# DIET SELECTION AND FORAGING EFFICIENCY OF NGUNI GOATS IN THE ZULULAND THORNVELD, KWAZULU-NATAL

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# DIET SELECTION AND FORAGING EFFICIENCY OF NGUNI GOATS IN THE ZULULAND THORNVELD, KWAZULU-NATAL

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By

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## DECLARATION

I (**Ntuthuko Raphael Mkhize**) hereby declare that this thesis is entirely my original work with the exception of such references and quotations that have been attributed to their authors or sources. This thesis has never been submitted for any degree of examination in any other university.

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## DEDICATION

I whole heartedly dedicate this thesis to each and every South African child who lives in absolute poverty, born by two, but raised by a single, illiterate and unemployed parent. This should prove that despite their difficult situation, with enough intent, action, focus, faith, dedication and commitment they too can achieve their aspirations. "The race is not to the swift or the battle to the strong nor does food come to the wise or wealth to the brilliant or favour to the learned; but **time and chance** happen to them all..."

Ecclesiastes 9: 11

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Ntuthuko Raphael Mkhize

#### SUMMARY

## Diet Selection and Foraging Efficiency of Nguni Goats in the Zululand thornveld, KwaZulu-Natal

by

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Supervisor: Prof. Peter F. Scogings

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Foraging efficiency and diet selection are central processes in plant-herbivore interactions. An understanding of these important parameters of foraging behaviour underpins sustainable vegetation management and profitable animal production. As a step towards better understanding the browse-browser interactions in a sub-humid subtropical savanna, a Nguni goat breed was used as a model browser in cafeteria-style experiments.

The primary objective of the study was to determine the seasonal and plant species patterns of foraging efficiency (indexed by short-term intake rates) and diet selection (indexed by intake). The secondary aim was to investigate how potential explanatory variables such as plant morphology (spinescence, long vs. short shoots and broad vs. fine leaves), phenology (evergreen vs. deciduous species) and plant chemistry (nitrogen, neutral detergent fibre, acid detergent fibre, acid detergent lignin, condensed tannin, cellulose and hemicellulose) are related with the observed patterns.

Six browse species (*Acacia natalitia*, *A. nilotica*, *Dichrostachys cinerea*, *Grewia occidentalis*, *Gymnosporia maranguensis* and *Scutia myrtina*) were used in two experiments to estimate (1) short-term intake rates and (2) intake patterns at four times during the year (i.e. early, middle and late wet season and dry season).

Intake rates varied significantly (P = 0.022) among plant species, with broad leaved species being consumed at higher rates than fine leaved ones. Intake rates were highest during the dry season (mean: 0.18 g s<sup>-1</sup> ± SEM: 0.012 g s<sup>-1</sup>) and lowest in the late wet season (mean: 0.15 g s<sup>-1</sup> ± SEM: 0.009 g s<sup>-1</sup>). Bite size was found to be the key variable influencing the intake rate of Nguni goats. No significant relationships were found between intake rate and either nitrogen, neutral detergent fibre, acid detergent fibre, acid detergent lignin, cellulose or hemicellulose concentrations. Condensed tannin concentration (% DM) was positively correlated with both intake rate (r = 0.65, P = 0.001, n = 24) and bite size (r = 0.53, P = 0.007, n = 24).

Diet selection was affected by the interactions between the seasons and browse species (P = 0.001). S. myrtina and G. occidentalis were consistently among the most preferred species through out all seasons, while the opposite was true for G. maranguensis and A. nilotica. During the dry season, A. natalitia ranked third among the avoided species and inconsistently featured among the most preferred species later in wet seasons. The opposite was observed for D. cinerea. A positive relationship was also observed between intake (an index for diet selection) and condensed tannin (r = 0.27, P = 0.001, n = 144).

Both foraging efficiency and diet selection were influenced more by the leaf and shoot morphology than spinescence. Plant chemistry did not clearly explain either foraging efficiency or diet selection patterns. These results have important implications for vegetation management and goat production in the Zululand Coastal Thornveld.

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#### **CHAPTER 1**

#### GENERAL INTRODUCTION

#### Background

Savannas cover 54% of southern Africa and 60% of sub-Sahara Africa (Scholes, 1997; Scholes and Archer, 1997). Being widespread in Africa, savannas support large, rapidly growing human populations and their associated livestock (Scholes and Archer, 1997). Thus the socio-economic value of the world's savannas is huge. However, human factors have led to extensive modification of savannas, either through vegetation removal for livestock grazing, wood harvesting and crop production, or through plant invasions caused by fire suppression, reduction of wild ungulates and overgrazing by domestic livestock (Scholes and Archer, 1997). There is thus a clear need for improved understanding of the impacts of management on savanna systems.

The domestic goat is probably the most important browser in the savannas of Africa (Nyamangara and Ndlovu, 1995; Bosman et al., 1996). Goats are important for meat, milk and hide production and are commonly used for ritual slaughter in rural communities. However, they are often blamed for habitat destruction (Kerley et al., 1995; Reid and Ellis, 1995), which can lead to the reduction of biodiversity and enhanced competition with wild ungulates that depend on scarce resources (Ekblad et al., 1993; Hamann, 1993; Parkes, 1994; Norton, 1995). In contrast to their negative image, however, goats are also considered as useful biological agents of woody plant control in savannas, especially following fire or mechanical clearing (Trollope et al., 1989; O'Connor, 1996). Therefore, it is important to develop a sound understanding of the tree-goat interaction in Africa.

A level of understanding of browse-browser interactions in savannas, that allows highly confident predictions to be made, would be extremely valuable for the conservation and management of savannas, for either the production of browse, or the control of woody plant invasions. However, the understanding of these interactions in savannas is weak. Relative to the research effort given to browse-browser interactions in boreal and temperate woodlands and forests, few studies have been conducted in tropical or subtropical savannas (Scogings, 2003; Rooke et al., 2004).

