than sheep under the same conditions (Dove, 2010). They consume high tannin diets without ill effects and excrete less in faeces, suggesting that goats have some unidentified mechanism of degrading and deactivating them. Previous studies reporting the presence of tannin binding salivary proteins (TBSP) have failed to prove (Dove, 2010), but loss of CT between ingestion and excretion is persistent. It emerged from the study of incremental dietary supplementation of Boar goat rations with condensed tannins (Mbatha, 2001), that they lacked the means to detoxify them. However, there was a decrease in intake with increasing CT. Given the wide occurrence of tannins in browses and forbs, mammalian herbivores only retain them below a certain threshold (Jansen et al., 2007).

Goats crave for variety thereby further raising the possibility of mixing and reducing the overall CT concentration in diet consumed to within some ineffective threshold (Dove, 2010). Provenza *et al.* (2003) reported the consumption of a variety of forages by herbivores as means of acquiring sufficient nutrients (complementary effect) and variable toxins, whose effect may not be additive. Increase in diversity of browse species and associated phytochemicals increases intake and a reduction in variety causes the opposite effect (Rogosic *et al.*, 2008) in herbivore diet. There is the likely hood that toxin interaction from different forage sources may neutralize some of the potential toxic outcomes. There is evidence that herbivores acquire the ability to forage, but apparently do not acquire the ability to select a variety given options (Provenza *et al*., 2003). The intake of three tannin rich shrubs fed to goats individually was low, but when fed collectively, it more than doubled (Rogosic *et al*., 2006). Garry Waghorn (2008) recommended the dilution of tannin rich forages with low tanniferous ones but insisted it can only yield beneficial results with supplemental proteins.

2.3.4 Fibre

Fibrousness of browse forage imposes physical toughness and reduces the rate of foliar biomass harvesting by herbivores. Fibre refers to structural carbohydrates as opposed to readily fermentable non-structural carbohydrates. They exert a strong influence on ruminal microbial fermentation of browse depending on the different proportions of fibre components (Papachristou *et al*., 2005), rumen motility and health.

The determination of forage structural carbohydrates is by separating soluble cell contents by solubilizing away materials in neutral detergent solution yielding neutral detergent fibre (NDF) (Van Soest *et al*., 1991). Neutral detergent fibre represents absolutely all fibre present in plant cell wall and comprises of cellulose, hemicelluloses and lignin. When solubilization is done in an acid detergent medium, the residue is acid detergent fibre (ADF); which is NDF less hemicellulose (Solaiman and Owens, 2010). Neutral detergent fibre is, therefore, relatively more fermentable than ADF. Acid detergent fibre content of any diet is negatively related to energy digestibility of that feed (Codron *et al*., 2006) and further solubilization in acid medium yields acid detergent lignin.

Lignin is widely reported to be indigestible (Codron *et al*., 2006; Waghorn, 2008) as opposed to cellulose which is slowly fermented by rumen cellulolytic microflora. Association of cellulose with lignin which is polyphenolic (Duncan *et al*., 1998) and indigestible (Papachristou *et al*., 2005) reduces browse fermentation. Fermentation of forage browse NDF depends on the proportion of its component hemicellulose, cellulose, and lignin (Solaiman and Owens, 2010). There is therefore a gradation of indigestibility from NDF through ADF to ADL. Relative browse utility is reported to be dependent on the protein/fibre ratio (Ben Salem and Smith, 2008), with high protein to fibre ratios showing higher degradability.

2.3.5 Browse crude protein

The socioeconomic and nutritional importance of goats in the arid and semi arid zones highlights the importance of protein as an essential nutrient for survival and productivity. Proteins are the sources of amino acids for animal structural, enzyme and hormone make-up. They are regarded as the primary determinant of quality of browse and to a larger extent diet quality (Mokoboki *et al*., 2005). Inadequate CP reduces dry matter forage intake and utilization (Ben Salem and Smith, 2008). Herbivore dietary protein is recommended to be high in fibrous forages to counter the negative effects of CT and enhance degradability and digestion (Garry Waghorn, 2008).

2.3.6 Spinescence

Spinescence is the presence of spines, thorns, or prickles (Schindler *et al*., 2005) on some shrub and tree forages as deterrents to herbivory by ungulates (Wilson and Kerley, 2003b). They serve as morphological defence as opposed to PSM, which are phytochemical alternatives. Spinescence does not prohibit but mitigates herbivory (Wilson and Kerley, 2003a) by restricting access to leaf biomass and reducing mammalian herbivore nutrient intake. This limits physical damage to shrubs and trees enhancing their survival. *Sitka spruce* develops increased needle-span as a deterrent to browsing by Red deer (Duncan *et al*., 1998).The possession of thorns, spines, and prickles is widely considered to be an evolutionary response to browsing by ungulates. The semi-arid thicket of Gauteng is highly spinescent (Personal observation) and therefore harvesting of most browse foliages is deterred, reducing instantaneous intake rate. Ungulate foraging behaviour is influenced by the presence of mechanical and chemical defence (Papachristou *et al*., 2003; Wilson and Kerley, 2003b).

2.4 Foraging behaviour of goats

There is ample empirical evidence attesting to goats' highly selective nature of their diet (Devendra and Burns, 1983; McDonald *et al*., 2011). Goats consume and digest a wider array of browse species, trees, herbaceous plants, than either sheep or cattle (Solaiman, 2010).The resulting diet differs in botanical composition from the average of the available feed (Dove, 2010). They have mobile thin lips and accurate tongue movements that enhance gleaning of foliar herbage between thorns.

This foraging behaviour equips goats to survive and thrive in harsh environments than its other counterparts (Alexandre and Mandonnet, 2005). It can be postulated that the wide scope of goats feed resources enable them to mobilize nutrients which are variable in quantity and quality resulting in a diet capable of meeting their requirements for maintenance, growth and reproduction (Provenza *et al*., 2003). On the other hand, diversity has the added advantage of mitigating the effect of toxins and plant secondary compounds which are present in high concentrations in some forage species. Diversity of nutrients and chemical deterrents is as much reflected at intra-specific level, resulting to goat preference of some browse forage parts than others (Papachristou *et al*., 2003).

Mammalian herbivores use mechanical and chemical cues to decide which plant species or plant parts to choose or avoid on range (Papachristou *et al*., 2003),on account of their nutrient and PSM content. Remarkably, there is change in perpetuity at the level of the animal, environment, forage nutrient content, kind and level of toxins in different plant parts, physical defence and differences in canopy shape (Provenza and Launchbaugh, 1999). This result to some browse species being selected sometime and rejected during the other. However, goats are inquisitive, independent, adventurous, hard to confine, intelligent and unconventional (Peacock and Sherman, 2010), rendering them the most adapted domestic herbivores in harsh climatic ecosystems and marginal lands. They can keep track of change and are at brace with chemical and morphological changes. The question that arises is how goats circumvent or counter toxic and inhibitory plant secondary compounds to meet their nutrient requirements. Insight into how goats interact with their diet resources, toxins, and PSM can be gained by examining their foraging behaviour vis-à-vis optimum foraging theory and diet selection.

2.4.1 Optimal foraging theory and diet selection

Optimal foraging theory attempts to predict the behaviour of animals while they are foraging (Pyke, 1984). It states that animals forage in such a way as will maximize their expected fitness, subject to any functional constraints (Stephen and Krebs, 1986). The implication is that, animals that are ill-equipped to forage efficiently will have little chance of competition and survival (Ydenberg et al., 2007), therefore promoting natural selection. Though some intra-specific variations to foraging behaviour may exist, they are assumed to be insignificant allowing for more uniform specific population foraging behaviour. Fundamentally, the optimal foraging theory considers browse and herbage resources as vehicles or bearers of nutrients and the nutrients as currency or animal reward (Simpson *et al.*, 2004), given the role of the later to metabolic activities.

Optimal foraging theory possesses the following qualities: an objective goal or function, which may be energy or some nutrient; a set of choice variables under the control of the animal and constraints on the available set of choices that may be based on genetic, physiological, sensory, morphological make-up, and chemical and physical interaction. Young animals manifest innate preferences and aversions for some foods whose nutrient, chemical and physical status changes with seasons reversing acceptability or rejection (Forbes, 2007).

Optimality in foraging mammalian herbivores entails selecting from a wide variety of browse species and herbage that vary in nutrient content and kind, as well as digestibility mitigating or poisonous PSM. Plant secondary metabolites are plant chemical components which do not have any major contribution to primary metabolic activities. On range, there are encounters with complementary foods, in which case, herbivores select the mixture that lead to an intake level corresponding to the summit of fitness (Simpson *et al.*, 2004). Optimal foraging theory, therefore, forms the basis for diet selection in mammalian herbivores (Dziba, 2000).

2.4.1.1 Diet selection

In-depth knowledge of why browsing ruminants select some plants and avoid others is crucial in the management of rangelands and animal productivity. Vegetation composition and spatial distribution of browse is heterogeneous, comprising of browse species at different stages of growth, variable nutrient and PSM profiles (Hattas *et al.*, 2011), and various morphological and phenological traits (Newman, 2007). This promotes herbivore diet selection at different spatial scales; from patch through herbage and browse species, to different parts of the same plant in view of meeting its nutritional requirements.

Goats have been noted for seeking variety in their ingesta for various reasons, the most important of which is to maintain the rumen environment within certain physiological and microbiological range (Morand-Fehr, 2005) in order to enhance efficient functioning. Provenza *et al.* (2003) suggested that variety presents options for animals that are morphologically and physiologically similar to eat different combinations of food that will yield the same productive outcome. Mammalian herbivores use both morphological and chemical cues to either choose or avoid plant species (Papachristou *et al*., 2003).

Vegetation composition and distribution influences diet selection. Diet preference is on the other hand, diet choice that is free of environmental constraints (Newman, 2007). Diet preference therefore refers to choice at specific and intra-specific level. Single plant foods lack nutrient variety and quantity to support growing animals to maturity (Newman, 2007). Nutrient imbalances in plants promote selection in order to complement and meet goat nutritional needs. Phylogenetically related species have different phenolic profiles (Hattas *et al*., 2011) and obviously nutrients. The implication is that herbivores still select given a continuous field of phylogenetically related species. The choice of diet, pace of foraging, and time spent eating depend on the state of the animal, available forage, plant architecture and distribution.

2.4.2 Functional response

Mammalian herbivore foraging behaviour can be better explained by examining how their nutritional goals and constraints function or operate. The foraging process determines the nutrient intake of herbivores on range, location and intensity on vegetation (Baumont *et al*., 2004). Interaction between mammalian herbivore foraging traits and those of their diet resources is referred to as functional response (Searle and Shipley, 2008) and elicits foraging behaviour. The morphological and physiological characteristics of herbivores and their associated diet resources give rise to specific foraging behaviour. Plant biomass/goat interaction involves various components, some of which relate to the goats, the available plant resources, and the extent to which the system of livestock management permit the processes of diet selection and intake rate to proceed (Newman, 2007). For example, goats are morphologically apt to select diets because of their narrow muzzle, long tongue, and flexible muscular lips (Searle and Shipley, 2008), whereas spinescent browse species regulate herbivory by limiting foliar biomass prehension and stripping (Schindler *et al*., 2003; Sebata and Ndlovu, 2010) and finally intensive browsing or grazing will result to smaller bite sizes and reduced intake (Baumont *et al*., 2004), as a result of depleting foliar biomass. Herbivore/plant interaction can be described as the relationship between resource abundance and the rate of intake (Gordon, 2003). Components of herbivore functional response include biomass harvesting time, bite size, chewing investment and chewing rates, and the rate of encounter with bites of vegetation. These components will be briefly explored.

2.4.2.1 Bite size

A thorough understanding of the foraging behaviour of mammalian herbivores, and the potential production out-come demands a spatial description of the distribution of bites in the environment (Gordon, 2003). Bite size, is the quantity of browse/herbal biomass dry matter cropped per bite. Bite size influences intake (Searle and Shipley, 2008) and has a huge implication on nutritive outcome or functional response. The bite size is highly variable and dependent on plant architecture, foliar biomass, spinescence and, the size and morphology of its mouth as well as the vegetation species composition.

2.4.2.2 Intake rate

Goat intake rate is the product of encounter rate, handling time and bite mass (Newman, 2007). Browse species have different architecture and morphological defence allowing goats to harvest varying number and size of bites thus leading to highly variable intake rates (Sebata and Ndlovu, 2010). Intake rate can be divided into two phases: short term intake rate indexed as a basis of diet selection and long term intake rate as a consequence of diet selection (Newman, 2007).

2.4.2.3 Biomass harvesting time

The prehension and severing bites of vegetation is dependent on the fibre composition, the distribution of plant parts, and the structural defence of plants (Searle and Shipley, 2008). Grasses have more cellulose and various proportion of silica relative to browses which have less cell wall cellulose and more lignin especially in the woody components (Searle and Shipley, 2008). Cellulose, lignin, and silica all impart toughness on forage biomass requiring herbivores to exert greater force and spend more time to sever a bite (Shipley and Yanish, 2001). The daily intake is the product of bite rate and foraging time.

2.4.2.4 Rate of encounter with vegetation

The spatial distribution of browses on range allows for movement to encounter other browse species, prehend and sever bites, demanding time in the process. Morphological browse defence such as the development and possession of thorns and spines has been strongly implicated in slowing biomass harvesting (Wilson and Kerley, 2003a; and Illius *et* *al*., 2002), and in the process increasing foraging time and encounter rate. Animal handle thorny or spiny plants carefully and slowly in their mouths to avoid pain and injury.

Research is therefore required to determine the influence of browse morphological traits such as spinescence relative to non-spinescence, deciduousness as opposed to evergreen, long shoots as opposed to short shoots, and fine leaves as opposed to broad leaves on diet selection and foraging efficiency of Nguni goats. The effect of browse chemical components such as crude protein, NDF, ADF, ADL and PSM such as condensed tannins on diet selection and foraging efficiency of Nguni goats are as well, essential components that demand research. This will enable prediction of vegetation forage potential and productivity of Nguni goats in this agro-ecological zone within and between seasons. The overall study will enable managerial inputs to enhance goat production as well as vegetation browse species composition.

2.5 Methodology

2.5.1 Study site

The study was conducted in Roodeplaat, South Africa. Roodeplaat is located 30km North East of Pretoria (Panagos and Van Staden, 1995). The area is situated between south latitudes 25° 20´-25° 40´, and between east longitudes 28° 17´-28°25´. The average annual rainfall of this area is 646mm. The temperature attains a maximum range in January 29°C-20°C and a minimum range in July 16°C-2°C. The area is described as Bushveld savannah (Mucina and Rutherford, 2006).

2.5.2 Study plants

The study was based on the following browse plants, all of which are representative of the most abundant species in the study site and have various combinations of shoot morphology, leaf size, leaf life span and physical defence: (1) *Acacia nilotica* carries bipinnate leaves with fine tiny leaflets on both old and new shoots. It is deciduous and armed with long straight thorns; (2) *Acacia caffra* has drooping pinnate leaves and tiny leaflets on both new and old shoots. It is deciduous and carries short hooked thorns; (3) *Acacia robusta* has bipinnate leaves with leaflets that are relatively bigger than either of *Acacia nilotica* or *Acacia caffra*. It is deciduous and has long and some short straight thorns; (4) *Combretum apiculatum* grows new broad leaves mainly on new shoots, is deciduous and thornless; (5) *Dichrostachys cinerea* has bi-pinnate leaves, which are borne on new and old shoots. The leaves are tiny and shade at the approach of winter or drought. *Dichrostachys cinerea* carries long straight thorns of relatively low density (6) *Ehretia regida* grows new leaves on new and older parts of the shoots. The tree is deciduous, has broad leaves, and is thornless; (7) *Euclea crispa* has broad tough evergreen leaves which are borne on new shoots and parts of the old twigs close to the new growth. It is thornless. ; (8)*Gymnosporia buxifolia* carries broad leaves on new and old shoots, it is evergreen and has long straight thorns;(9)*Rhus lancea* is evergreen, has broad leaves and grows new leaves on mainly new shoots. It is thornless. ; And (10) *Ziziphus mucronata* has broad leaves which are borne mainly on new shoots and is deciduous. It carries both hooked and straight thorns at close interval rendering prehensibility by goats difficult.

2.5.3 Study goats

Nguni goats are used as model browsers in this research. They are indigenous goats of small-framed bodies, with a short-hair coat. Nguni goats are one of the dominant indigenous breeds in South Africa (Rumosa Gwaze *et al*., 2009), very hardy prolific, and adapted to all agro-ecological zones. They compete with other ungulates for food on range and are useful for controlling bush encroachment (Devendra and Burns, 1983). Foraging on tops of trees and shrubs by domestic and wild herbivores increases the nutrient content and palatability of some shrubs stimulating below canopy growth of grasses and forbs (Schindler *et al*., 2003). The coat colours range from brown, black and white to variegated combination of the three.

2.6 General hypothesis

It is expected that Nguni goat productivity will be improved upon, given, a better understanding of their foraging behaviour in relation to browses in diet selection and foraging efficiency respectively within and among seasons**.**

CHAPTER THREE

DIET SELECTION OF NGUNI GOATS IN AN ARID SUB-TROPICAL SAVANNAH, SOUTH AFRICA

Abstract

Primarily, the seasonal and plant species trends of diet selection by Nguni goats indexed by intake and secondly the potential implications of plant chemical components, phenological and morphological traits on diet selection were investigated in cafeteria style. Six browse plants: *Acacia nilotica*, *Acacia robusta, Dichrostachy cinerae*, *Erhetia rigida, Rhus lancea* and *Ziziphus mucronata* were used in the dry and rainy seasons. Diet selection was affected by a significant interaction between species and seasons ($p < 0.05$). Intake was not significantly higher in the rainy season relative to the dry season, 3.94 ± 0.42^a gDM compared to 3.57 ± 0.42^a gDM. *Rhus lancea* and *A. robusta* were the most selected species in both seasons, while *Z. mucronata* was more selected in the dry season than *E. crispa* but at early rainy season it was the opposite. *Dichrostachys cinerea* and *A. nilotica* were least selected in both seasons, but with improved intake of *D. cinerea* in the rainy season, whereas that of *A. nilotica* declined significantly. Intake of long shoot plant species, which were concomitantly broad leafed was significantly higher than that of species with short shoots (t= -3.99; df= 65.80; p= 0.0002). Similarly, intake of deciduous species was significantly lower than that of evergreen counterparts (t= 5.22; df= 34.02; p< 0.0001). Intake was higher for spineless than spinescent species (t= 5.22; df= 34.02; p< 0.0001). In the rainy season, cellulose positively correlated with intake (r= 0.85; n= 6; p= 0.031), bite number (r= 0.98; n= 6; p= 0.001) and browsing time (r= 0.93; n= 6; p= 0.007). In the dry season, there was no correlation between plant chemical components and intake, except cellulose that correlated with intake-variable of bite size (r= 0.87; n= 6; p= 0.023). The following regression equation was derived from correlation to model intake: Intake= 0.68 + BS (3.07), (r^2= 0.71; p< 0.05); where BS= bite size. Diet selection tended to be driven more by shoot and leaf morphology than by either of spinescence or plant chemistry.

3.1 Introduction

Browse forage in African savannas is an essential diet resource for mammalian herbivores (Ben Salem and Smith, 2008). It is rich in protein and other nutrients (Assefa *et al*., 2008; Estell, 2010). Given that browses are available throughout the year, especially in arid environments where there is seldom herbage, they constitute an important source of essential forage resources. Browse is widely reported to be heavily defended against mammalian herbivory (Kaitho, 1997; Rogosic *et al*., 2008; Estell, 2010). Range forage composition is heterogeneous and diverse in nutrients, secondary metabolites, morphological traits and flavours (Skarpe *et al*., 2007; Wang *et al*., 2011). Diversity is further accentuated by differences in nutrients and PSM content of phylogenetically related browse species (Youngentob *et al*., 2010) and regular changes in climatic conditions that place plant chemical composition and plant canopy in a state of flux.

The interaction between abiotic and biotic components of vertebrate herbivore ecosystem influences diet selection trends and animal distribution on range (Alexandre and Mandonnet, 2005). Mammalian herbivores are in essence inextricably linked to herbaceous and browse forage resources which serve as their primary sources of essential nutrients and energy to support life processes (Papachristou e*t al*., 2005; Iason and Villalba, 2006). For them to thrive, they must respond appropriately to their constantly changing nutritional needs in place and time. It is imperative to understand why herbivores select some food items in preference to others, and the underlying mechanisms influencing choice. This knowledge is fundamental to developing predictive models for effective rangeland management (Ungar, 1996) and animal productivity.

For efficient production, mammalian herbivores must of necessity select and constitute a diet adequate in proteins, energy and nutrients (Skarpe *et al*., 2007) and minimal in PSMs (Provenza *et al*., 2003). Some PSMs serve as defence against pathogen invasion and others as deterrents to herbivory (Solaiman, 2010). Diet selection indexed by intake is therefore critical to ruminant productivity on range by determining how much protein, energy and other nutrients are derived from forage to support further activity and production. Tannins, fibre, and nutrients are the main components of forage leaf chemistry that affect diet selection by herbivores (Cooper *et al*., 1988), but there are other PSMs that exert various effects on herbivory (Estell, 2010). Plant secondary metabolites occur in all browse species and forbs (Foley and Moore, 2005) but may not be very significant in some to exert any influence (Rogosic *et al*., 2008) on the nutritional and physiological status of herbivores (Solaiman, 2010).

Common PSMs in forages include tannins, alkaloids, saponins, terpenes and lignin, of which, Condensed tannins are the most prevalent. They affect forage value and digestibility while alkaloids impart bitter taste (Assefa *et al*., 2008). They bind to proteins, carbohydrates and minerals reducing forage value and digestibility (Ben Salem et al., 2005; Dove, 2010; Estell, 2010). While on the other hand, minimal concentrations of condensed tannins improve protein use efficiency by tentatively binding and increasing supply to the glandular abomasum and small intestine for enzymatic digestion and absorption (McAllister *et al*., 2005; Solaiman and Owens, 2010). Condensed tannins in browses of hot and arid environments are apparently always detrimental to ruminants because of their high concentration and chemical structure relative to those of temperate regions (Waghorn, 2008).

Plant secondary metabolites occur widely in forages alongside nutrients (Rogosic *et al*., 2008). However, mammalian herbivores have to maximize nutrient and energy intake while concurrently regulating the former. This is a special attribute of adapted mixed herbivores such as goats. Goats that are adapted to consuming tanniferous black brush develop the capacity to degrade and excrete uronic acid, which is the end product of CT detoxification (Estell, 2010) than naive ones (Provenza and Launchbaugh, 1999), therefore exhibiting a developed and enhanced ability to detoxify PSMs. Condensed tannin concentration and their chemical structure influence astringency, digestion, nutritive value and nematicidal effects (Foley and More, 2005; Waghorn, 2008). Browsers may consume a high level of some CTs whose impact on herbivore nutrition and digestion is minimal relative to others. Lignin as well, is a polyphenolic plant secondary metabolite of forages whose presence in plant cell wall prevents fibre digestion (Solaiman and Owens, 2010).

There is apparently no knowledge of diet selection of goats in the semi-arid Bushveld of Gauteng, South Africa. Irrespective of the rich seasonal herbage and perennial browse forages, the province has the lowest number of goats (National Department of Agriculture, 2011). If ruminant herbivore production has to be efficient and optimal, diet selection and preference must of prime necessity be investigated to enhance forage availability, utility, and management of range land resources. Results obtained will enable us to predict and model potential production outcomes in the province and related agro-ecological zones world wide.

The broad objective of this study was to investigate the plant species patterns of diet selection within and between the dry and rainy seasons, and the influence of chemical components, secondary metabolites, phenology and morphology.

The specific objectives included:

- The plant species trends of diet selection by Nguni goats indexed by intake and the role of plant structural components such as spines/thorns and shoot morphology;
- The role of plant chemical components such as proteins, fibre and tannins in browse intake; and
- How these effects are relate to seasons.

It is hypothesised that:

- Different plant species by being deciduous or evergreen will have different intake within and amongst seasons (Papachristou *et al*., 2003);
- Spinescence will negatively affect intake (Papachristou *et al*., 2003; Wilson and Kerley, 2003a) but ‘spinelessness will positively affect intake (Dziba, 2000; Papachristou *et al*., 2003); additionally, species with new leaves on long shoots will be selected and foraged upon more than those with new growth on old short shoots. (Scogings *et al*., 2004), whereas fine leafed species will negatively affect instantaneous intake as opposed to broad leafed species (Sebata and Ndlovu, 2010).
- Tannins and fibre will negatively affect intake (Papachristou et al., 2003); but protein will positively affect intake (Dziba *et al*., 2003; Provenza *et al*., 2003).

3.2 Materials and methods

This study investigated the factors affecting diet selection of Nguni goats fed six common browses in the Bushveld of semiarid subtropical Gauteng. They included, *Acacia nilotica, Acacia robusta, Dichrostachys cinerea, Euclea crispa, Rhus lancea,* and *Ziziphus mucronata,* all fed collectively in cafeteria style under shade during two seasons: dry season in July and rainy season in December. It is perceived that plant nutrients, secondary metabolites, phenological and morphological traits will influence diet selection.

3.2.1 Study site and vegetation

The study was conducted in Roodeplaat, South Africa. Roodeplaat is located 30km North East of Pretoria. The area is situated between south latitudes 25° 20´-25° 40´, and between east longitudes 28° 17´-28°25´ (Panagos and Van Staden, 1995). The average annual rainfall of this area is 646mm. The temperature attains a maximum range in January 29°C-20°C and a minimum range in July 16°C-2°C. The vegetation is described as Bushveld savannah (Mucina and Rutherford, 2006).

3.2.2 Study plants

The study was based on plants that are representative of the most abundant species in the study site and have various combinations of shoot morphology, leaf size, leaf life span and physical defence. These plants included: (1) *Acacia nilotica* which is characterized by bipinnate leaves with fine tiny leaflets on both old and new shoots, and is also deciduous and armed with long straight thorns. (2) *Acacia robusta* has bipinnate leaves with leaflets which are relatively bigger than those of *Acacia nilotica.* It is also deciduous with long and some short straight thorns. (3) *Dichrostachys cinerea* has bi-pinnate leaves which are borne on new and old shoots. The leaves are tiny and shade at the approach of winter or drought. *Dichrostachys cinerea* carries long straight thorns of relatively low density. (4) *Euclea crispa* is thornless with broad tough evergreen leaves. They are mostly borne on new shoots and parts of the old twigs close to the new growth. (5) *Rhus lancea* is an evergreen browse plant which has broad leaves and grows new leaves on mainly new shoots. It is thornless; and (6) *Ziziphus mucronata* has broad leaves which are borne mainly on new shoots and is deciduous. It carries both hooked and straight thorns at close interval rendering prehensibility by goats difficult.

3.2.3 Study goats

Six Nguni goats were used as model browsers in this research. They are indigenous goats of small-framed bodies, with a short-hair coat. Nguni goats are one of the dominant indigenous breeds in South Africa (Rumosa Gwaze *et al*., 2008), hardy prolific, and potentially adapted to all agro-ecological zones (Nyamukanza and Scogings, 2008). They have coat colours ranging from brown, black and white to a variegated combination of the three.

They compete with other ungulates for food on range and are useful for controlling bush encroachment (Devendra and Burns, 1983). Foraging on tops of trees and shrubs by domestic and wild herbivores deters growth lengthwise but improves nutrient content and palatability of some shrubs, given the new sprouts. New growth in browses is associated with increase nutrient content and intake by goats (Papachristou *et al*., 2003) Browsing thus stimulates below canopy growth of grasses and forbs (Schindler et al., 2003).

3.2.4 Conditioning and adaptation of goats

Prior to the trial during the rainy season in December and dry season in July respectively, the goats were allotted a maximum period of two weeks of adaptation to the experimental procedure. First, they were placed individually in pens 3×1.5m under shelter, which differed from collective confinement that was common practice on the farm. The shelter was open to one side, with three solid walls raised to a corrugated roof, inclined lengthwise to the open side to protect the animals from wind and rain. Buckets were provided for pellets, hay and water. Those for pellets and hay were fixed and held in place with wire rings to prevent goats from throwing out content in the course of eating.

Goats were maintained on lamb/ewe ration from Epol, a division of Rainbow Farms (Pty) Ltd, South Africa, and 100g daily allowance of lucerne hay. The lamb/ewe pelleted ration contained 13% crude protein, 12% moisture, 14% fibre, 2.5% minimum fat, 1.5% calcium, 0.2% Phosporus, urea 1%, other NPN (non protein nitrogen) sources 0.5% and vitamin A 10000 IU/IE/kg. The goats were subsequently served freshly cut branches of the different browses as part of the experimental diet. The conditioning was done in two phases; first for foraging efficiency trial because it preceded diet selection.

Goats were run through the experimental procedure of diet selection. Six 2 year old ewes of mean weight 22.5±2.14kg were selected randomly from amongst the most acquainted and compliant of the initial 14. Base line dry matter intake data were collected and calculated to ensure that goats received sufficient feed to meet their daily maintenance requirements.

Goats were served 100g lucerne hay regularly and 500g of pellets that was incrementally adjusted by 10% in the event of total consumption or reduced by the same quantity given that, pelleted diet was not consumed in its entirety.

3.2.5 Diet selection experiment

Diet selection experiment was conducted over six days in the dry and rainy seasons. Thirty nine freshly cut branches of each of the six browse species with mean length 53.5cm (SEM: 0.55cm) were cut in the morning of every experimental day. Cut ends of branches were placed into buckets containing fresh water and kept under shade to minimize transpiration loss. Thirty six branches of each species were used for the experiment and three reserved for chemical sampling. The trial was conducted with six goats per day. Six distinct randomised arrangements of the six browse species per treatment for each goat per experimental day were served.

The experiment was run between 08.00 and 13.00h on each of the six experimental days. Individual branches of all six species were offered clamped in holes on a foraging board (Dziba *et al.*, 2000) and spaced to minimize searching time as well as overlapping. To control for ordering effects, branches of each browse species were placed equally in the first, second, and third order across individual goats during the experiment. A 6×6 latin Square design was applied to obtain six unique arrangements as treatments per goat. The arrangement on the board was such that, no branch of a given species appeared in the same position more than once for each goat nor did it occur next to the same species more than twice in the entire trial. This design ensured that there was an equal opportunity for goats to select from all available options with very little movement.

Each branch was weighed before serving and after foraging. From the conditioning phase, a maximum of three minutes was allotted to each goat to forage granted that no branch was depleted and the goat did not stop foraging either. Bite count per species were taken using a tally counter. Fresh weights of branches were subsequently converted to dry matter (DM) to determine intake dry matter (gDM) as an index of diet selection (Haschick and Kerley, 1997). Video footages of the different bouts were taken to subsequently determine browsing time for the respective branches in the entire experiment. Bite rate and intake rate of the different branches by goats were calculated from bite number, bite size, intake and browsing time.

Prior to video recording, information relating to goat number, feeding bout and date were displayed to mark the beginning or transition from one bout to another. Each goat was released periodically to the foraging area and video recording commenced from point of entry (weighing crate) to the end of the feeding bout. The actions of the goat as it browsed from one branch to another were marked with audio description to enhance subsequent data collection and processing.

Following audio identification of species by the video recorder and visual confirmation from the footages, respective browsing times were taken using a stop clock. Goats foraged from one species to another and sometimes switched intermittently. Cumulative browsing time per branch of each feeding bout were recorded, pausing the video at every transition to the next one and stopping the stop-clock to take stock of specific browsing time per species branch.