Research on browse-browser interactions in semi-arid subtropical savannas on the eastern seaboard of South Africa shows that diet selection is mainly governed by shoot morphology and then by associated chemical traits (Dziba et al., 2003; Scogings et al., 2004).

#### **Literature Review**

The objective of this section is to discuss the utilization of woody plants in relation to their nutritive value and anti-quality factors that are believed to act as plants defence mechanisms against herbivory. The optimal utilization of woody plant species in savannas depends on a better understanding of plant-animal interactions (Dziba et al., 2003). Many woody plants have defensive strategies (morphological or chemical defence traits) against herbivores. As a result, herbivores face on a regular basis the challenge of harvesting sufficient nutrients to evade starvation and produce viable offspring while avoiding the negative effects of phytochemicals or other anti-quality factors (Launchbaugh, 1996). Therefore, understanding how several plant biochemical mechanisms, physical defenses, growth forms or distribution patterns affect herbivory and how herbivores respond to these factors is critical to our understanding of the role that herbivores play in our grazing systems. This section therefore discusses different ways in which browsers are adapted to change their feeding behaviours as a strategy to deal with anti-quality factors in forages.

#### Browse utilization in the African savannas

Most of the Southern African countries are blessed with a diverse range of browsing game animal species, which have an enormous intrinsic and commercial value (Topps, 1997). Lack of adequate year-round feed resources is probably the most important factor contributing to low growth rates and subsequently low animal production, especially during the dry season in subtropical and tropical regions (Sawe et al., 1998; Makkar and Becker, 1998). The use of browse species as forage for ruminants (such as goats and wild herbivores) is increasingly becoming important in many parts of the tropics (Aganga and Tshwenyane, 2003). Browses have multiple roles in farming systems, as animal feed, fire wood, mulch and are useful in soil conservation and improvement (Kaitho, 1997; Topps, 1997). In the communal areas of northern KwaZulu-Natal, farmers use trees for medicinal purposes such as to treat worm infestations and coughs and for increasing milk production in their livestock (Kunene et al., 2003).

#### Browse as forage

This discussion is restricted only to the use of woody plants as forage for mammalian herbivores. Although good statistical evidence on the magnitude of this feed source is lacking (Wilkins, 2000), browse is clearly a major component of the diets of goats and other browsers (Pawelek et al., 2008). Browse species are more important for ruminant production during dry seasons when the nutritive value and quantity of herbaceous plants decline (Abdulrazak et al., 2000a). The parts of trees that are commonly used as feed include leaves, tender shoots or twigs, fruits, pods and seeds (Aganga and Tshwenyane, 2003).

Nutrient and energy intake of browses directly depends on the chemical composition of the leaves and young twigs of trees (Ferwerda et al., 2006). According to Mokoboki et al. (2005) many browse species are of good nutritive value and have a potential for integration into livestock feeding systems. Tree leaves may have crude protein (CP) content up to 250 g kg<sup>-1</sup> DM and, in addition to their direct contribution to nutrient supply, may increase the digestibility of the low-CP basal diet (Wilkins, 2000). Many other studies (Aschalk et al., 2000; Mokobiki et al., 2005; Abdulrazak et al., 2000b; Kallah et al., 2000: Makkar and Becker, 1998; Sawe et al., 1998) support the notion that browse leaves from various species are a good source of crude protein and energy. Moreover, a positive growth response in goats fed leguminous woody plants and pods of Acacia albida as dietary supplements has been reported (Sawe et al., 1998). Supplementation with Dichrostachys cinerea fruits resulted in increased digestibility, nitrogen-retention and subsequently improved goat performance (Smith et al., 2005). However, in contrast to the beneficial effects of woody plants as forages, some of the plant species have been reported to have detrimental effects to livestock if consumed in large quantities (Kunene et al., 2003: Kellerman et al., 1988). The presence of phenolic compounds and other anti-quality factors in browse species has a negative effect on their nutritive value and on intake by herbivores (Abdulrazak et al., 2000a b; Wilkins, 2000).

#### Anti-quality factors in browses

Plants have co-evolved with predator populations of bacteria, insects, fungi and grazing animals and have developed defence mechanisms which assist their survival (Aganga and Tshwenyane, 2003; Kaitho, 1997). This section is solely dedicated to briefly discussing the different types of anti-quality factors that are used by woody plants as defence mechanisms against mammalian herbivores. Some effects of these factors on herbivore production and the ways in which animals deal with anti-quality factors, are discussed briefly.

Morphological structures of rangeland plants (e.g. spines, thorns and prickles) are largely reported to act as plant defence against herbivory and have been shown to affect the foraging behaviour of mammalian herbivores (Cooper and Owen-smith, 1986; Papachristou et al., 2003). Some forms of spinescences (especially, hooked thorns) catch on lips, tongues and ears and, therefore, require animals to carefully manipulate the plants in their mouths to avoid pain and injuries. Feeding rates by herbivores browsing on species armed with thorns, spines or prickles are significantly reduced compared to when browsing on spineless species (Cooper and Owen-Smith, 1986). Gowda (1996) reported a negative correlation between the feeding rate and spine density, which showed that spine density, protects the twigs of the plants, but not necessarily the leaves from being browsed. Moreover, Milewski et al. (1991) proposed that increased spine length may be an induced defence aimed at protecting the leaves of the plants against ungulates (giraffe and goats). It is clear from above that, the varying forms of spinescence differ in their effectiveness against different species and sizes of ungulates, and in relation of the feeding strategies of the animals.

Cooper and Owen-Smith (1986) also reported some influences of growth stages of the whole plant and its leaves, soil nutrient and light availability and previous defoliation history, on woody plant acceptability. The way in which leaves and stems are arranged in space determines the size and arrangement of bites (Shipley and Yanish, 2001).