3.2.6 Sampling and chemical analyses

Three branches of predetermined size for each browse species were weighed and each of them put in a separate paper bag. Paper bags were labelled with species code, date and objective of the sample, to distinguish them from the rest. Labelled samples were oven dried to constant mass for three days at 60°C. The mean moisture content of the respective extra branches was subsequently used to convert fresh weight of served branches to dry weight. Dry leaves were pooled for all branches per day per species and each day taken as a replicate. Proportion of dry mass of foliage and inter-thorn distances for the spinescent species was used to test for their respective effect on intake.

Pooled oven dried leaf material of the three branches of each species was milled to pass through a 1mm sieve and subsequently analysed for nitrogen (N), condensed tannins (CT), neutral detergent fibre (NDF), acid detergent fibre (ADF), and acid detergent lignin (ADL). Hemicellulose and cellulose were determined by difference. All the chemical analyses were done in the Animal Science Laboratory of the University of Kwazulu Natal, Pietermaritzburg.

Crude protein was determined by the AOAC (16th edition 1997) method 990.03 using LECO. FP2000, Nitrogen analyser. Neutral detergent fibre (NDF), (ADF) and (ADL) were in turn determined ash inclusive (Van Soest *et al*., 1991) using ANKOM$^{200/220}$ fibre analyzer (ANKOM Corporation® Technology, Fairport, New York). HCl-butanol pronathocyanidin assay (Porter *et al*., 1986) was used to determine condensed tannins as leucocyanidin equivalent (Makkar, 1995) and absorbances read at visible wavelength of light 550nm using Beckman DU®640 Spectrophotometer.

3.2.7 Calculations and statistical analysis

All data were analysed using SAS 9.1. Data were tested for normality and for diet selection variables, only intake required transformation. Intake was square root transformed; whereas for leaf chemical components, hemicellulose was log transformed. All transformed data were back transformed for presentation in tables.

The data were subjected to analysis of variance using the general linear models (GLM) procedure of SAS (2002) in a two season × 6 feeds Latin square design with six replicates. The model used was:

$$Y_{ijk} = \mu + s_i + p_j + (sp)_{ij} + \varepsilon_{ijk};$$

Where Y_{ijk} is the observation, μ is the population mean, s_i is the season effect (i= 1-2), p_j is the plant species effect (j = 1-6), $(sp)_{ij}$ is the interaction between seasons and plant species and ε_{ijk} is the residual error. Scheffé test was used post hoc for mean separation. To test the effect of plant traits including, long shoots and short shoots, fine and broad leaves, deciduous and evergreen species, and, spinescent and spineless species on intake and intake variables, T-test was used.

Pearson correlation analysis was used to determine the relationships between intake, intake related variables and chemical variables. Significant associations were regressed to model the relationships. The level of significance was standardized at maximum probability $p<0.05$ for all statistical test. Our choice of Scheffé test post hoc was because sample sizes were unbalanced, and the analysis fairly complex.

3.3. Results

3.3.1 Effect of seasons and plant species on intake

Intake of Nguni goats was significantly affected by species ($F_{5,60} = 31.87$; $p < 0.05$) and interaction of seasons and species ($F_{5,60} = 2.52$; $p = 0.04$; Figure 3.1). Intake in the dry season can be partitioned into three tiers; first, *R. lancea* was the most significantly selected species, followed by a middle tier of *A. robusta, Z. mucronata*, and *E. crispa*, whose respective intakes were significant but not significantly different from each other. The bottom tier of *D. cinerea* and *A. nilotica* had the least intake.

In the rainy season, *R. lancea* was consistent as the most selected plant species, followed by *A. robusta* and *E. crispa* with improved intake from that of the dry season. They were followed by *Z. mucronata* and *D. cinerae* which had close intake and *A. nilotica*; that was consistent with dry season's selection as the least.

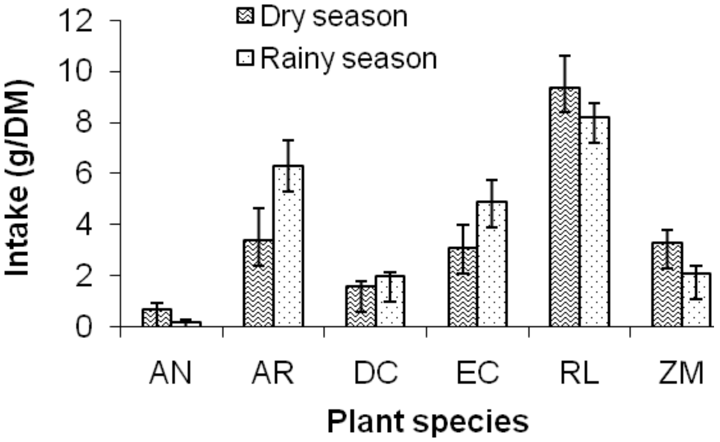

Figure 3.1 Intake dry matter of pooled species samples by Nguni goats for the dry and rainy seasons. AN= ***Acacia nilotica*****, AR=** ***Acacia robusta*****, DC=** ***Dichrostachys cinerea*****, EC=** ***Euclea crispa*****, RL=** ***Rhus lancea*****, ZM=** ***Ziziphus mucronata*****, error bars = standard error, n=6.**

3.3.2 Effect of shoot/leaf morphology, phenology and spinescence on intake

Intake of browse species notably, *E. crispa, R. lancea and Z. mucronata* with new leaves mainly on long shoots (n = 36), which were coincidentally broad leafed (appendix 3) was significantly higher than species (*A. nilotica, A. robusta and D. cinerae*) with new leaves mainly on short (n= 36) shoots (t = -3.99; df =65.80; p = 0.0002). Species with leaves on short shoot were typically fine leafed in nature (appendix 3). Similarly, intake of deciduous species (n = 48) was significantly higher than that of evergreen (n = 24) species (t = 5.22;

.df = 34.02; p<0.0001). Interthorn distances of Spinescent species were significantly different ($F_{3,20}$= 5.43; p< 0.007) Interthorn distances were significantly different for *Z. mucronata* and *D. cinerea*, and not significantly different for *A. nilotica* and *A. robusta*. Additionally, intake of spineless species (n = 24) relative to spinescent (n = 48) ones was significantly higher (t = 5.22; df =.34.02; p < 0.0001). Leaf mass fractions were highest for *R. lancea*, closely followed by *E. crispa* and *A. robusta, while Z. mucronata* had leaf mass that was intermediate but higher than *D. cinerae* and *A. nilotica* respectively (Table 3.1).

3.3.3 Effect of seasons on intake and intake related variables

Mean intake (table 3.2) of the different species in the dry season, was high for *R. lancea*, *Z. mucronata* and *E. crispa,* whereas *D. cinerea, A. nilotica* and *A robusta* were less selected (Table 3.1). In the rainy season, the selection trend was high for *R. lancea, A. robusta* and *Z. mucronata* relative to *D. cinerea* and *A. nilotica* that were less selected. Selection trends indicated a higher selection of *E.crispa*, *R. lancea* and *Z. mucronata,* all of which had long shoots. Conversely, *A. nilotica* and *D. cinerea* with characteristic short shoots yielded lower intake, except *A. robusta* that had intake comparable to that of species with long shoots. Marked improvement in selection of *A. robusta* in the rainy season relative to the dry season is suggestive of the influence of factors other than the presence of foliage. Bigger bite sizes were cropped from *E.crispa, R. lancea, A. robusta* and *Z. mucronata* relative to smaller bites from *D. cinerea* and *A. nilotica* in the dry season. On the other hand, bite sizes cropped by goats in the rainy season were high for *E. crispa, A. robusta* and *R. lancea*, and low for *Z. mucronata, D. cinerea* and *A. nilotica*. Bite sizes were smaller for spinescent species including *Z. mucronata*, *D. cinerea* and *A. nilotica* relative to non spinescent species such as *E. crispa* and *R. lancea* Bite rates in the dry season were high for *Z. mucronata, D. cinerea* and *R. lancea* compare to those of *A. robusta, A. nilotica* and *E. crispa*. In the rainy season, the trend exhibited gradation into three distinct tiers. The higest bite rates were cropped from *D. cinerea* and *A. robusta*, followed by a middle tier of *Z. mucronata, R. lancea* and *E. crispa*, and the bottom tier comprised of *A. nilotica*. Bite rates were also high for some of the spinescent species in both the dry and rainy seasons, notably, *Z. mucronata* and *D. cinerea*. Conversely, bite rates were low in the dry and rainy seasons for non-spinescent *R. lancea* and *E. crispa*. Intake rate trends by goats for the dry season, presented three different levels. The higest intake rate were taken from *E. crispa* and *R. lancea,* followed by *A. robusta* and *Z. mucronata,* and the least from *D. cinerea* and *A. nilotica*. In the rainy season, the highest intake rates were derived

Table 3.1 Means (±SEM) of interthorn distance(cm), leaf mass, bite size (gDM), intake (gDM), bite rate (bites^{-1}) and intake rate (gs^{-1}DM) of the different species

Species	n	Interthorn(cm)	Leaf mass(g)	n	Bite size(g)	n	Intake(gDM)	n	Bite rate(bitess^{-1})	n	Intake rate(gDMs^{-1})
A. nilotica	18	2.14±0.068^{C}	2.73±0.0161^{B}	12	0.10±0.068^{C}	12	0.45±0.730^{D}	12	0.15±0.032^{C}	12	0.04±0.028^{C}
A. robusta	18	2.11±0.089^{C}	10.32±1.620^{A}	12	0.48±0.068^{BA}	12	4.85±0.730^{B}	12	0.29±0.032^{BA}	12	0.22±0.028^{A}
D. cinerea	18	3.15±0.216^{B}	3.87±0.442^{B}	12	0.16±0.068^{C}	12	1.81±0.730^{CD}	12	0.37±0.032^{A}	12	0.08±0.028^{BC}
E. crispa	18	0.00±0.000^{D}	12.49±1.592^{A}	12	0.59±0.068^{A}	12	3.97±0.730^{CB}	12	0.34±0.032^{BC}	12	0.22±0.028^{A}
R. lancea	18	0.00±0.000^{D}	13.25±1.622^{A}	12	0.58±0.068^{BA}	12	8.79±0.730^{A}	12	0.29±0.032^{BA}	12	0.16±0.028^{BA}
Z. mucronata	15	3.78±0.455^{A}	6.16±1.132^{B}	12	0.26±0.068^{BC}	12	2.66±0.730^{CBD}	12	0.32±0.032^{A}	12	0.10±0.028^{BC}

SEM= standard error of mean; g= gram metric weight; n=sample size; superscript=significant mean differences from *A. robusta, E. crispa* and *R. lancea*, followed by *Z. mucronata* and *D. cinerea*, and the least from *A. nilotica*. Intake rate for both seasons were high for non-spinescent, evergreen *E. crispa* and *R. lancea,* as well as the leafy/deciduous *A. robusta* relative to spinescent/deciduous Z. mucronata, D. cinerea and *A. nilotica*. Intake related variables such as number of bites cropped were diverse with the highest number from *R. lancea* followed by *D. cinerea, Z. mucronata, A. robusta, E. crispa and A. nilotica*.

Table 3.2 Means (±SEM) of bite size (g), intake (g), bite rate (bites^{-1}) and intake rate (g s^{-1}) of the different species for the dry and early rainy seasons

Season	Species	n	Bite size(g)	Intake (g)	Bite rate (Bites s^{-1})	Intake rate (g s$^{-1)}$
Dry	*A. nilotica*	6	0.10±0.016	0.67±0.241	0.16±0.036	0.02±0.001
	A. robusta	6	0.32±0.051	0.43±1.245	0.17±0.037	0.09±0.013
	D. cinerea	6	0.15±0.012	1.64±0.201	0.22±0.014	0.05±0.000
	E. crispa	6	0.61±0.156	3.07±0.932	0.14±0.037	0.15±0.045
	R. lancea	6	0.59±0.045	9.36±1.217	0.21±0.020	0.12±0.016
	Z. mucronata	6	0.27±0.011	3.25±1.243	0.27±0.043	0.07±0.000
Rainy	*A. nilotica*	6	0.10±0.037	0.23±0.075	0.13±0.036	0.06±0.022
	A. robusta	6	0.64±0.111	6.26±1.001	0.41±0.027	0.35±0.063
	D. cinerea	6	0.16±0.019	1.98±0.118	0.52±0.027	0.10±0.024
	E. crispa	6	0.75±0.101	4.86±0.835	0.34±0.04	0.28±0.040
	R. lancea	6	0.57±0.027	8.21±0.586	0.36±0.026	0.19±0.012
	Z. mucronata	6	0.25±0.030	2.06±0.280	0.37±0.034	0.13±0.018

SEM= standard error of mean; g= gram metric weight; n=species sample size

3.3.4 Correlations of leaf chemical components with intake and intake related variables

In the rainy season, cellulose positively correlated with intake (r = 0.85; n=.6; p= 0.031), bite number (r= 0.98; n= 6; p= 0.001) and browsing time (r= 0.93; n=.6; p= 0.007). In the dry season, cellulose as well correlated with bite size (r= 0.87; n= 6; p= 0.023). (Table 3.3).

Table 3.3 Correlation coefficient (r) and probability difference (p) of levels of association of intake, time, bites, and bite size with leaf chemical components and secondary compounds. (n=6)

Season	Chem Com		Time (s)	Intake(gDM)	Bites	Bite size(gDM)
Dry	Protein	r	0.09	-0.28	0.27	0.73
		p	0.870	0.590	0.607	0.100
	NDF	r	0.10	0.43	0.10	0.49
		p	0.849	0.389	0.845	0.317
	ADF	r	0.08	0.44	-0.04	0.74
		p	0.877	0.378	0.945	0.090
	ADL	r	0.12	0.26	-0.21	0.63
		p	0.828	0.613	0.692	0.181
	Hem	r	0.18	0.30	-0.37	-0.04
		p	0.728	0.561	0.476	0.939
	Cellulose	r	0.49	0.76	0.34	0.87
		p	0.314	0.079	0.506	0.023*
	CT	r	0.41	0.46	0.31	0.53
		p	0.420	0.358	0.545	0.275
Rainy	Protein	r	-0.19	-0.43	0.33	-0.64
		p	0.718	0.394	0.949	0.171
	NDF	r	0.37	0.56	0.66	0.42
		p	0.475	0.245	0.150	0.402
	ADF	r	0.59	0.69	0.76	0.54
		p	0.210	0.128	0.077	0.274
	ADL	r	0.30	0.49	0.51	0.40
		p	0.561	0.329	0.300	0.428
	Hem	r	-0.04	0.83	0.24	-0.01
		p	0.934	0.875	0.641	0.984
	Cellulose	r	0.93	0.85	0.98	0.61
		p	0.007*	0.031*	0.001*	0.196
	CT	r	0.45	0.25	0.47	0.02
		p	0.369	0.628	0.342	0.967

n=.sample size; chem. com. = plant chemical component; NDF= neutral detergent fibre; ADF= acid detergent fibre; ADL=.acid detergent lignin; Hem= hemicellulose; CT= condensed tannins; *=significant correlations

The following regressions were modelled from the correlations, figure 3,2 ,3.3 ,3.4 and 3.5.

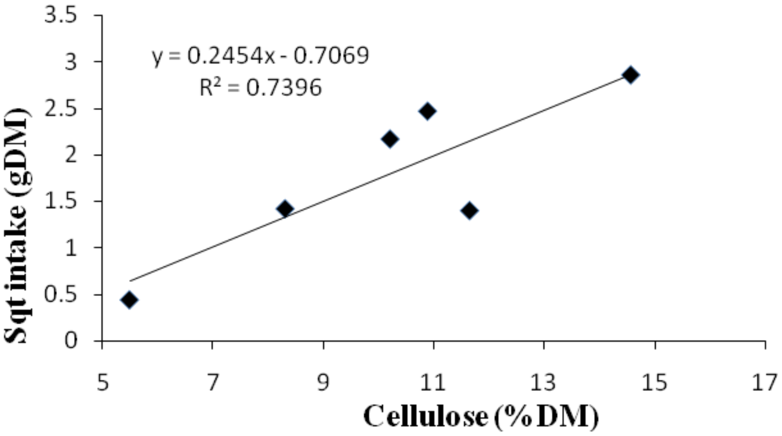

Figure 3.2. Regression between short term intake and percentage cellulose dry matter of Nguni goats from a pooled multi-species data set in the rainy season. (n=6).

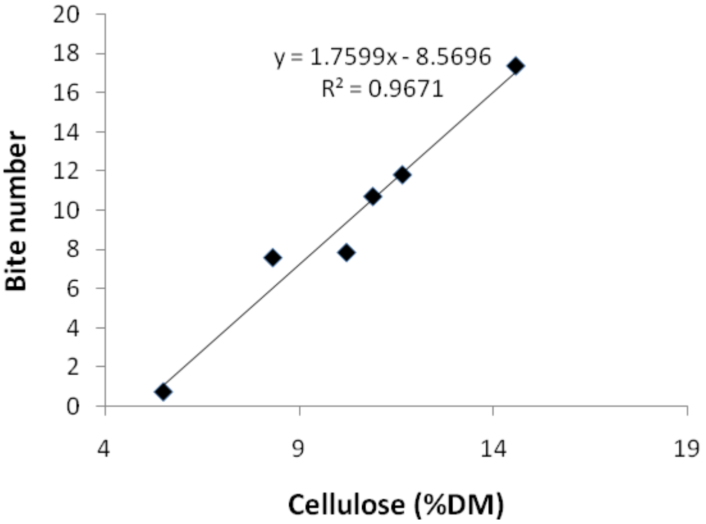

Figure 3.3. Regression between cellulose dry matter and mean number of bites cropped of Nguni goats from a pooled multi-species data set in the rainy season.(n=6)

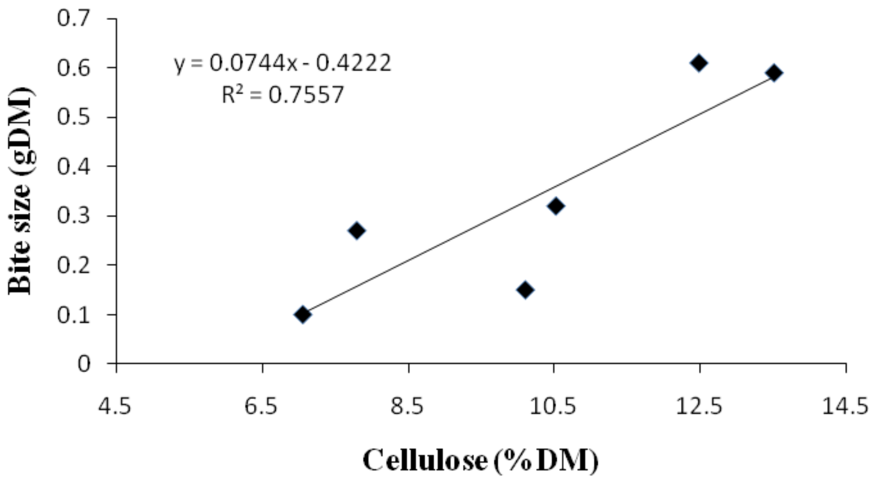

Figure 3.4. Regression of bite size and percentage cellulose of Nguni goats on a pooled multi-species data set during the dry season (n=6).

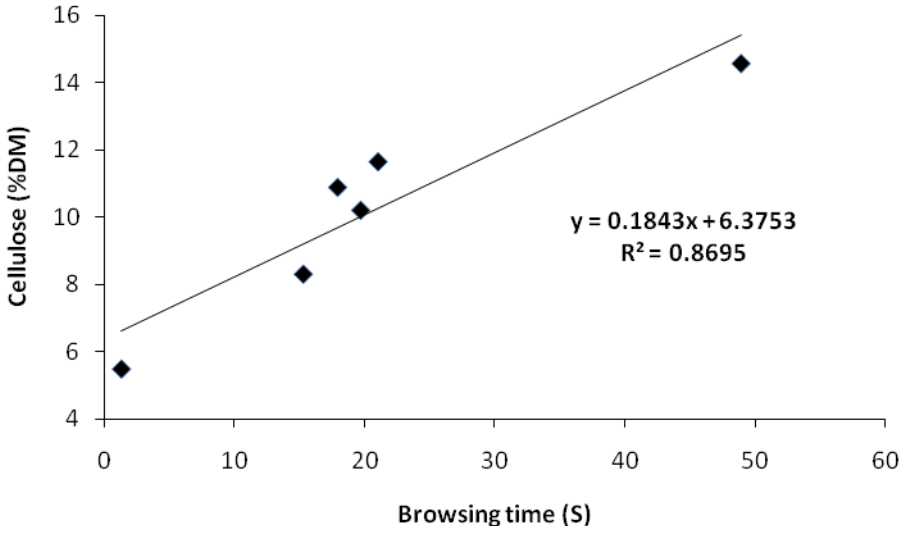

Figure 3.5 Regression of percentage cellulose dry matter of browses and mean browsing time of Nguni goats on a pooled multi-species data set in the rainy season. (n=6).

3.4 Discussion

3.4.1 Effect of plant species on intake

Congruent with our expectation, diet selection indexed by intake, was significantly influenced by species (Figure 3.1), with the following ranking in the dry and rainy seasons respectively: *R. lancea* > *A. robusta* > *Z. mucronata* > *E. crispa* >.*D. cinerea* > *A. nilotica* and *R. lancea* > *A. robusta* > *E. crispa* > *Z. mucronata* >.*D. cinerea* > *A. nilotica*. Similar results whereby species influenced intake were observed in the Thornveld of the Eastern Cape (Dziba *et al*., 2003), the shrublands of the Mediterranean (Papachristou et al., 2003), and the Zululand Thornveld. (Mkhize, 2008). Plant species are inherently different in canopy structure, leaf and shoot morphology, phenology, structural deterrents to mammalian herbivory, plant secondary metabolites (condensed tannins) and toxins, and nutrients. Species differences, in addition to changes brought about by different seasons, tend to influence diet selection and intake. Goats therefore, select to various extent, given the opportunity to choose from various options (Mkhize, 2008; Basha *et al*., 2011). Shoot morphology tended to have significantly influenced diet selection by Nguni goats in the present study as it did in the arid savannah of the Eastern Cape (Dziba *et al*, 2003). Species with new leaves on long shoots *E. crispa, Z. mucronata,* and *R. lancea* featured amongst the most selected, including *A, robusta* that had high foliar mass fraction (Table 3.1). Similar results were observed in the False Thornveld of the Eastern Cape (Bakare and Chimonyo, 2011); in the Zululand Thornveld (Mkhize, 2008) and in semiarid South Western Zimbabwe (Sebata and Ndlovu, 2010). Plant species with long shoots enhanced and maximized short term intake by presenting goats the opportunity to crop young nutritive leaves (Sebata and Ndlovu, 2010) alongside succulent twigs than would be cropped from species with new leaves on old short shoots. Selection of *A. robusta* improved from dormancy 3.4 ± (SEM= 1.25) gDM in the dry season to 6.3 ± (SEM= 1) gDM in the rainy season coupled with the growth of some new long shoots. Similar improvement in selection of *E. crispa* also occurred in the rainy season. Conversely, there was marginal decline in the selection of *R.lancea*, attributable to active growth of new shoots and partial loss of foliage in the rainy season (Personal observation). *Ziziphus mucronata* as well declined in intake from dry to rainy season, though with the growth of new long shoots. These declines in intake are suggestive of factors other than foliage or shoot structure. Coincidentally, species with new leaves on new long shoots were broad leafed in nature.

3.4.2 Effect of physical traits, shoot and leaf morphology on intake

Broad leaf species (appendix 3) featured amongst the most selected in both seasons, they included *E. crispa*, *R. lancea* and *Z mucronata*. Incidentally, *A. robusta* that has fine leaves was consistently highly selected in the dry and rainy seasons. Its high selection by Nguni goats could be attributed to the high presence of foliar biomass. Relative to *E. crispa* and

R. lancea that are spineless, *Z. mucronata* was less selected in the rainy season, consistent with observations that Nguni goats will select more of spineless broad leafed species relative to spinescent ones (Mkhize, 2008). *Ziziphus mucronata* is deciduous in addition to being spinescent and had little foliage during the dry season. Selection patterns showed strong inclination towards species with high foliar mass fraction

Our results also depict a significant selection of deciduous species relative to evergreen ones (Appendix 3). Deciduous species including *A. nilotica*, *A. robusta*, and *Z.mucronata*, all carried considerable foliage in the dry season, except *D. cinerea* that had very little leaf material. Out of all the six species that were used in the diet selection trial two, *E. crispa* and *R. lancea* were evergreen. The former had marginally lower selection in the dry season relative to *A. robusta* and *Z. mucronata*, both of which were deciduous but the later was highly selected (figure 3.1). These results concur with similar observations in the Zululand Thornveld, (Mkhize, 2008), where deciduous species carried leaves longer into the dry season and were relatively highly selected. Contrary to observations in the False Thornveld of the Eastern Cape and the Zululand thornveld, evergreen browses in the present study featured amongst the most selected in both dry and rainy seasons, consistent with Shipley *et al*. (1998).

Additionally and in partial accord with our expectation that spinescence will negatively affect intake, whereas spinelessness will positively affect intake, spinescent *D. cinerea* and *A. nilotica* were the least preferred in both dry and rainy (Table 3.3) seasons. Generally, spinescent species had diverse levels of selection in both seasons, *A. robusta* and *Z. mucronata* were highly selected during the dry season, whereas *D. cinerea* and *A. nilotica* were least selected in both seasons. *Acacia nilotica* was the least selected in the dry season and *D. cinerea* the least selected in the rainy season in the Zululand Thornveld (Mkhize, 2008). Intake of *Z. mucronata* declined in the rainy season. Low selection of *D. cinerea* in the current study contrasts with high selection that was observed in the wet season and lower intake in the dry season in the Zululand Thornveld (Basha et al., 2011). Sanon et al. (2007) reported very low intake of *D. cinerea*, concurring with observations in the current study. Marked divergent selection of *D. cinerea* in various ecological zones can be attributed to the effect of climate and soil on plant morphology, phenology and leaf chemistry.

Various levels of selection of spinescent browse species can be attributed to the nature of shoots, leaves and thorns, and their different levels of deterrence amongst other factors from browsing by goats. Diverse thorn morphology has been observed to present different levels and extent of deterrence to herbivory by mammalian herbivores (Shipley and Yanish, 2001). Long straight spines were observed to affect intake significantly (Mkhize, 2008). *Acacia robusta* which was highly selected in both seasons had straight thorns, but with leaf morphology that enhanced intake, whereas *Z. mucronata* with straight and hooked thorns at relatively close interval, especially at actively growing portions of the branches had lower selection. Spinescence was also observed to deter herbivory by influencing bite size of common duiker, bushbuck and Boer goats (Wilson and Kerley, 2003a).

3.4.3 Effect of plant chemical components and secondary compounds on intake

Inconsistent with our prediction that crude protein will positively affect intake (Dziba *et al*., 2003; Provenza *et al*., 2003), there was no correlation between intake and crude protein in the current study in both the dry and rainy seasons (Table 3.3). Conversely, Mkhize (2008), observed a very weak positive relationship between intake and crude protein in a similar study in the Zululand Thornveld in the dry season.

Crude protein content of the six browse species across seasons was within close range, except *E. crispa* that was significantly low in the dry and rainy seasons respectively (appendix 3.4). This close variation rendered distinct selection difficult, granted that it was potentially on the basis of browse species crude protein content (Alonso-Diaz *et al*., 2008). Shoot and leaf morphology were observed earlier in the study to have had overbearing influence on preference, suggesting that goats' primary objective function was intake maximization and crude protein was secondary in the event of a lag. However, there is empirical report of a positive association of intake and crude protein (Dziba *et al*., 2003; Ganqa, 2005; Baraza *et al*., 2008).

Cellulose positively correlated with bite size in the dry season, whereas there was a positive correlation between cellulose intake and bite size in the rainy season. All of the other fibre components, NDF, ADF, hemicellulose and ADL had no statistically discernable effect on intake and associated intake variables. The observed results contrast with our prediction that fibre will negatively affect intake (Papachristou *et al*., 2003).

In the dry season, cellulose correlated with bite size given that the biggest bites were taken from species characterized by growth of new long shoots relative to those with new growth on old short shoots. Though in the dormant season, cellulose was present as structural fibre to lend plant physical support and offered goats a greater opportunity to crop more foliage and twigs from species with long shoots. Meantime, in the rainy season, dormancy ceded to active growth with a proliferation of new long shoots and increased cellulose as structural fibre. This also culminated to increase intake (figure 3.1) from *A. robusta, E. crispa, R. lancea* and *Z. mucronata*, all of which grew new leaves on long shoots. Furthermore, increase intake from these species is associated with larger bite sizes owing to shoot and leaf morphology. Species with new leaves on long shoots were broad leaf in the majority except *A. robusta* that bore fine leaves. Fermentable fibre at 19% is reported to enhance passage rate and also improve butter fat (Solaiman, 2010). Forage fibre will therefore become prohibitive at levels exceeding the 19% mark. The cellulose content of all plant species was below 19% in both the dry and early rainy seasons (see appendix 1).

Inconsistent with our prediction that condensed tannins will negatively affect intake (Papachristou *et al*., 2003), there was no significant correlation of condensed tannins and intake in both dry and rainy seasons. Condensed tannins at concentrations higher than 5% in browse plants have been reported to negatively affect intake (Dove, 2010; Muir, 2011). However, in the present study there was no discernable effect in utter defiance of this widely observed trend. These observations are consistent with similar ones in the Zululand Thornveld (Mkhize, 2008).

Close examination of the different species show that condensed tannin concentration of *D. cinerea, E. crispa*, and *R. lancea* exceeded 5% concentration level and had no specific effect on their respective intake or selection relative to those with lower concentrations such as *A. nilotica, A. robusta* and *Z. mucronata*. In the dry season, *E. crispa* and *R. lancea* featured amongst the most preferred species and was consistent in the rainy season, whereas, *D. cinerea* was one of the least selected in both seasons as well. Therefore the thresh-hold of 5% condensed tannins as a bar to effective intake and utilization of tanniferous browses is not tenable in the present study. Goats have been reported to be more tolerant to tanniferous browses than sheep (Dove, 2010).

The increase importance of browse with aridity (Ben Salem et al., 2005) and associated goat husbandry (Assefa *et al*., 2008) is likely to have developed in them the ability to accommodate and efficiently utilize tannin rich browses. Additionally, goats consume a variety of browses and plant secondary compounds (Provenza *et al*., 2003; Iason and Villalba, 2006), some of which may neutralize or dilute (Iason and Villalba, 2006; Rogosic *et al.*, 2006) the effects of condensed tannins on intake and utilization of browses. Condensed tannin rich browses were taken in low quantity when fed to goats individually, but when fed collectively, more was consumed (Rogosic *et al*., 2006). The absence of any primary influence of condensed tannins on intake is suggestive of a secondary remote role in the current study. Baraza *et al*. (2008), postulated that in short term studies condensed tannins would be a secondary signal for short term intake regulation. However, in cafeteria trials wherein animals have many options to choose, the association of particular effects with specific plant species is apparently impossible (Alonso-Diaz *et al*., 2008), given that all of them contain condensed tannins. Goat ability to consume and utilize tannin rich browse reasserts their role as very important biological controllers of bush encroachment and invasive alien species (Scogings *et al*., 2004).

3.5 Conclusion

Diet selection of Nguni goats was significantly influenced by plant species and seasons in the current study. Other related factors included, spinescence which exerted partial influence and shoot/leaf morphology which influenced diet selection significantly. On the other hand, cellulose influenced diet selection in the rainy season, whereas protein and condensed tannins had no significant influence on intake in both seasons. These results suggest that the influence of crude protein, condensed tannins and other leaf fibre components may be secondary to intake of browse by Nguni goats in the bushveld of Gauteng.

Goat ability to consume and efficiently utilize tanniferous browses, earmarks them as appropriate biological controllers of bush encroachment and invasive alien plant species, coupled to their universally acclaimed socioeconomic importance as animals and food of the poor.