High fibre (e.g. cellulose, hemicellulose and lignin) content is a seminal attribute of plants that exhibit high structural anti-quality (Laca et al., 2001). Forage plants with high fibre contents are often difficult for herbivores to bite because of the physical toughness associated with fibres. Although structural factors are not associated with deaths, they reduce forage intake (Shipley and Yanish, 2001), digestibility (Edwards and Ullrey, 1999), or both, such that animal performance is adversely influenced. According to Laca et al. (2001) structural anti-quality factors may actually promote sustainability of grazing systems by preventing severe or complete defoliation, or by providing refuges for highly desirable forages. It may not, therefore, be desirable to completely counteract their effects.

Plants possess a wide variety of chemicals that can reduce forage value, cause toxicities (resulting to sicknesses and even deaths) and serve as feeding deterrents. These chemicals are not involved in the primary metabolic processes supporting plant growth, development or reproduction and they are termed secondary compounds (Launchbaugh, 1996). However, plant secondary compounds, sometimes called phytotoxins, have a negative impact on the fundamental biochemical processes, survival, growth or selective behaviour of herbivores (Launchbaugh, 1996). The major classes of plant secondary compounds include terpenes, oxalates, tannins, alkaloids, and glycosides (Cheeke, 1998; Pfister et al., 2001; Majak et al., 2001). Not all chemicals are equally effective at deterring herbivory, and a chemical effective against one herbivore may not affect grazing/browsing by another (Launchbaugh, 1996). Even though most of these chemicals occur in almost all groups of plants, tannins are mainly found in woody species and probably have the largest influence on the nutritive value of browse as forage. Moreover, tannins have been seen as a major reason why woody plants are little used as sole livestock fodder (Makkar, 2003; Abdulrazak et al., 2000b). This study focuses on tannins as a very influential group of plant secondary compounds in African savannas and hence the following section specifically discusses the tannins and their influence on animal production.

#### Tannins

Tannins are naturally occurring plant polyphenols that can have a large influence on the nutritive value of forages (Reed, 1995). They are commonly divided into two groups, hydrolysable and condensed tannins (Butter et al., 1999). Hydrolysable tannins (HT) are water-soluble polyesters of phenolic acids and glucose or quinic acid and are susceptible to acid and glucose hydrolysis (Butter et al., 1999). Condensed tannins (CT) are formed by the condensation of flavan-3-ols and produce coloured anthocynidins on treatment with acid alcohol hence are named proanthocynidins (PA). The HT and CT differ in their nutritional significance and toxicity effects, but both precipitate proteins. While CT reduce forage quality, the HT cause poisoning in animals if sufficient quantities are consumed (Krebs et al., 2003). Condensed Tannins are considered the primary antinutritional factors of woody plants (Reed, 1995, 2001), hence more focus of this review is placed on CT and their effects on ruminant production.

Several factors affect both the levels and solubility of CT in leaves of woody plants. According to Krebs et al. (2003) the amount of CT found in foliage may vary with plant genotypes, seasons, the age of plant and age of foliage. Makkar et al. (1991) found that CT increases with maturity of leaves in oak species. However, Provenza et al. (1990) found that current season's growth had higher tannin concentrations in black brush. Moreover, soil fertility and acidity also affect CT levels, with low pH associated with higher CT levels (Krebs et al., 2003). According to Hagerman (2002) the solubility of CT is dependent on factors such as seasonal changes in leaf morphology and moisture content, and chemistry of the CT such as a molecular weight as well as the chosen method of forage preservation.

Although tannins apparently do not function in "primary" metabolism such as biosynthesis, biodegradation and other energy conversions of intermediary metabolism, they do have diverse biological activities ranging from toxicity to hormonal mimicry and may play a role in protecting plants from herbivory and diseases (Hagerman, 2002). The ability of tannins to form strong complexes with proteins and polysaccharides is the most important aspect of their anti-nutritional effects. The ability of CT to form insoluble complexes with proteins and polysaccharides affects the fibre digestion (Reed, 2001). They bind with at least four groups of proteins in the ruminant: dietary proteins, salivary proteins, endogenous enzymes and gut microbes including microbial enzymes (Krebs et al., 2003). The general effects of tannins include the decrease in in-vivo nutrient utilization and in particular protein utilization, decrease in growth, decrease in palatability and subsequently feed intake (Abdulrazak et al., 2000a b) or decrease in various enzyme activities (Makkar, 2003). Only very high levels of tannin intake by animals can produce toxicity and even cause death (Butter et al., 1999).

The presence of CT in forages could act either as an anthelmintic or improve the nutritional environment in which the host can flourish (Butter et al., 1999). The capacity of condensed tannins to bind with protein could enable soluble proteins to bypass the rumen and increase the duodenal protein supply once the complex dissociates in the acidic conditions of the abomasums, hence increasing the protein supply to the host (Krebs et al., 2003; Abdulrazak et al., 2000b). Additional protein supply in the parasitized animal helps the host to expel the worm burden from the gastro-intestinal tract more rapidly (Butter et al., 1999). Furthermore, based on the knowledge of tannin chemistry, it is likely that tannins act as potential biological antioxidants (Hagerman, 2002). Antioxidants are widely believed to be an important line of defence against oxidative damage, which has been implicated in a range of diseases.

Various studies have been conducted on the ways in which the detrimental effects of tannins can be dealt with while preserving the benefits. The approaches are discussed extensively in a recent review of the effects and fate of tannins in ruminants (Makkar, 2003). These include using woody ash as a cheap source of alkali and manipulating the storage and drying conditions for detannification of tannin-rich forages. Extractions with aqueous organic solvents, fermentation of leaves, and incorporating polyethylene glycol (PEG), which is considered to break the tannin-protein complexes, are some of the approaches that have been considered to either inactivate or remove tannins from forages. However, although various chemical treatments have been shown to effectively reduce tannins in forages, high cost and labour requirements make their use impractical or uneconomic (Krebs et al., 2003).

If plant species containing CT are to be utilized successfully as a source of feed for ruminants, then a greater understanding of the factors that influence CT content and activity within a plant species is necessary (Krebs et al., 2003). This together with knowledge of the interactions between CT levels and nutrients in forages would assist in the development of management strategies.

#### Foraging Behaviour

Goats, unlike all other domestic livestock species are versatile in diet selection and in consuming a diet. They are very active and inquisitive in their foraging behaviour. Like many wild herbivores, goats discriminate between plant fractions or feed particles that appear identical, consuming one and leaving the other (Huston, 1998). Their mobile lips and precise tongue movement make it possible to sort through the feed, literally pushing the unchosen plant or plant fragments aside while taking only the most preferred (Illius et al., 1999). Many wild browsing herbivores and domestic goats are opportunistic feeders. Given an opportunity to be selective, these animals will graze or browse from some plant or plant types and avoid some.

Adaptive mechanisms for avoiding toxicosis include behavioral skills which limit the quantity of toxins ingested and internal systems that detoxify or tolerate the phytoxins that are ingested (Launchbaugh, 1996). Moreover, foraging behaviour (diet selection and intake rate) is not affected only by the plant characteristics as discussed above, animal anatomical features (e.g. body size, mouth and tooth dimensions. stomach structure and digestive capabilities) also influence intake rate and diet selection for a particular plant species (Haschick and Kerley, 1997).

#### Diet selection

The understanding of how or why browsing ruminants select some plants and avoid others could be a useful tool for management of grazing lands. Foraging behaviour is thus central to understanding plant-herbivore interactions, efficient management of grazing systems and eventually profitable livestock enterprises (Ungar, 1996). Foraging behaviour can be explained differently at different temporal and spatial levels (Laca and Demment, 1996). How animals know which plants to avoid is a question of considerable debate. Several hypotheses have been formulated to explain diet selection by mammalian herbivores, focusing on the maximization of nutrient intake, the minimization of plant secondary compounds, or the satiety hypothesis (Jansen, 2007). According to Provenza (1995) animals accomplish these decisions by relating plant flavours to positive or negative digestive consequences (post-ingestive feedback). Some experiments have advocated diet selection based on intake rate (Illius et al., 1999). Furthermore, livestock live in multi-generational groups in which dietary information can be passed from experienced to inexperienced animals (Provenza and Ropp, 2001). Moreover, ecologists studying wild herbivores have used optimal foraging theory (OFT) to predict animal responses to the changing food resource and environmental factors (Belovsky, 1978). Diet selection is discussed in a more detailed manner in chapter 3 of this thesis.

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Intake

Intake is a major determinant of animal behaviour and subsequently animal production. Ultimately, better understanding of intake should facilitate better management. The rate at which an animal can gather food during active foraging bout is a function of the capacity of its gathering apparatus and the abundance of the food. The relationship between intake rate and abundance is termed as the functional response (Illius, 2006). Approaches to studying intake, range from the comparison of controlled experimental treatments to the gathering of data from a single natural or managed study area (Gordon, 1995; Ungar, 1996). The bite is the fundamental unit of intake. Biting, or the taking of a bite, is defined as the series of head and mouth-part movements that precede and include the severance and bringing of herbage into the mouth (Ungar, 1996). Intake rate is also discussed in more detail in the following chapter.

### Aims and outline of this thesis

The primary aim of this study is to determine the seasonal and plant species patterns of diet selection and foraging efficiency of Nguni goats among a group of six common browse species in the Zululand Coastal Thornveld. The possible effects of plant chemistry, phenology and morphology on diet selection and foraging efficiency are investigated as a secondary objective.

**Chapter 2** determines the seasonal and browse species patterns of foraging efficiency under controlled conditions. This chapter also investigates the possible effects of different plant traits on the observed patterns.

**Chapter 3** deals with the effects of season and plant species on diet selection of Nguni goats under similar conditions as chapter two. Plant chemistry, phenology, spinescence, leaf and shoot morphology are used as the possible explanatory variables of animal preference.

**Chapters 2 and 3** are written as separate manuscripts for submission to a peer-reviewed journal, after some minor changes. Therefore, there is some unavoidable overlap between these two chapters.

**Chapter 4** summarises the two experiments and interprets and contextualizes the results in terms of foraging behaviour, browse-browser interactions, vegetation management and animal production in the sub-humid subtropical savannas.

#### **CHAPTER 2**

# FORAGING EFFICIENCY OF NGUNI GOATS IN RELATION TO SEASON AND PLANT SPECIES IN A SUB-HUMID SUBTROPICAL SAVANNA

#### Abstract

The dual aims of this study were to (1) determine the seasonal and plant species foraging efficiency patterns, indexed by browse short-term intake rate of Nguni goats and (2) investigate how some potential explanatory variables influence these patterns. Six browse species (Acacia natalitia, Acacia nilotica, Dichrostachys cinerea, Grewia occidentalis, Gymnosporia maranguensis and Scutia myrtina) were used in a cafeteriastyle experiment during four periods of the year (early, middle and late wet season and dry season). Short-term intake rates were calculated as the product of bite sizes and bite rates. The relationships between the intake rates and chemical variables were determined by Pearson's correlation analysis. Goats achieved higher intake rates from broad leaf and long shoot species than their counterparts. Intake rate increased with increasing bite size making an asymptotic relationship. Intake rates were highest during the dry season (mean: 0.18 gs<sup>-1</sup>  $\pm$  SEM: 0.012 g s<sup>-1</sup>) and lowest in the late wet season (mean: 0.15 g s<sup>-1</sup>  $\pm$  SEM: 0.009 g s<sup>-1</sup>). Of all the chemicals studied, only condensed tannin concentration (% DM) was positively correlated with both intake rate (r = 0.65, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 24) and bite size (r = 0.53, P < 0.001, n = 0.001, P < 0.001, n = 0.0010.010, n = 24). Foraging efficiency was influenced more by leaf and shoot morphology than spinescence. Plant chemistry and season did not clearly explain the foraging efficiency patterns.