Given the results obtained when browses were presented to goats in cafeteria style, the proceeding section will examine the maximum achievable biomass intake when they are served individually relative to nutrients, PSM, morphological and phenological traits.

CHAPTER 4

FORAGING EFFICIENCY OF NGUNI GOATS IN RELATION TO PLANT SPECIES AND SEASONS IN AN ARID SUB-TROPICAL SAVANNA, SOUTH AFRICA

Abstract

The objectives of this study were two fold: (1) Determine the seasonal and plant species trend of foraging efficiency indexed by browse short term intake rate (IR) of Nguni goats; and (2) investigate how spinescence, phenology, leaf and shoot morphology, and leaf chemistry will potentially explain the observed trends. The study was carried out in the dry, early rainy and late rainy seasons. Ten plant species were presented to goats individually under shade. Instananeous intake rate varied amongst species ($p< 0.05$) and seasons ($p< 0.05$). *Acacia caffra, Acacia robusta* and *Rhus lancea* featured amongst species with the highest IR in all three seasons, *Ehretia rigida* and *Acacia nilotica* were consistent as the least efficiently foraged. *Gymnosporia buxifolia* that was efficiently foraged in the dry season, declined to amongst the least in the early and late rainy seasons. Browses with long shoots were more efficiently foraged relative to those with short shoots ($t= -3.2$; $df= 284.64$; $p< 0.002$). Evergreen plant species yielded higher intake rate compared to deciduous species ($t= 2.02$; $df= 278.01$; $p< 0.044$). Intake rate of spinescent relative to spineless species was not significantly different but more bites were cropped from spinescent relative to spineless species ($t= 2.80$; $df= 256.77$; $p= 0.006$). Bite sizes were smaller for spinescent relative to spineless species ($t= -3.30$; $df= 227.4$; $p= 0.001$). There were significant positive correlations of cellulose with IR ($r= 0.71$; $n= 10$; $p= 0.023$), and also with condensed tannins (CT) ($r= 0.71$; $n= 10$; $p= 0.023$) in the dry season. Additionally, cellulose also had a positive correlation with bite size in the same season ($r= 0.73$; $n= 10$; $p= 0.016$). At early rainy season, there was no correlation of intake with any of the plant chemical components, whereas, NDF ($r= 0.65$; $n= 10$; $p= 0.044$), hemicellulose ($r= 0.76$; $n= 10$; $p= 0.012$) and CT ($r= 0.68$; $n= 10$; $p= 0.032$) all correlated positively with browsing time at early rainy season. Regression equations were derived from correlations to model IR and related variables: The following regression equations were derived to model intake rate and some intake rate related variables: (1) intake rate= 0.433 + BSDM (0.081), $r^2= 0.68$, $p< 0.05$ and BSDM= bite size dry matter; (2) Bite rate= 0.503 –BSDM (0.147), $r^2= 0.597$, $p< 0.05$ and BSDM= bite size dry matter; (3) Bite size dry matter=

1.713 – BR (4.210), r^2= 0.597 ,$p< 0.05$ and BR= bite rate, and (4) Intake dry matter= 3.804 + BSDM (0.865), r^2= 0.607, $p< 0.05$ and BSDM= bite size dry matter.

4.1 Introduction

Baumont *et al*. (2000) and Gordon, (2001) acknowledged the importance of maximizing forage intake in order to optimize production of mammalian herbivores and promote fitness in confinement or on range. Goats have socio-economic importance in South Africa (Rumosa Gwaze *et al*., 2008) and global subsistence agriculture (Devendra and Solaiman, 2010), and their vital role as biological controllers of bush invasion (Devendra and Burns, 1983; Scogings and Mopipi, 2008). Foraging efficiency is the maximum quantity of feed or forage that can be eaten by an animal within a particular time (Baumont *et al*., 2000). Forage intake rate is regulated by plant physical traits (Dziba *et al*., 2003; Wilson and kerley, 2003; Hanley *et al*., 2007), plant secondary metabolites (Hattas *et al*., 2011) and nutrients (Baumont *et al*., 2000); the former determines plant biomass harvested in the short term, and the later is mediated by short term accumulation of nutrient and PSMs, and the resulting feedback (Solaiman and Owens, 2010). Incidentally, seasonal changes in quantity and quality of both herbaceous and browse forages demand that ruminants maximize intake rate during periods of abundance (Sebata and Ndlovu, 2010) to stock large reserves of nutrients for periods of acute scarcity such as the dry season.

Factors affecting foraging efficiency in the bushveld are unclear. Empirically, thorns and spines are known to influence herbivory by browsing ruminants (Schindler et al., 2003; Wilson and Kerley, 2003a; Mutjinde *et al*., 2006; Hanley *et al*., 2007) and chewing (Papachristou *et al*., 2005), thus serving as important drivers of intake rate. Likewise, fibre content affects herbivory (Hanley *et al*., 2003) by influencing plant biomass harvesting and handling time, as well as microbial forage degradation in the rumen (Solaiman, 2010). In the same vein, the presence and distribution of leaves on browse affects instantaneous intake rate (Dziba *et al*., 2003; Sebata and Ndlovu, 2010) with regards to how much leaf biomass is cropped per bite taken. Browse instantaneous intake rate is the product of bite size and bite rate (Sebata and Ndlovu, 2010). Plant chemicals which do not take part in primary metabolism such as tannins have been reported to affect intake rate (Solaiman, 2010).

Condensed tannins in forages at levels of 6% and above have the potential of depressing intake (Muir, 2011) and, by implication, intake rate. They reduce forage intake rate by their instantaneous astringent sensation, concurrent reduced palatability and ruminal microbial degradation, and post ruminal digestion by their ability to irreversibly bind proteins, some minerals and cabohydrates (Solaiman, 2010; Muir, 2011). Contrary, lower levels have been largely reported to be beneficial to ruminant nutrition because they increase protein use efficiency (Nsahlai *et al*., 1998; Solaiman, 2010; Muir, 2011) by reversibly binding and increasing protein supply to the small intestine for enzymatic digestion and absorption. In addition to tannins, protein content have been linked to forage intake, microbial degradability and digestion (Solaiman, 2010), enhancing ruminant function and production. Browse crude protein decreased from rainy season to dry season (Papachristou *et al*., 2005), suggesting that this trend might have implications to intake rate and intake.

The main objective of this trial was to investigate the seasonal trends of ten commonly browsed species, plant physical and chemical factors affecting intake rate when presented to goats individually under shade. Plant chemical, phenological and morphological traits are expected to influence intake rate of browses by goats. The specific objectives of this study are twofold: (1) to investigate the role of plant chemical components such as protein, fibre, and condensed tannins on instantaneous intake rate of goats within and among seasons; and (2) to investigate the role of plant physical traits such as shoot and leaf morphology, spinescence, and fibrousness on instantaneous intake rate within and among seasons.

It was hypothesized that:

- ❖ Instantaneous intake rate vary with species (Rogosic *et al*., 2008) and seasons (Bakare and Chimonyo, 2011);
- ❖ Spinescence will negatively affect instantaneous intake rate (Wilson and kerley, 2003b; Hanley *et al*., 2007) while long shoot and broad leaf morphology will exert a positive effect (Dziba *et al*., 2003; Sebata and Ndlovu, 2010); additionally, evergreen species will positively affect intake, whereas deciduous species will negatively affect intake (Basha *et al*., 2011) and
- ❖ Goats will crop more of high protein browses (Mokoboki *et al*., 2005) and less of highly fibrous (Hanley *et al*., 2005), as well as tanniferous ones (Papachristou *et al*., 2003).

4.2 Materials and methods

4.2.1 Study site and vegetation

The study was conducted in Roodeplaat, South Africa. Roodeplaat is located 30km North East of Pretoria. The area is situated between south latitudes 25° 20´-25° 40´, and between east longitudes 28° 17´-28°25´ (Panagos and Van Staden, 1995). The average annual rainfall of this area is 646mm. The temperature attains a maximum range in January 29°C-20°C and a minimum range in July 16°C-2°C. The vegetation is described as Bushveld savannah (Mucina and Rutherford, 2006).

4.2.2 Study plants

The study was based on 10 browse plants per treatment, which were served to each goat individually relative to 6 that were served collectively in six different arrangements per treatment in the former study. The plants are representative of the most abundant species in the study site and have various combinations of shoot morphology, leaf size, leaf life span and physical defence: (1) *Acacia nilotica* carries bipinnate leaves with fine tiny leaflets on both old and new shoots. It is deciduous and armed with long straight thorns; (2) *Acacia caffra* has drooping pinnate leaves and tiny leaflets on both new and old shoots. It is deciduous and carries short hooked thorns; (3) *Acacia robusta* has bipinnate leaves with leaflets that are relatively bigger than either of *Acacia nilotica* or *Acacia caffra*. It is deciduous and has long and some short straight thorns; (4) *Combretum apiculatum* grows new broad leaves mainly on new shoots, is deciduous and thornless; (5) *Dichrostachys cinerea* has bi-pinnate leaves, which are borne on new and old shoots. The leaves are tiny and shade at the approach of winter or drought. *Dichrostachys cinerae* carries long straight thorns of relatively low density (6) *Ehretia regida* grows new leaves on new and older parts of the shoots. The tree is deciduous, broad-leafed, and thornless; (7) *Euclea crispa* has broad tough evergreen leaves which are borne on new shoots and parts of the old twigs close to new growth. It is thornless. (8) *Gymnosporia buxifolia* carries broad leaves on new and old shoots. It is evergreen and has long straight thorns; (9) *Rhus lancea* is evergreen, has broad leaves and grows new leaves on mainly new shoots. It is thornless; and (10) *Ziziphus mucronata* has broad leaves which are borne mainly on new shoots and is deciduous. It carries both hooked and straight thorns at close interval rendering prehensibility by goats difficult.

4.2.3 Study goats

Ten 2 years old female Nguni goats of average weight 22.6±2.15kg were used as model browsers in this study. For a description of the goats, refer to section 1.4.2. They are indigenous goats of small-framed bodies, with a short-hair coat. Nguni goats are one of the dominant indigenous breeds in South Africa (Rumosa Gwaze *et al*., 2008), very hardy, prolific and adapted to all agro-ecological zones. They compete with other ungulates for food on range and are useful for controlling bush encroachment (Devendra and Burns, 1983; Scogings and Mopipi, 2008). Goats and browsing mammalian ungulates have the advantage of improving on browse forage quality, by taking bites from existing shoots and promoting axillary sprouts which are richer in nutrients than the old growth (Scogings *et al*., 2004).The coat colours range from brown, black and white to variegated combination of the three.

4.2.4 Conditioning and adaptation of goats

Prior to the trial during the respective seasons, the goats were allotted a maximum period of two weeks of adaptation to the experimental procedures. First, they were kept in individual pens under shelter which differed from collective confinement that was common practice on the farm. Goats were served a maintenance lamb/ewe ration from Epol, a division of Rainbow Farms (Pty) Ltd, South Africa (refer to section 3.2.4), and 100g of lucerne hay after every test run. The lamb/ewe pelleted ration contained 13% crude protein, 12% moisture, 14% fibre, 2.5% minimum fat, 1.5% calcium, 0.2% Phosporus, urea 1%, other NPN (non protein nitrogen) sources 0.5% and vitamin A 10000 IU/IE/kg.

On every conditioning day, each goat was served ten branches individually, representing different browse species. Each branch was clamped and held in place by two pieces of wood using G-clamp. The weight of pellets was adjusted daily to meet each goat's maintenance requirements following previous day's intake from an initial base of 500g.
Animals were first served freshly cut branches of different browses as part of adaptation process to the experimental diet. When they had fully adapted, ten two year old ewes of mean weight 22.38±2.00kg were randomly selected from the initial fourteen.

4.2.5 Foraging efficiency

Foraging efficiency experiment was done immediately, after conditioning for 10 days. Thirteen freshly cut branches of each of the 10 browse species with mean length 53.5±0.55cm were cut in the morning of every experimental day. The cut ends were put into buckets containing fresh water and placed under shade to minimize transpiration loss. Whereas, the three extra branches for each species were weighed, put into clearly labelled paper bags, oven dried at 60°C for three days. Dry weights were taken to convert fresh weights to dry matter. Dry leaf material was finally separated from twig for chemical sampling and analyses. Some of the species including: *Acacia nilotica*, *Dichrostachys cinerea, Erhetia rigida and Ziziphus mucronata* did not have enough leaf material during the dry season and so were pooled together for chemical sampling and analyses.

The experiment was done between 08.00 and 13.00h of each of the ten experimental days. Individual branches of all ten species were offered tightly clamped between two pieces of wood held in place by G-clamps. A 10×10 Latin Square design was applied to come out with 10 unique arrangements as treatments. The arrangement was such that, the order of succession of the 10 browse branches, served to different goats for every experimental day were different. This design ensured an even opportunity for goats to browse on all the browse species. The branches were weighed before serving and after foraging. They were subsequently put into paper bags, clearly marked with goat number, species code and date for identification. These packaged branches were all oven-dried for three days at 60°C to constant weight as determined in the preliminary trial and the dry weights recorded. The study was carried out in the early and late rainy seasons in December and March, and dry season in July respectively.

From the conditioning phase a maximum of three minutes was allotted to each goat to forage given that the branch was not depleted and the goat did not stop eating either. Bite counts and time were taken for any of the branches served and eaten by goats using a tally counter and stop watch for subsequent calculation of intake rate and bite rate. The fresh weights of the branches were subsequently converted to dry matter to determine intake rate dry matter ($DMgs^{-1}$) as an index of instantaneous intake rate (Haschick and Kerley, 1997).

4.2.6 Sampling and chemical analyses

Three freshly cut branches of predetermined size for each browse species were weighed, each of them put in a separate paper bag and oven dried to constant mass for three days at 60°C. Mean moisture content of the respective extra branches was subsequently used to convert fresh weight of served branches to dry weight. Dry leaves were pooled for all branches per day per species. Proportion of dry mass of foliage and inter-thorn distances for the spinescent species was used to test for their respective effect on intake rate, bite rate, intake and bite size.

Pooled oven dried leaf material was centrifuge-milled to pass through a 1mm sieve and subsequently analysed for nitrogen (N), CT, NDF, ADF, and ADL. Hemicellulose was calculated as the difference between NDF and ADF, and cellulose as the difference between ADF and ADL. All the chemical analyses were done in the animal science laboratory of the University of KwaZulu Natal, Pietermaritzburg.

Crude protein was determined by the AOAC (16th edition 1997) method 990-03 using LECO. FP2000. Nitrogen-analyzer. Neutral detergent fibre, ADF and ADL were in turn determined ash inclusive (Van Soest et al., 1991) using ANKOM$^{200/220}$ fibre analyzer (ANKOM Corporation® Technology, Fairport, New York). HCl-butanol proanthocyanidin assay (Porter *et al*., 1986) was used to determine condensed tannins as leucocyanidin equivalent Makkar, 1995) and absorbances read at visible wavelength of light 550nm using a Beckman DU®640 Spectrophotometer.

4.2.7 Calculations and statistical analysis.

Data were analyzed using SAS 9.1. The prerequisite of homogeneity of variance was not met by all variables. All foraging efficiency variables: bite, intake, bite rate, intake rate were square root transformed whereas bite size was log transformed. On the other hand, leaf chemical components such as, condensed tannins, proteins, NDF and ADF did not require transformation, while ADL and cellulose were square root transformed, and hemicelluloses log transformed.

The general linear model (GLM) was used to determine effects of seasons and species on intake rate, square root bite rate, log bite size among the independent variables of species and seasons, and interaction of seasons and species. The model used was:

$$Y_{ijk} = \mu + s_i + p_j + (sp)_{ij} + \varepsilon_{ijk}$$

Where Y_{ijk} is the observation, μ is the population mean, s_i is the season effect (I = 1-3), p_j is the plant species effect (j = 1-10), $(sp)_{ij}$ is the interaction between season and plant species and ε_{ijk} is the residual error.

Treatment means with significant differences were compared post hoc using Scheffe's test, especially because the samples were unbalanced. For pair wise comparisons such as long versus short shoots, deciduous versus evergreen, spinescent versus spineless, T-test were used.