### Introduction

Goats (*Capra hircus*) are common domestic browsers in African savannas and their nutrition depends mainly on the utilization of woody plant species occurring in these rangelands (Dziba et al., 2003). The process of finding and harvesting food dominates the lives of mammalian herbivores (Shipley et al., 1994). Goats spend nearly half of their feeding time browsing and supplement their intake of intact browse by feeding on fallen leaf litter during the dry season (Owen Smith and Cooper, 1987). However, goats are mixed and opportunistic feeders and therefore, will both graze and browse depending on food quality and availability.

Feed intake is the most important factor influencing the feeding value of roughages and, therefore, determines the performance of grazing livestock (Meissner et al., 1999; Shipley and Spalinger, 1992; Haschick and Kerley, 1997). Rate of food consumption by herbivores determines how much time they invest in feeding to meet their metabolic requirements for energy and nutrients (Shipley et al., 1994). Accordingly, food intake rate determines the time available to invest in other non-feeding activities such as resting or mating. Moreover, food nutritional quality and intake rate (i.e. bite size and bite rate) affect the rate of nutrient release in the gut (i.e. postingestive feedback) (Provenza, 1995).

An understanding of foraging efficiency and the factors affecting the rate of intake by animals on rangelands is therefore very important for efficient vegetation management and profitable animal production. Although some research has been conducted in the semi-arid parts of South Africa, little is known about this important parameter of foraging behaviour for Nguni goats in the sub-humid subtropical savannas of KwaZulu-Natal. Approximately 54% of KwaZulu-Natal is covered by the savanna biome (Breebaart et al., 2002). This province with 13% of the national goat population ranks third after the Eastern Cape (49%) and Limpopo (14%) in terms of goats numbers (Anon, 2004).

The objectives of this study were, firstly, to determine the seasonal and plant species patterns of short-term intake rates of Nguni goats fed six browse species common in Zululand Coastal Thornveld (Mucina and Rutherford, 2006) and secondly, to investigate how some potential explanatory variables such as certain chemical components (nitrogen, neutral detergent fibre, acid detergent fibre, acid detergent lignin, condensed tannin, cellulose and hemicellulose), morphology (spinescence, long vs short shoots and broad vs fine leaves) and phenology (deciduous vs evergreen) are related with short-term intake rates. To achieve these objectives, the cafeteria-style experiment was designed and seasonally conducted to test the following hypotheses:

- Season affects short term intake rates because plant species should change in palatability, morphology and chemistry throughout the year (Owen-Smith and Cooper, 1987).
- Short-term intake rates vary among different plant species because of intrinsic differences in shoot morphology (Dziba et al., 2003), leaf morphology (Haschick and Kerley, 1997; Dziba et al., 2003), spinescence (Cooper and Owen-Smith, 1986; Gowda, 1996) and leaf chemistry (Scogings et al., 2004; Owen- Smith and Cooper, 1987).

#### **Materials and Methods**

#### Study Area

The experiment was conducted during the dry season (late July/early August 2006), early wet season (late November/early December 2006), mid wet season (late January/early February 2007), and late wet season (late March/early April 2007) at Owen Sitole College of Agriculture (OSCA). OSCA is situated 12.5 km north of Empangeni, on the old Mtubatuba road KwaZulu-Natal (KZN), South Africa. The 672 ha farm averages 3.2 km in width from east to west and 2.2 km from north to south. The area extends between latitudes 28°57'45"-28°57'22"S and between longitudes 31°55'31"-31°57'22"E (van der Linden et al., 2005). The mean annual rainfall of OSCA is 995 mm, with 75% of it falling between October and April (Figure 1). The rainfall data were obtained from OSCA station (03047277) weather records held by the South African Weather Services. OSCA falls within two Bioresource Units (BRU), namely Moist Coastal Forest, Thorn and Palmveld (BRU 1) and Moist Zululand Thornveld (BRU 19) (Camp, 1999). Acocks (1988) placed OSCA under Coastal Forest and Thornveld (Veld Type 1). Mucina and Rutherford (2006) have recently placed the study area under the Zululand Coastal Thornveld.



Figure 1. Average monthly precipitation for 1979-2007 (shaded bars) and monthly precipitation during a diet selection and foraging efficiency study at OSCA in 2006-2007 (open bars).

#### Study animals

Nguni goats were used for this experiment. These goats are small-framed animals with a characteristic mixture of colour patterns throughout the body. Goats are often blamed for habitat destruction (Kerley et al., 1995; Reid and Ellis, 1995), which can lead to the reduction of biodiversity and enhanced competition with wild ungulates that depend on scarce resources (Ekblad et al., 1993; Hamann, 1993; Parkes, 1994; Norton, 1995). However, in contrast to their negative image, goats are also considered as useful biological agents of woody plant control in savannas, especially following fire or mechanical clearing (Trollope et al., 1989; O'Connor, 1996). Moreover, goats are generally kept for meat, milk and hide production and are commonly used for ritual slaughter in rural communities.

Indigenous (Nguni) goats particularly are well suited to harsh environments (Ramsay et al., 2001).

#### Study Plants

Short-term feed intake rates of goats were determined using six browse species commonly found in the Zululand Coastal Thornveld. The species were Acacia natalia (formerly part of A. karroo, Coates Palgrave, 2002), A. nilotica, Dichrostachys cinerea, Grewia occidentalis, Gymnosporia maranguensis (=G. senegalensis var. maranguensis, Coates Palgrave, 2002) and Scutia myrtina. Although all six species are common and widespread throughout the study area, A. natalitia, A. nilotica and D. cinerea are dominant where grazing and fire management have not been effectively implemented (van der Linden et al., 2005) while S. myrtina is normally present in bush clumps where it grows vigorously and makes the area inaccessible.

All species but *S. myrtina* and *G. maranguensis* are deciduous. *Acacia natalitia* and *A. nilotica* have long, straight spines, *G. maranguensis* and *D. cinerea* have long, straight "stem-spines" that bear leaves, while *S. myrtina* has irregularly distributed small hooks and *G. occidentalis* is spineless. *Acacia natalitia*, *A. nilotica* and *D. cinerea* are fine-leaved legumes having bi-compound leaves, while *G. maranguensis*, *S. myrtina* and *G. occidentalis* are broad-leaved. *Scutia myrtina* and *G. occidentalis* cannot add new leaf area without extending the internodes of new long-shoots (Scogings et al., 2004). In contrast, *A. natalitia*, *A. nilotica*, *D. cinerea* and *G. maranguensis* can add new leaf area without shoot elongation and thus produce most of their new leaves in clusters on short-shoots (spurs).

#### Conditioning of animals

In each season, goats were allowed two weeks of conditioning to the experimental procedure. During this period, six castrated males that were two years old and weighed 26 kg (SEM:  $\pm 1.3$ ) were penned individually under a shelter. The shelter had a solid roof and two semi-solid sides to protect the goats from rain and wind. Goats were maintained on hay and "meat goat semi-complete" pellets manufactured by Meadow Feeds (Pty) Ltd. Pellets contained (per kg dry matter) 150 g protein, 26 g fat, 150 g fibre, 120g moisture, 10-12 g calcium and 5 g phosphorus. Animals were also offered fresh branches of browse as part of the diet to familiarize them with the browse species to be used in the experiment. Furthermore, animals were run through the experimental procedure in a "foraging arena" in the same shelter where they were housed to condition them to the research protocol.

Baseline dry matter (DM) intake data were collected and calculations made daily (including the experimental days) to ensure that animals were individually fed sufficient amounts of feed to meet their maintenance requirements. Water was provided *ad libitum* to all the animals.

#### Experimental Design

After the conditioning period, the short-term intake rate experiment was conducted between 08:00 and 11:00 in the morning of each of the 12 experimental days. This experimental procedure is largely modelled after Dziba et al. (2003); Haschick and Kerley (1997) and Wilson and Kerley (2003). At least six unbrowsed branches of each species were collected in the morning of each experimental day. Based on a sample of 72 branches, mean branch length and diameter were 52.50 cm (SEM:  $\pm 0.760$ ) and 7.85 mm

(SEM:  $\pm 0.980$ ) respectively. The branches were kept in water to reduce transpiration loss. Three branches of each species were used for the experiment and the other three branches were kept aside for chemical analysis. The experiment was conducted on three goats per day (six replicates of two days) with six consecutive treatments (browse species) per goat per day. Branches of each species were offered individually to each goat by mounting a branch on a foraging board (Dziba et al., 2003). To control for the ordering effects, branches of each browse species were placed equally in the first, second, and third order across individual animals during the experiment (Appendix 1). A 6x6 Latin Square was used to reduce carryover effects of one treatment following another (Zar, 1999). Animals were allowed to consume each branch for a maximum of one minute while bites were recorded. Preliminary tests had indicated that allowing the goats to feed for longer than one minute prevented the detection of differences in foraging efficiency because the browse became severely depleted. Branches were individually weighed before and after browsing and the weights converted to dry mass. After each experimental day, all the branches were dried in an oven at 60 °C for 24 hours (based on preliminary tests) to determine their DM. Intake rates, in grams (g) dry mass per second (gDMs<sup>-1</sup>) were estimated as the product of bite rate (number of bites taken per second) and bite size (gDM removed per bite) (Ungar, 1996: Haschick and Kerley, 1997; Dziba et al., 2003).

#### Chemical Sampling and Analysis

To relate short-term intake rates with plant chemistry, leaf samples from the three completely unbrowsed branches collected daily for chemical analysis were analyzed for nitrogen (N). condensed tannins (CT). neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), cellulose and hemicellulose. All chemical analyses were done at the animal science laboratory of KwaZulu-Natal University, Pietermaritzburg. N was determined by the micro-Kjeldahl method and NDF, ADF and ADL were determined as ash-free fractions by the methods described by Van Soest et al. (1991) using the ANKOM fibre technology. Cellulose was calculated as the difference between ADF and ADL and hemicellulose as the difference between NDF and ADF. The acid-butanol proanthocyanidin assay (Porter et al., 1986) was used to determine CT (%DM) as leucocyanidin equivalent (Makkar, 1995).

#### Statistical Analysis

All data were analyzed using SYSTAT 10 (SPSS, 2000). For all variables except for intake rate, N, NDF, ADF and ADL, the assumptions of homogeneity of variances and normality were not met. As a result, bite rate and hemicellulose were log-transformed while CT, bite size and cellulose were square-root (SQR) transformed (Zar, 1999). The general linear model (GLM) option was used to compare the dependant variables, intake rate, log (bite rate), and SQR (bite size) among the independent variables, season and plant species. Treatment means with significant differences were compared using the Scheffe's test. To test the effects of plant traits such as broad vs fine leaves, or long vs short shoots, on intake rates, bite rates and bite sizes, t-tests were done.

To determine the possible relationships between foraging efficiency variables of Nguni goats and chemical variables of browse leaves, the Pearson's correlation analysis was used. Regression analysis was done only when correlations were significant in order to
model the relationship. Significant effects in all tests were declared at the probability level of P < 0.050.