To determine the probable relationship between foraging efficiency variables of Nguni goats and leaf chemical components, Pearson's correlations were computed to ascertain the level of association Regression analyses were run to model relationships that correlated significantly. The level of significance was standardized at probability $p < 0.05$ for all statistical tests.

4.3 Results.

4.3.1 Effect of seasons and species on instantaneous intake rate

There were significant differences in the intake rate amongst species ($F_{9,270}= 28.52$; $p< 0.05$), as well as seasons ($F_{2,270}= 16.28$; $p< 0.05$). Intake rate of browse species for the dry season were highest from *A. caffra*, and *G. buxifolia*, followed by *C. apiculatum, R. lancea, E. crispa, A. robusta* and *Z. mucronata* in the middle tier, and least from *E. rigida, D. cinerea* and *A. nilotica* (Figure 4.1)

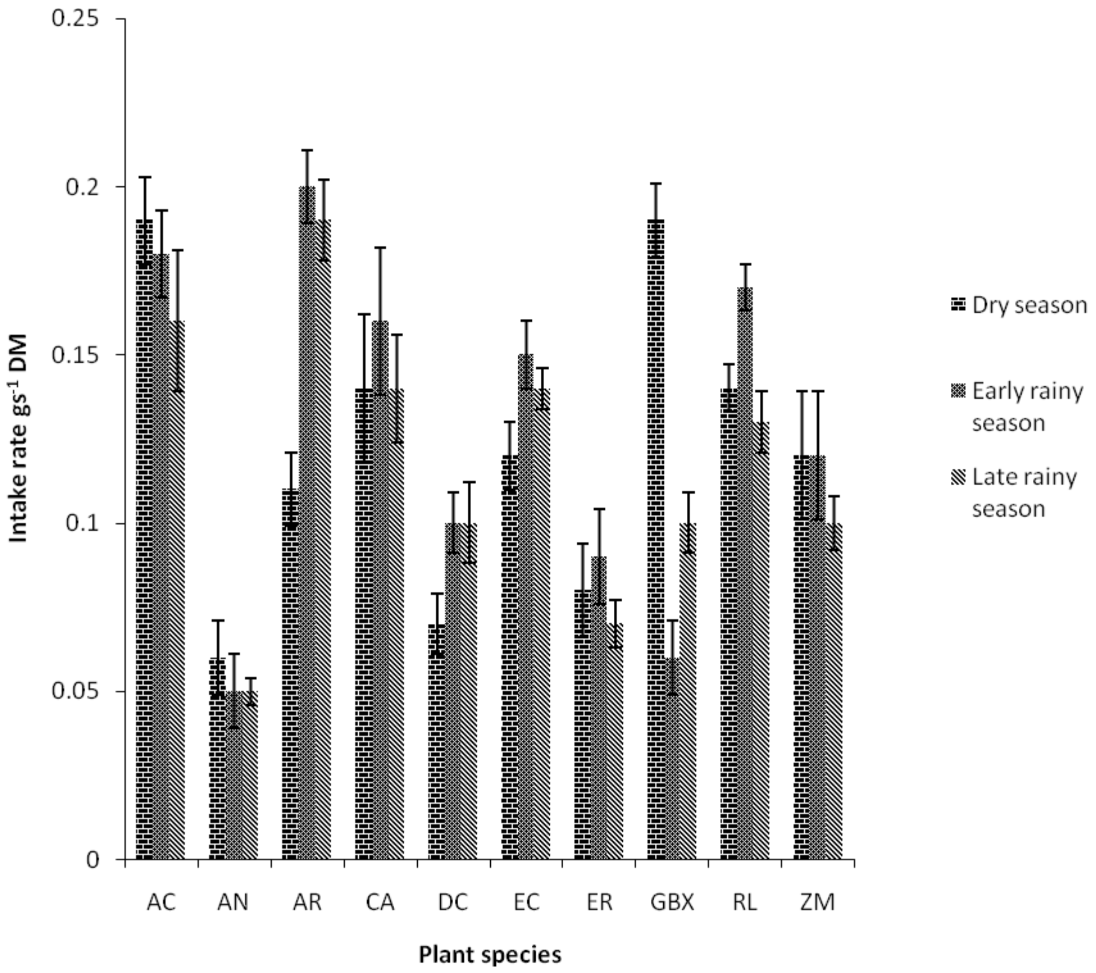

Figure 4.1 Intake rates (gs^{-1}DM) of pooled plant species samples for the dry, early rainy and late rainy seasons. AC= *Acacia caffra*, AN= *Acacia nilotica*, AR= *Acacia robusta*, CA= *Cumbretum apiculatum*, DC= *Dichrostachys cinerea*, EC= *Euclea crispa*, ER= *Erhetia rigida*, GBX= *Gymnosporia buxifolia*, RL= *Rhus lancea*, ZM= *Ziziphus mucronata*, n=10

At onset of the rainy season (Figure 4.1), the highest intake rate was taken from *A. robusta, A. caffra,* and *R. lancea,* followed by another set comprising of *C. apiculatum, E. crispa* and *Z. mucronata.* The set with the lowest intake rate comprised of *D. cinerea, E. rigida, G. buxifolia* and *A. nilotica*. At late rainy season, the intake rate trends showed three distinct sets: the first of which included *A. robusta, A. caffra, C. apiculatum, E. crispa* and *R. lancea* with the highest intake rate, followed by *D. cinerea, G. buxifolia,* and *Z. mucronata* in the second, and the last set with the least intake rate included E. *rigida* and *A.*

nilotica. In the dry season, *A. caffra*, and *G. buxifolia* yielded the highest intake rate, followed by the set of *A. robusta, C. apiculatum, E. crispa, R. lancea* and *Z. mucronata.* The lowest intake rate, were derived from *A. nilotica, D. cinerea* and *E. rigida*. *A. caffra*, .*A. robusta*, *R. lancea, C. apiculatum* and *E. crispa* featured amongst species with highest intake rate in all three seasons, whereas *G. buxifolia* that offered one of the highest intake rate in the dry season declined to amongst one with the least intake rate at both early and late rainy seasons. *Ehretia rigida*, *D. cinerea* and *A. nilotica* were consistent in all three seasons as the least efficiently foraged by goats. Intake rate across seasons show three distinct groupings. The highest intake rate by Nguni goats was taken from *A. caffra, A. robusta* and *R. lancea*, while, the second set of species with significantly similar intake rate comprised of *C. apiculatum, E crispa, G. buxifolia* and *Z. mucronata*. The bottom tier with low intake rate was made of *A. nilotica*, *D. cinerea* and *E. rigida*.

Bite rate of goats from the different species had basically two groups. The upper group of *A. nilotica, D. cinerea, E. rigida, G. buxifolia* and *Z. mucronata*, and the lower group comprising of *A. caffra*, *A. robusta*, *C. apiculatum*, *E. crispa* and *R. lancea*. Many bites were taken from *A. nilotica*, *D. cinerea*, *E. rigida, G. buxifolia* and *Z. mucronata*, whereas fewer bites were taken from *A. caffra*, *A. robusta*, *C. apiculatum*, *E. crispa* and *Rhus lancea.*

Table 4.1 Means (±SE) of bite size(g), bite rate (bitess^{-1}), intake(g) and intake rate(gs^{-1}) of the different species for the dry, early rainy and late rainy season

Season	Species	n	Bite size(g)	Bite rate(bs^{-1})	Intake (g)	Intake rate (gs^{-1})
Dry	*A. caffra*	10	0.93±0.083	0.23±0.001	16.4±1.19	0.19±0.013
	A. nilotica	10	0.21±0.057	0.44±0.023	3.2±0.32	0.06±0.011
	A. robusta	10	0.49±0.039	0.28±0.012	8.2±0.71	0.11±0.011
	C. apiculatum	10	0.89±0.098	0.18±0.013	8.1±0.96	0.14±0.022
	D. cinerea	10	0.21±0.016	0.35±0.035	3.6±0.46	0.07±0.001
	E. crispa	10	0.74±0.053	0.20±0.015	10.1±0.80	0.12±0.010
	E. rigida	10	0.27±0.040	0.40±0.034	2.9±0.37	0.08±0.014
	G. buxifolia	10	0.44±0.043	0.52±0.021	14.6±0.96	0.19±0.011
	R. lancea	10	0.57±0.041	0.28±0.015	12.5±0.60	0.14±0.001
	Z. mucronata	10	0.40±0.063	0.38±0.014	9.4±1.34	0.12±0.019
Early rainy	*A. caffra*	10	0.57±0.036	0.040±0.048	14.0±1.25	0.18±0.018
	A. nilotica	10	0.09±0.001	0.57±0.082	2.4±0.40	0.05±0.001
	A. robusta	10	0.56±0.315	0.54±0.073	11.9±4.53	0.20±0.080
	C. apiculatum	10	0.57±0.106	0.44±0.072	10.9±1.50	0.16±0.022
	D. cinerea	10	0.17±0.016	0.68±0.044	5.3±0.25	0.10±0.001
	E. crispa	10	0.41±0.049	0.48±0.055	11.9±0.82	0.15±0.011
	E. rigida	10	0.12±0.001	0.84±0.082	5.0±0.39	0.09±0.001
	G. buxifolia	10	0.08±0.001	0.76±0.061	4.4±0.47	0.06±0.001
	R. lancea	10	0.56±0.061	0.41±0.039	14.6±0.45	0.17±0.001
	Z. mucronata	10	0.27±0.047	0.61±0.060	9.2±0.79	0.12±0.010
Late rainy	*A. caffra*	10	0.47±0.068	0.36±0.013	8.9±1.17	0.16±0.021
	A. nilotica	10	0.11±0.012	0.48±0.031	2.9±0.24	0.05±0.001
	A. robusta	10	0.44±0.044	0.46±0.021	10.0±0.60	0.19±0.012
	C. apiculatum	10	0.47±0.056	0.33±0.012	8.3±0.70	0.14±0.016
	D. cinerea	10	0.19±0.024	0.52±0.023	4.8±0.62	0.10±0.012
	E. crispa	10	0.43±0.034	0.35±0.019	7.9±0.35	0.14±0.001
	E. rigida	10	0.13±0.015	0.57±0.035	3.2±0.26	0.07±0.001
	G. buxifolia	10	0.19±0.020	0.56±0.023	5.9±0.59	0.10±0.001
	R. lancea	10	0.44±0.041	0.34±0.017	8.2±0.58	0.13±0.001
	Z. mucronata	10	0.22±0.020	0.49±0.016	4.8±0.47	0.10±0.001

n = species sample size

4.3.2 Effect of spinescence on instantaneous intake rate and intake rate related variables

There was a significant difference of interthorn distance amongst spinescent species ($F_{5,30}$=19.02; p<0.05). Interthorn distances of the respective species ranged as follow: *A. caffra> Z. mucronata> D. cinerae> A. nilotica> A. robusta> G. buxifolia* (table 4.1).

T-test showed no significant difference between mean intake rate as well as intake of spinescent and spineless species, whereas, many bites were cropped from spinescent (n=180) than spineless (n=120) plant species (t= 2.80; df= 256.77; p= 0.006). Bite size cropped by goats were smaller for spinescent relative to spineless species (t= 3.69; df= 283.57; p= 0.0003). Additionally, bite rate were higher for spinescent compared to spineless species (t= -3.30; df= 227.42; p= 0.001).

4.3.3 Effect of shoot/leaf morphology and phenology on instantaneous intake rate

Browse species with new leaves borne on long shoots (n= 120) were more efficiently foraged relative to those with new leaves on old short shoots (n= 180), (mean: 0.14 vs mean: 0.11gs^{-1}; t= -3.2; df.= 284.64; p< 0.002). The trait of growing new leaves on long shoots is typical of *E .crispa*, *C. apiculatum*, *R. lancea* and *Z. mucronata*, whereas that of growing new leaves on old short shoots is characteristic of *A. nilotica*, *D. cinerea*, *E. rigida* and *G. buxifolia*. *Acacia robusta* carried much leaf biomass and was relatively less spinescent featuring amongst species with the highest intake rate by goats. Browse species with new leaves on long shoots featured within the upper tier of intake rate ranking of all three seasons, as well as pooled intake rate ranking. Browse species with new leaves predominantly borne on old short shoots had *A. caffra* with outstanding intake rate in the dry, early rainy and late rainy seasons, while *G. buxifolia* was highly foraged upon during the dry season, and the rest featured in the lower tier. Evergreen species (n= 91) on the other hand, were consumed at a higher intake rate relative to deciduous (n=.209) ones (mean: 0.13 vs. mean: 0.12; t= 2.02; df = 278.01; p= 0.04). Incidentally, most of the evergreen species including *E. crispa* and *R. lancea* except *G. buxifolia* tended to be those with new leaves borne on new long shoots and were concurrently broad leafed.

4.3.4 Correlation of intake rate and intake rate related variables with leaf chemical components

Table 4.2 shows that, there was a significant positive correlation of intake rate and cellulose content of browse species (r= 0.71;.n=10; p= 0.023).in the dry season. Similarly, there was as well a significant positive correlation of condensed tannins and intake rate (r= 0.71; n= 10; p= 0.022) in the same season. Cellulose also had a significant positive correlation with bite size (r= 0.73; n=.10; p= 0.016) in the dry season. On the other hand, there was no correlation between intake rate and plant chemical variables at early rainy season, whereas, NDF(r= 0.65; n= 10; p= 0.044), hemicelulose (r= 0.76; n= 10; p= 0.012) and condensed tannins (r= 0.68; n= 10; p= 0.032) all had significant positive correlations with browsing time at early rainy season.

Regression equations modelling significant correlations of intake rate and related variables were:

(1) intake rate= 0.433 + BSDM (0.081), r^2 = 0.68, $p< 0.05$ and BSDM= bite size dry matter; (2) Bite rate= 0.503 –BSDM (0.147), r^2 = 0.597, $p< 0.05$ and BSDM= bite size dry matter; (3) Bite size dry matter= 1.713 – BR (4.210), r^2 = 0.597 ,$p< 0.05$ and BR= bite rate, and (4) Intake dry matter= 3.804 + DSDM (0.865), r^2 = 0.607, $p< 0.05$ and BSDM= bite

Table 4.2 Correlation coefficients (r) and probability difference(p) of levels of association of intake rate(gS^{-1}DM) time(S), bite rate(BitesS^{-1}) and bite Size dry matter(gDM) with leaf chemical components and plant secondary compounds

Season	Chemical components		Time (s)	Int R(gDMs^{-1})	Bite rate	Bite size(gDM)
Dry	Protein	r	-0.17	-0.08	-0.17	-0.04
		p	0.639	0.834	0.648	0.891
	NDF	r	0.32	0.31	-0.28	0.27
		p	0.364	0.382	0.426	0.444
	ADF	r	0.43	0.28	-0.51	0.42
		p	0.212	0.431	0.128	0.227
	ADL	r	0.29	0.03	-0.35	0.15
		p	0.423	0.936	0.323	0.673
	Hem Cel	r	0.05	0.29	0.17	-0.02
		p	0.883	0.415	0.642	0.963
	Cellulose	r	0.57	0.71	-0.54	0.73
		p	0.087	0.023*	0.108	0.016*
	C. Tannins	r	0.58	0.71	-0.39	0.61
		p	0.078	0.022*	0.271	0.061
Early rainy	Protein	r	-0.19	0.05	0.10	0.00
		p	0.599	0.898	0.778	0.992
	NDF	r	0.65	0.39	0.09	0.33
		p	0.044*	0.267	0.790	0.353
	ADF	r	0.14	0.18	-0.01	0.11
		p	0.689	0.619	0.989	0.759
	ADL	r	0.33	0.25	0.06	0.18
		p	0.354	0.485	0.856	0.619
	Hem Cel	r	0.76	0.37	-0.11	-0.35
		p	0.012*	0.288	0.762	0.316
	Cellulose	r	-0.46	-0.12	0.13	-0.12
		p	0.179	0.743	0.714	0.738
	C. Tannins	r	0.68	0.14	0.21	0.15
		p	0.032*	0.690	0.558	0.686

IntR(gDM)= intake rate gram dry matter; NDF= neutral detergent fibre; ADF= acid detergent fibre; ADL= acid detergent lignin; Hem. Cel= hemicellulose; C.Tannins= Condensed tannins; n= 10; *= significant correlation

The regression in Figure 4.2 was modelled, showing square root intake rate ($gDMs^{-1}$) and square root cellulose (%DM)

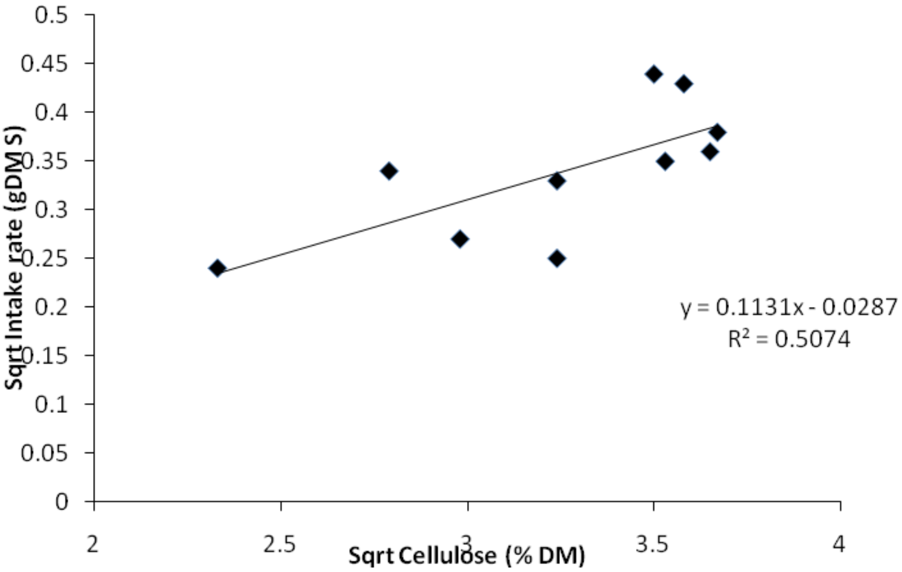

Figure 4.2 Scatter plot showing the regression between square root intake rate and square root cellulose dry matter of Nguni goats from a pooled multi-species data set for the dry season.

Similarly, the regression in Figure 4.3 was modelled from the correlation between square root intake rate ($gDMs^{-1}$) and percentage condensed tannins.

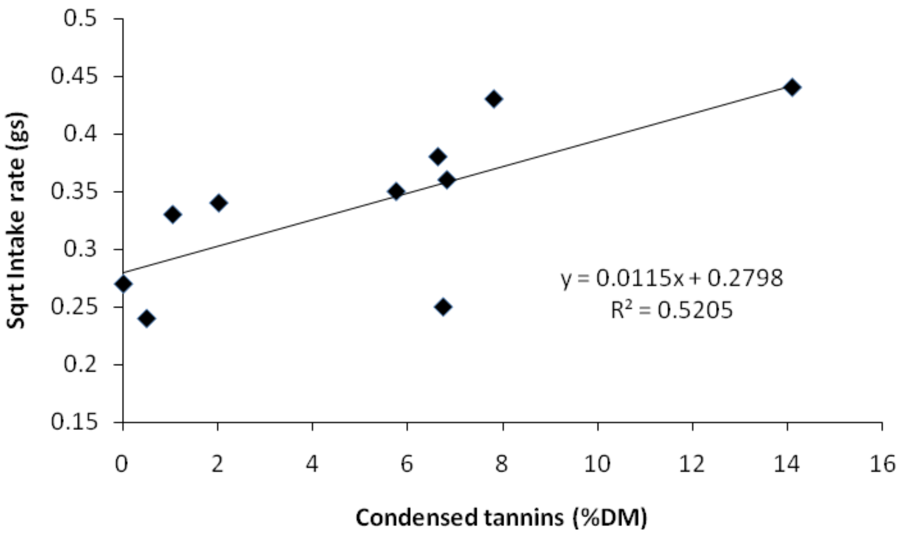

Figure 4.3 Regression between square root intake rate and percentage condensed tannins dry matter of Nguni goats from a pooled multi-species data set for the dry season.

Additionally, the regression below was modelled from the correlation between square root cellulose and log bite size dry matter of Nguni goats

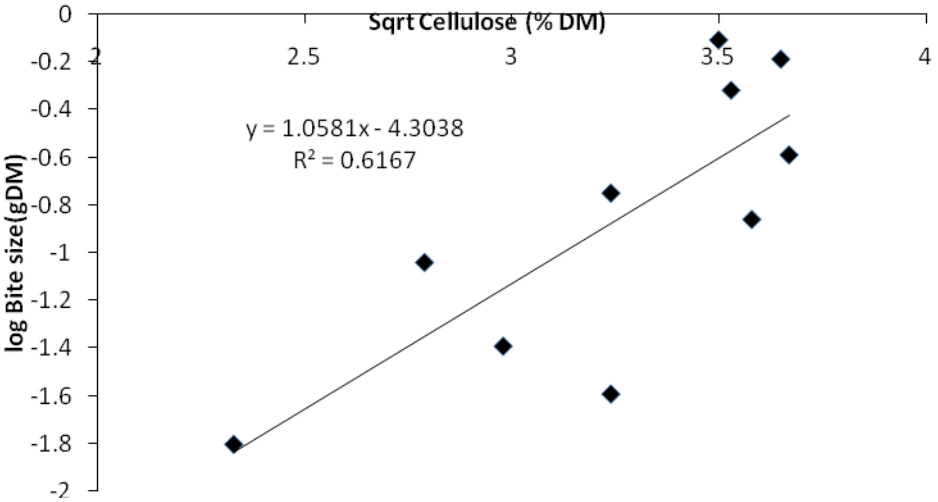

Figure 4.4 Regression between log bite size dry matter and square root cellulose percentage dry matter of Nun goats from a pooled multi-species data set for the dry season.

4.4 Discussion

4.4.1 Effect of seasons and species on instantaneous intake rate

Consistent with our prediction, short term intake rates varied amongst species (Scogings *et al*., 2004; Rogosic *et al*., 2006) and seasons (Bakare and Chimonyo, 2011). Instantaneous intake rate were highest at early rainy season, declined in the dry season and were lowest at late rainy season. These observations are consistent with those of (Dziba *et al*., 2003) in the Thornveld of the Eastern Cape and (Mkhize, 2008) in the Zululand Thornveld, KwaZulu - Natal.

Instantaneous intake rate of species during the different seasons, show that, during the dry season: *A. caffra* > *G. buxifolia* > *C. apiculatum* > *Z. mucronata* > *R. lancea* >.*E. crispa.* > *A. robusta* > *E. rigida* > *D. cinerea* > *A. nilotica*, whereas at early rainy season the trend was as follow*: A. robusta* > *A. caffra* > *R. lancea* > *C. apiculatum.*>.*E. crispa* >.*Z. mucronata* > *D. cinerea* > *E. rigida* > *G. buxifolia* > *A. nilotica*, and at late rainy season *A. robusta* > *A. caffra* > *C. apiculatum* > *E. crispa* > *R. lancea* > *Z. mucronata* > *D. cinerea* > *G. buxifolia* > *E. rigida* > *A. nilotica.* Seasonal intake rate trends had diverse ranking during the dormant dry season and the growing rainy seasons Instantaneous intake rate of some species was marginal in the dry season and subsequently improved markedly at early rainy season, notably, instantaneous intake rate of *A. robusta* and *R. lancea* were improved remarkably from dry to early rainy season. Bite rates were highest at early rainy season which coincided with the growth of new shoots and leaves, followed by late rainy season and lowest in the dry season. Early rainy season during which the highest bite rates were taken by Nguni goats in the current study, contrasts with the dry season (Yayneshet *et al*., 2008) in a semiarid region of Ethiopia where similar observations were registered. Both studies lay credence to the variation of bite rate of different plant species with seasons, though observations were made in different agro-ecological zones. Concurrent with our observations (Yayneshet *et al*., 2008), bite rates were influenced by species and seasons.

4.4.2 Effect of physical traits on instantaneous intake rate

Contrary to our expectation that intake or intake rate will be lower for spinescent than spineless plant species (Wilson and Kerley, 2003a; Hanley *et al*., 2007), there was no significant difference between the mean intake rate of spinescent and spineless plant species. Spinescent species with significant contribution to intake rate such as *A. caffra* and *A. robusta* featured amongst spineless species with high consumption rate. However, spinescence exerted various effects on intake rate related variables. More bites were cropped from spinescent than spineless species, given that goats had to pluck leaves in between thorns and spines. This gave rise to smaller bites than would be taken from spineless species with no physical or structural barrier to browsing by goats. This observation was consistent with that of Wilson and kerley (2003a) on bite diameter selection by Blue duiker, Bushbuck, Common duiker, Boar goat, Kudu and Black rhinoceros. Bite rates were significantly higher for spinescent than spineless species, compensating for less foliage cropped and equilibrating the higher intake from spineless species. Furthermore, shoot and leaf morphology that has been observed to have strong implications on intake rate (Dziba *et al.,* 2003; Scogings *et al*., 2004), can be evaluated relative to spinescence inorder to ascertain which of the two traits has stronger influence. *Acacia robusta* had higher intake rate relative to *Z. mucronata,* both had new leaves and were respectively spinescent. While the former had fine leaves on old short shoots, the later had broad leaves. Intake rate, therefore, might have been influenced more by leaf morphology than by the presence of spines (Mkhize, 2008).

In accordance with our expectation that shoot morphology would exert a positive influence on intake rate/consumption rate (Dziba *et al*., 2003), species with new long shoots had higher intake rates than those with new leaves on short old shoots. Plant species with new long shoots were dominantly broad leafed in nature (appendix 3), except *A. robusta* that had fine leaves. Therefore, goats had higher intake rate from broad than fine leaf species in all three seasons. This observation is consistent with those of Haschick and Kerley (1977), Dziba *et al*. (2003), Wilson and kerley (2003a) and Mkhize (2008), whereby higher intake rates were obtained from broad leafed species as well as those with long shoots.

4.4.3 Effect of plant chemical and secondary components on foraging efficiency

Except for cellulose that correlated positively with intake rate and bite size in the dry season, NDF, ADF, hemicellulose and ADL had no significant interaction with intake rate and intake rate related variables. The results of the current study thus partially agree with our expectation that fibre will negatively affect intake rate as observed from previous studies by Hanley et al (2005), though the effect emerged rather positive for cellulose than negative. Mkhize (2008), reported a positive correlation between intake rate and fibrousness in dry season in similar studies in the Zululand Thornveld. Cellulose is structural fermentable fibre that lends support to browse and herbage, and was significantly higher in browse in the dry season compared to early rainy season. In addition, species from which consumption rate was higher emanating from large bite sizes grew new long shoots and were broad leafed to a larger extent, availing the opportunity for goats to consume more cellulose alongside browse forage. The cellulose content of most browse species in both dry and early rainy season was below the 19% threshold (Solaiman, 2010), beyond which cellulose becomes prohibitive to intake rate and utilization of browse (Appendix 2).

Contrary to our expectation, there was no significant interaction between crude protein and intake rate /foraging efficiency. This observation concurred with those of (Scogings *et al.***,** 2004; Mkhize, 2008), whereby there was no correlation between crude protein and intake rate. This is suggestive that, if goat primary objective function was to maximize intake rate by foraging more on species with new long shoots and broad leaves (Dziba *et al*., 2003; Scogings *et al*., 2004; Mkhize, 2008) concurrently, therefore, crude protein becomes a secondary objective function sought after as a result of post ingestive feed back(appendix 2).

Contrary to expectation, condensed tannins correlated positively with intake rate in the dry season and browsing time at early rainy season. Concomitant increase of intake rate and condensed tannins was also observed in studies by Scogings *et al* (2004), in the semi-arid subtropical savannah of the Eastern Cape and the Zululand Thornveld Mkhize (2008). Increase in intake of tanniferous browses under short term confined experiments, indicate the inability of condensed tannins to deter intake rate. Several reasons have been advanced in previous studies to support goat ability to consume and utilize tanniferous plants and are relevant to the present study. The prevalence of condensed tannins in virtually all browses (Muir, 2011), and the inability of goats to completely avoid them, given their dependence on browse in semiarid and arid savannahs. Goats exhibit greater tolerance to consume (Dove, 2010), manage and utilize (Rogosic *et al*., 2006) tanniferous browses relative to sheep (Dove, 2010). They, therefore, have a stronger inclination to browse and crave for variety (Provenza *et al*., 2003), that is as well associated with diverse plant secondary metabolites and toxins. Some of these toxins and secondary metabolites potentially interact and neutralize others thus increasing intake rate and long term intake (Rogosic *et al*., 2006). Remarkably, most of the browsing time was spent on plants that grew new leaves on new shoots, all of which contained significant levels of condensed tannins.

Similar to crude protein, condensed tannins were not primary drivers of short term intake rate. Suggesting that, goat primary objective function in the short term was to maximize cumulative nutrient intake regardless of subsequent post ingestive feedback (Scogings *et al*., 2004), hence high instantaneous intake of tanniferous browse plants. Conversely, *D. cinerea* emerged differently from the trend, though with significant concentration of condensed tannins, suggesting the interaction of some other plant secondary compound to exert deterrence to instantaneous intake rate. It also highlighted diverse effect of plant chemistry on short term intake rate and seasons, given that this positive correlation of intake rate and condensed tannin was in the dry season and not at early rainy season.

Instantaneous intake rate ranking of the same species for different seasons differ considering the chemical and morphological changes that take place within and between seasons. Even when there is marginal or no chemical change with regards to condensed tannins levels, instantaneous intake rate still differ rendering understanding and prediction of foraging efficiency on the basis of plant chemistry difficult The outcome is strongly suggestive of the influence of a suite of plant secondary compounds and nutrients, some of which have not been examined in the present study. This study gives us greater insight into browse/browser interaction in subtropical savannahs and potential inputs that can improve on range and herbivore ecological management. There is therefore need to broaden the scope of plant secondary compounds examined and their potential interaction with different nutrients components.

4.5 Conclusion

Foraging efficiency by Nguni goats was significantly influenced by plant species and seasons. Efficient foraging demanded that, they selectively foraged on browses that enabled them to maximize instantaneous intake rate and nutrients, before proceeding to browses with less vegetative material. Condensed tannins did not significantly influence intake rate. Similarly, spinescence did not affect intake rate, given that more bites were taken from spinescent species to compensate for large bites from spineless leafy species.

Plants generally differ in quality, quantity and type of nutrients, different proportions of fibre and PSM. Each browse species therefore makes an important contribution to the nutrient pool that makes up the diet in one season or the other. Their interaction in the diet, potentially mitigated deterrence or poisoning when a variety of forage resources was available, thus, promoting the use of both rich and poor quality browse plants, This, therefore reaffirms the need for rich species vegetation composition and management inputs that will enhance its conservation.

Foraging efficiently can therefore be accomplish when there is variety of phenological, morphological and chemically different forages, and good ecological balance with grass herbage which is seasonal. Therefore, managerial approaches that seek to promote browse species variety optimum stocking rate and judicious browsing will as well enhance efficient foraging in the semiarid savannah.

CHAPTER 5
GENERAL DISCUSSION

5.1 Summary of aims and results

The trial was conducted to determine the seasonal trends of diet selection and foraging efficiency of Nguni goats on a group of six browse plants in the former and ten browse plants in the later, commonly found in the Bushveld of Gauteng. It was a secondary aim to study how plant morphology, phenology and chemistry can potentially explain the observed patterns. Short term intake and intake rate were used as indices of diet selection and foraging efficiency respectively. Diet selection experiment was done in cafeteria style, whereas in foraging efficiency experiment, browse species branches were presented to goats individually. Both experiments were done under shade.