## Results

#### Effects of season and plant species

Intake rates varied significantly ( $F_{3, 120} = 3.33$ ; P = 0.022) among seasons (Table 1). The mean intake rate was highest during the dry season (mean: 0.18 g s<sup>-1</sup> ± SEM: 0.012) and least during the late wet season (mean: 0.15 g s<sup>-1</sup> ± SEM: 0.009). Bite rates also significantly varied between the seasons ( $F_{3, 120} = 21.09$ ; P < 0.001; Table 1). Goats had faster bite rates during the mid and late wet seasons than during the dry season and early wet season.

Table 1. The mean bite rates and intake rates (± standard error) of Nguni goats during four seasons (different superscripts indicate significant mean differences)

Season	Bite rate (bite s <sup>-1</sup> )	Intake rate (g DM s <sup>-1</sup> )	
Dry	$0.48 \pm 0.014^{a}$	$0.18 \pm 0.012^{a}$	
Early wet	$0.47 \pm 0.011^{a}$	$0.15 \pm 0.008^{b}$	
Mid wet	$0.56 \pm 0.016^{b}$	$0.17 \pm 0.008^{ab}$	
Late wet	$0.57 \pm 0.015^{b}$	$0.15 \pm 0.009^{b}$	

In line with the predictions. significant differences in intake rate ( $F_{5, 120} = 11.43$ ; P < 0.001) were observed among the plant species (Table 2). S. myrtina, G. occidentalis, A. natalitia and G. maranguensis had higher intake rates than A. nilotica and D. cinerea. The

*t*-tests showed higher intake rates for broad leaf species than fine-leaf ones (mean:  $0.18 \pm$  SEM: 0.052 vs mean:  $0.14 \pm$  SEM: 0.055g s<sup>-1</sup>; t = -5.27; df = 141.7; P < 0.001). Species that produce new leaves on new long shoots were consumed at higher rates than those that produce new leaves on short shoots (mean:  $0.19 \pm$  SEM: 0.054 vs mean:  $0.15 \pm$  SEM: 0.056 g s<sup>-1</sup>; t = -4.07; df = 96.9; P < 0.001). Although animals were offered branches with similar diameter and length across the seasons, evergreen species were consumed at higher rates than deciduous ones (mean:  $0.19 \pm$  SEM: 0.052 vs mean:  $0.15 \pm$  SEM: 0.052 g s<sup>-1</sup>; t = -4.74; df = 99.7; P < 0.001).

Plant species also affected the bite rates of goats ( $F_{5, 120} = 15.04$ ; P < 0.001; Table 2). *A. natalitia* and *A. nilotica* allowed the fastest bite rates while *S. myrtina* and *G. occidentalis* offered the slowest bite rate. Faster bite rates were observed for fine leaf than broad-leaf species (t = 3.93; df = 139.1; P < 0.001). Species that produce new leaves on new long shoots had slower bite rates than those that produce new leaves on short shoots (mean:  $0.46 \pm \text{SEM}$ : 0.060 vs mean:  $0.55 \pm \text{SEM}$ :  $0.096 \text{ bite s}^{-1}$ ; t = 6.95; df = 134.4; P < 0.001). Plant phenology did not significantly affect the bite rates.

Browse species	Bite rate (bite s <sup>-1</sup> )	Intake rate (g DM s <sup>-1</sup> )
A. nilotica	$0.52 \pm 0.017^{a}$	$0.12 \pm 0.010^{a}$
G. occidentalis	$0.45 \pm 0.012^{a}$	$0.17 \pm 0.010^{a}$
G. maranguensis	$0.55 \pm 0.016^{b}$	$0.18 \pm 0.010^{b}$
D. cinerea	$0.53 \pm 0.018^{b}$	0.13 ±0.010 <sup>b</sup>
A. natalitia	$0.60 \pm 0.024^{b}$	$0.17 \pm 0.010^{b}$
S. myrtina	0.46 ±0.013 <sup>a</sup>	$0.20 \pm 0.011^{a}$

Table 2. The mean bite rates and intake rates (±standard error) of six browse species (different superscripts indicate significant mean differences).

There was a significant effect of interaction between the plant species and season on bite sizes of Nguni goats ( $F_{15, 119} = 2.14 P = 0.012$ ; Figure 2). During all seasons except for the early wet season, goats had bigger bite sizes from *S. myrtina*, *G. occidentalis* and *G. maranguensis* than *A. nilotica*, *D. cinerea* and *A. natalitia*. During the early wet season, *A. natalitia* was one of the species from which the greatest bite sizes were obtained.



Figure 2. Interactions between seasons and plant species on bite sizes of Nguni goats (error bars represent standard errors).

Broad leaf species had bigger bite sizes than fine leaf species (mean:  $0.61 \pm \text{SEM}$ :  $0.107 \text{ g bite}^{-1} \text{ vs mean}$ :  $0.49 \pm \text{SEM}$ :  $0.106 \text{ g bite}^{-1}$ ; t = -6.81; df = 142; P < 0.001). Species that produce their new leaves on new long shoots offered greater bite sizes than those that produce their new leaves on short shoots (mean:  $0.64 \pm \text{SEM}$ :  $0.107 \text{ g bite}^{-1}$  vs mean:  $0.51 \pm \text{SEM}$ :  $0.108 \text{ g bite}^{-1}$ ; t = -6.55; df = 94.9; P < 0.001). Evergreen species offered bigger bite sizes than deciduous ones (mean:  $0.62 \pm \text{SEM}$ : 0.111 vs mean:  $0.52 \pm \text{SEM}$ : 0.117 gbite $^{-1}$ ; t = -4.04; df = 98.7; P < 0.001).