The order of selection of plant species in diet selection experiment was as follows: *R. lancea* > *A. robusta* >.*E. crispa.* > *Z. mucronata* > *D. cinerea* > *A. nilotica* and the seasons had the following pattern early rainy >dry season relative to intake Plant phenology affected intake, with evergreen plant species offering a higher mean significant intake than deciduous species. Broad leaf species also tended to be selected more than fine leaf ones. Spinescence had no significant effect on intake, whereas many bites tended to be taken from spinescent than spineless species. Intake as well tended to be higher for long shoot species than old short shoot counterparts Intake was positively related to cellulose at early rainy season as well as intake related variables such as browsing time and number of bites cropped. In the dry season, only cellulose from amongst plant chemical components had significant correlation with bite size.

In foraging efficiency experiment, intake rate was in the order*: A. caffra* > *A. robusta* > *R. lancea* > *C. apiculatum* > *E. crispa* > *G. buxifolia* > *Z. mucronata* > *D. cinerea* > *E. rigida* > *A. nilotica*. In terms of seasonal trends of intake rate the order was: early rainy > late rainy >dry. There tended to be a strong positive correlation between bite size and intake rate, whereas there was a negative relation between bite rate and intake rate. Goats achieved higher intake rate from plant species with leaves on long shoots relative to those on old short shoots. Coincidentally, plant species with long shoots were broad leafed in nature and obviously had the same effect on intake rate. Contrary to our prediction, goats did not forage less efficiently from spinescent species relative to spineless ones.

Correlation between plant chemical components and foraging efficiency variables indicated that in the dry season, cellulose had a positive relation with intake rate and bite size. Similarly, condensed tannins had a positive correlation with intake rate. At early rainy season, there was no relation between plant chemical components and intake rate, whereas NDF, hemicellulose and condensed tannins correlated positively with foraging efficiency variable of browsing time.

5.2 Interpretation and potential implications

Given that diet selection experiment was cafeteria designed, whereas foraging efficiency presented unique opportunities to forage from individual browse species under shade, considerable caution has to be exercised at extrapolating the results to natural vegetation. Natural vegetation on range is inherently complex and dynamic with a suite of different factors ranging from climate, precipitation, humidity, temperature, soil fertility, vegetation species composition and distribution, and topography affecting forage availability and quality. None the less, important insight is gained with regards to mammalian herbivore foraging behaviour when: (1) forage options increase or decrease, as is the case from dry to rainy season and vice versa ; (2) morphological, phenological and chemical changes take place amongst the respective browse species; (3) Overgrazing occurs as a result of overstocking, further reducing choice and restricting animals to very limited and poor quality forage resources or ideally when deciduous species lose foliage reducing vegetation species composition; (4) Intra-seasonal and extra-seasonal changes take place, thus affecting the nutrients, component fibre composition, and plant secondary metabolite concentration of the respective browse species; (5) foraging occurs in arid and semi-arid regions, where generalist mammalian herbivores have browse as sole forage during all/some period of the year; and (6) management decisions have to be taken with regards to vegetation species composition.

The high intake of *R. lancea, A. robusta* and *E. crispa relative* to *Z. mucronata*, *D. cinerea* and *A. nilotica* in diet selection suggest that these evergreen species can serve as important source of forage for goats during the dry season. Additionally, lower preference of spinescent species also suggest goats initial quest to satisfy hunger by optimizing intake once its food resources have been identified and subsequently selecting species that yield lower intake. This enables them to compose a diet adequate in nutrients and minimal in plant secondary compounds. On the other hand, it is postulated that goats increase their bite rate when foraging from spinescent and less leafy species in order to compensate for inadequate access to foliage or sparse foliage and maximize their intake of nutrients. Evidently, mean intake and intake rate of spinescent and spineless species was not significantly different. Also, the high instantaneous intake rate of evergreen and spinescent *G. buxifolia* in the dry season and very low intake rate at onset of the rainy season is indicative of goat behavioural adjustments to accommodate less preferred species during periods of scarcity to optimize intake. The dynamic shift in selection with its associated changes in browse quality and canopy architecture, highlight the need to maintain vegetation species composition in order to ensure the availability of sufficient forage all year round.

The positive correlation of condensed tannins with intake rate in foraging efficiency is suggestive of goat ability to tolerate considerable levels of condensed tannins. This thus, equips them first to thrive on browse based diets with prevalent condensed tannins, and uniquely in the semi-arid vegetation of Gauteng, where it is virtually sole source of forage in the dry season. The high intake and intake rate observed at early rainy season relative to dry season in both diet selection and foraging efficiency, suggests that browse plants such as *R. lancea, A. robusta, E. crispa* and *Z. mucronata* have the potential of making important contribution to goat production and related ungulates. In the dry season, the trend is the same, but with *A. robusta* and *Z.mucronata* likely to lose foliage because of their deciduous nature.

5.3 Future Research

More work is required in the area of plant morphology especially spinescence, given that many different types of spines/thorns exist and will tend to offer different levels of deterrence. Some may be efficient, others partially and some ineffective at deterring herbivory by ungulates.

Research work is required to control the more preferred species especially those with long shoots from being consumed out of existence and disequilibrating vegetation species composition, ecological balance and long term goat production.

Plants with a wider distribution of condensed tannins and other identified secondary compounds should be used in trials to test and ascertain the critical level at which they become effective as detterents to herbivory by goats and other mammalian herbivores.
The nutrient composition of different species should be evaluated along a gradient in order to study their respect influences on selection.

Digestibility trials are required to determine the nutritional contribution of the studied species to goat production and productivity after confirming the results on free ranging counterparts. This will allow for a direct and precise measurement of plant species contribution to animal productivity.

Bush encroachment has become a critical problem in the savannahs of the world, given the scale of cattle ranging. Additionally, the use of chemical and mechanical methods to control invasive alien woody species is expensive and require periodic attention that adds to control cost availing the opportunity and need for goats to be used as biological agents of bush control. It is therefore strongly recommended that, goat husbandry should be promoted with necessary technical support.

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APPENDIX

Appendix 1: Mean values (±SEM) gkg^{-1} of plant leaf chemical components and secondary compounds of the different species for dry and early rainy season.

Spp. ID= species identity; n= species sample size; CP= crude protein; NDF= neutral detergent fibre; ADF=acid detergent fibre; H.Cell= hemicelluloses; Cell= cellulose; ADL= acid detergent lignin; C.Tannins= condensed tannins; AN= *Acacia nilotica*; AR= *Acacia robusta*; DC= *Dichrostachys cinerea*; EC= *Euclea crispa*; RL= *Rhus lancea*; ZM= *Ziziphus mucronata*

Season	Spp ID	n	CP	NDF	ADF	H.Cell	Cell	ADL	C.Tannin
Dry	AN	1	125(00.0)	181(00.0)	106(00.0)	75(00.0)	71(00.0)	35(00.0)	4.9(0.00)
	AR	5	114(15.5)	445(17.3)	234(4.8)	211(15.3)	105(3.7)	129(3.7)	10.4(1.05)
	DC	1	142(00.0)	414(00.0)	232(00.0)	182(00.0)	101(00.0)	131(0.0)	67.4(0.00)
	EC	7	99(13.6)	413(15.0)	313(10.3)	100(7.7)	125(4.7)	188(6.7)	57.5(5.44)
	RL	10	120(11.5)	375(15.2)	242(7.8)	133(8.5)	135(4.2)	107(4.8)	66.3(7.90)
	ZM	4	129(3.1)	280(19.0)	136(3.7)	144(11.9)	78(1.9)	58(1.9)	20.1(3.29)
rainy	AN	6	140(4.5)	220(15.1)	103(5.2)	117(14.6)	55(3.1)	48(3.2)	5.6(0.29)
	AR	6	143(6.1)	517(19.7)	256(2.8)	262(17.8)	109(1.5)	147(2.6)	12.8(1.00)
	DC	6	199(10.8)	494(11.0)	200(17.6)	194(17.0)	117(4.3)	184(16.2)	75.2(16.68)
	EC	6	81(6.6)	358(21.2)	270(16.8)	88(8.0)	102(9.2)	168(9.0)	70.0(8.85)
	RL	6	122(6.1)	389{13.4)	257(11.3)	132(7.7)	146(7.5)	111(11.7)	54.8(11.54)
	ZM	6	173(11.6)	377(23.6)	169(7.0)	208(22.3)	81(3.3)	88(5.8)	58.6(9.53)

Appendix 2: Mean values (±SEM) gkg^{-1} of plant chemical components and secondary compounds for the dry and early rainy seasons

Season	Spp ID	n	CP	NDF	ADF	HCell	Cell	ADL	C.tannin
Dry	A. caffra	10	149(10)	356(11.3)	231(14.4)	125(9.7)	123(7.2)	108(17.4)	141(11.97)
	A. nilotica	1	125(00.0)	194(00.0)	116(00.0)	78(0.0)	54(0.0)	62(00.0)	4.9(0.00)
	A. robusta	5	114(15.5)	446(17.3)	234(4.8)	211(15.3)	105(3.7)	129(3.7)	10.4(1.05)
	C. apiculatum	10	128(10.3)	287(6.8)	179(2.9)	108(5.4)	133(4.0)	45(3.4)	68.2(10.07)
	D. cinerea	1	142(00.0)	443(00.0)	265(00.0)	178(0.0)	105(0.0)	160(00.0)	67.4(0.00)
	E.crispa	7	99(13.6)	413(15.0)	313(10.3)	100(7.7)	125(4.6)	188(6.7)	57.5(5.44)
	E. rigida	2	116(24.0)	237(5.4)	127(9.3)	110(14.6)	89(9.0)	38(0.3)	00(0.0)
	G. buxifolia	5	102(2.1)	278(20.6)	199(3.7)	178(18.6)	128(3.5)	71(3.6)	78.1(4.88)
	R. lancea	10	120(10.6)	375(5.2)	242(7.8)	133(8.5)	135(4.2)	107(4.8)	66.(3.90)
	Z. mucronata	4	129(3.2)	280(9.0)	136(3.7)	144(1.9)	78(1.9)	58(1.7)	20.1(3.30)
Early	A. caffra	6	225(14.0)	388(51.8)	237(35.0)	152(26.4)	109(11.9)	127(25.3)	131(13.87)
Rainy	A. nilotica	6	140(4.5)	321(33.8)	197(22.4)	125(18.7)	110(15.2)	87(11.4)	4.7(0.97)
	A. robusta	6	143(6.1)	676(40.6)	229(18.5)	147(28.7)	111(5.6)	118(19.0)	12.8(1.00)
	C. apiculatum	6	152(2.7)	367(37.6)	210(29.1)	157(29.1)	108(14.8)	102(17.9)	21.9(3.31)
	D. cinerea	6	199(10.8)	401(27.8)	247(29.5)	153(16.6)	110(7.7)	137(26.7)	75.2(16.68)
	E.crispa	6	81(6.7)	371(60.0)	282(32.8)	152(35.4)	95(11.4)	124(23.7)	70.0(8.86)
	E. rigida	6	175(6.4)	346(25.7)	192(23.4)	154(8.4)	101(13.2)	91(14.0)	1.4(1.38)
	G. buxifolia	6	125(3.8)	399(43.7)	234(24.5)	165(31.9)	105(4.5)	129(23.1)	99.3(12.28)
	R. lancea	6	122(6.1)	392(39.7)	201(28.8)	191(20.7)	97(11.4)	103(22.5)	54.8(11.55)
	Z. mucronata	6	173(11.6)	387(30.4)	208(16.3)	95(15.3)	113(10.0)	95(15.3)	58.5(9.53)

Spp ID= species identity; n= species sample size; CP= crude protein; NDF= neutral detergent fibre; ADF= acid detergent fibre; HCell= hemicellulose; Cell= cellulose; ADL= acid detergent lignin; C Tannin= condensed tannins

Appendix 3: Plant phenology, leaf and shoot morphology in relation to pooled percentage means across seasons of chemical components (±SEM) and plant secondary compounds (±SEM) for diet selection experiment

	n	Dec Spec	n	Evergreen	n	Br. Leaf	n	Fine Leaf	n	LONS	n	LSS
C Protein	35	15.1±0.81^{a}	29	10.7±0.89^{b}	39	11.9±0.86^{b}	25	14.9±1.07^{a}	39	11.9±0.86^{b}	25	14.9±1.07^{a}
NDF	35	38.8±2.22^{a}	29	38.3±2.43^{a}	39	37.2±2.06^{a}	25	40.8±2.57^{a}	39	37.2±2.06^{a}	25	40.8±2.57^{a}
ADF	35	20.1±1.45^{b}	29	26.8±1.60^{a}	39	23.9±1.56^{a}	25	21.9±1.95^{a}	39	23.9±1.56^{a}	25	21.9±1.95^{a}
Hem. Cel	35	18.8±0.85^{a}	29	11.5±1.33^{b}	39	13.3±1.56^{b}	25	19.0±1.57^{a}	39	13.5±1.26^{b}	25	19.0±1.57^{a}
Cellulose	35	9.1±0.54^{b}	29	12.8±0.63^{a}	39	11.6±0.62^{a}	25	9.5±0.78^{b}	39	11.6±0.62^{a}	25	9.5±0.78^{b}
ADL	35	11.0±1.15^{b}	29	14.0±1.26^{a}	39	12.4±1.14^{a}	25	12.3±1.42^{a}	39	12.4±1.14^{a}	25	12.3±1.42^{a}
Tannin	34	3.3±0.70^{b}	29	6.3 ±0.76^{a}	39	5.9±0.67^{a}	24	2.8±0.85^{b}	39	5.8±0.67^{a}	24	2.8±0.85^{b}

C. Protein= crude protein; NDF= neutral detergent fibre; ADF= acid detergent fibre; Hem. Cel= hemicellulose; ADL= acid detergent lignin; n= sample size; DEC. Spec.= deciduous species; Evergreen= evergreen species; Br. Leaf= broad leafed species; Fine Leaf= Fine leafed species; LONS= long shoot species; LSS= short shoot species

Appendix 4: Plant phenology, leaf and shoot morphology in relation to pooled percentage means of chemical components (±SEM) and plant secondary compounds (SEM) for foraging efficiency experiment

Chem Com	n	Dec Spec	n	Evergreen	n	Br. Leaf	n	Fine Leaf	n	Lons	n	LSS
C Protein	69	15.6±0.60^{a}	42	10.9±0.77^{b}	74	12.7±0.63^{b}	37	16.1±0.89^{a}	55	12.4±0.75^{b}	56	15.2±0.75^{a}
NDF	69	35.5±1.42^{a}	42	38.0±1.82^{a}	74	35.9±1.38^{a}	37	37.6±1.95^{a}	55	35.9±1.60^{a}	56	37.0±1.59^{a}
ADF	69	20.8±1.0^{b}	42	23.3±1.29^{a}	74	21.3±0.98^{a}	37	22.7±1.39^{a}	55	21.8±1.15^{a}	56	21.8±1.14^{a}
Hem. Cel	69	14.7±0.92^{a}	42	14.7±1.1^{a}	74	14.6±0.88^{a}	37	14.9±1.25^{a}	55	14.4±1.02^{a}	56	15.3±1.01^{a}
Cellulose	69	11.1±0.43^{a}	42	11.5±0.55^{a}	74	11.4±0.42^{a}	37	11.0±0.59^{a}	55	11.5±0.48^{a}	56	10.9±0.48^{a}
ADL	69	9.8±0.84^{b}	42	11.8±1.08^{b}	74	10.0±0.82^{a}	37	11.7±1.15^{a}	55	10.2±0.96^{a}	56	10.9±0.95^{a}
Tannin	69	5.2±0.76^{a}	42	6.7±0.97^{a}	74	5.5±0.55^{a}	37	6.3±1.05^{a}	55	5.6±0.86^{a}	56	5.9±0.73^{a}

C. Protein= crude protein; NDF= neutral detergent fibre; ADF= acid detergent fibre; Hem. Cel= hemicellulose; ADL= acid detergent lignin; n= sample size; DEC. Spec.= deciduous species; Evergreen= evergreen species; Br. Leaf= broad leafed species; Fine Leaf= Fine leafed species; LONS= long shoot species; LSS= short shoot species