## Relationship between foraging efficiency variables

From a pooled data set, short-term feed intake rate was positively correlated to bite size of goats (r = 0.91; P < 0.001; n = 24; Figure 3). No significant correlation was

observed between short-term intake rate and bite rate. There was a negative correlation between bite sizes and bite rates of goats (r = -0.59; P = 0.002; n = 24; Figure 4). Similar patterns were observed when data were analyzed within seasons and for individual species.



Figure 3. Scatter plot showing the regression between the short term intake rates and bite sizes of Nguni goats on a pooled.multispecies data set.



Figure 4. Scatter plot showing the regression between the bite rates and bite sizes of Nguni goats on a pooled, multispecies data set.

# Foraging efficiency and chemical variables

From a pooled data set across the plant species and seasons, a positive correlation was observed between the intake rate of Nguni goats and condensed tannin percentages of browse leaves (r = 0.65; P = 0.001; n = 24; Figure 5). No significant correlations were observed between intake rate and nitrogen, NDF, ADF, ADL, cellulose and hemicellulose when data were pooled.



Figure 5. Scatter plot showing the regression between intake rates and condensed tannins of Nguni goats from a pooled, multispecies data set.

However, according to seasons across the plant species, NDF (r = 0.65; n = 36; P < 0.001), ADF (r = 0.42; n = 36; P = 0.012), hemicellulose (r = 0.39; n = 35; P = 0.020) and cellulose (r = 0.55; n = 35; P = 0.001) were positively correlated to short term intake rates only during the dry season.

Furthermore, according to species per season, intake rate for *G. occidentalis*, during the dry season was negatively related with N (r = -0.87; P = 0.027; n = 6) and positively related with NDF (r = -0.90; P = 0.017; n = 6) and CT (r = 0.82; n = 6; P = 0.046). Intake rate of *G. maranguensis* showed significant relationships with chemicals only during the early wet season and late wet season. In the early wet season, CT (r = 0.90; n = 6; P =0.015) and NDF (r = -0.82; n = 6; P = 0.044) were positively and negatively related with the intake rate of *G. maranguensis* respectively. During the late wet season, ADF (r = -0.86; n = 6; P = 0.029) was negatively related with the intake rate of the same species.

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During the dry season, the intake rate for *D. cinerea* was positively related with ADF (r = 0.94; n = 6; P = 0.016) while in the early wet season it was negatively related with CT (r = -0.96; n = 6; P = 0.002) and during the late wet season it was positively correlated with NDF (r = 0.82; n = 6; P = 0.045) and negatively related with N (r = -0.84; n = 6; P = 0.038). Intake rate for *S. myrtina* was significantly related with the chemicals only during the dry season and mid-wet season. During the dry season, cellulose (r = 0.81; n = 6; P = 0.048) and N (r = 0.83; n = 6; P = 0.040) were positively related with intake rate of *S. myrtina*. During the mid-wet season, intake rates (r = 0.87; n = 6; P = 0.023) increased with the increasing hemicellulose of the same plant species.

When data were pooled according to plant species across the seasons, the following relationships were observed. For *A. nilotica* the intake rate was positively correlated to N (r = 0.58; n = 24; P = 0.003), ADF (r = 0.42; n = 24; P = 0.041) and cellulose (r = 0.44; n = 24; P = 0.030). Intake rate for *G. occidentalis* was only positively related with CT (r = 0.72; n = 24; P < 0.001) while that of *G. maranguensis* did not have a significant relationship with any of the chemicals. For *D. cinerea* N (r = -0.47; n = 24; P = 0.022) and NDF (r = -0.42; n = 24; P = 0.047) were negatively related with intake rate, while no significant relationship was detected between the chemicals and short-term intake rate of *A. natalitia* and *S. myrtina*.

A positive correlation was observed between the bite size and CT (r = 0.53; P = 0.007; n = 24; Figure 6). Bite size was also positively correlated with NDF (r = 0.41; P = 0.048; n = 24; Figure 7). Correlations between bite sizes of Nguni goats and N, ADL, ADF, cellulose and hemicellulose of browse leaves were not significant.

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Figure 6. Scatter plot showing the regression between the condensed tannin and bite sizes of Nguni goats from a pooled, multispecies data set.



Figure 7. Scatter plot showing the regression between the Neutral Detergent Fibre and bite sizes of Nguni goats from a pooled, multispecies data set.

Bite rate did not significantly correlate with any other chemical variable except with hemicellulose (r = -0.44; P = 0.032; n = 24; Figure 8).



Figure 8. Scatter plot showing the regression between hemicellulose and bite rate of Nguni goats from a pooled data set.

## Discussion

# Effects of season and plant species

Short-term intake rates were higher during the dry season than the wet season, which agrees with other studies. Cooper and Owen-Smith, (1988) reported that certain woody species were rejected during the wet season and increased in acceptability during the coarse of the dry season. Moreover, Yayneshet et al. (2008) reported that bite rate was influenced by season and species, with the highest bite rates achieved during the dry season. Forage availability (lower) could have caused animals to increase their bite sizes of

whatever was available during the dry season. Although this study did not find any relationship between intake rate and bite rate, season also appeared to have influenced the bite rates.

It was predicted that plant morphology would influence the foraging efficiency as has been observed elsewhere (Shipley et al., 1999; Shipley and Spalinger, 1992; Cooper and Owen-Smith, 1986). It is evident from the results that goats achieved higher intake rates from broad-leaved species than the fine leaved ones, with the exception of A. natalitia. Goats obtained significantly larger bite sizes from broad-leaved species than their counterparts throughout the four seasons. This observation supported earlier findings by Haschick and Kerley (1997), Wilson and Kerley (2003) and Dziba et al. (2003) where animals took larger bites from large leaved plants, as well as from plant with terminal leaf clusters. The same studies reported an asymptotic relationship between the intake rates and bite sizes and a negative relationship between the bite sizes and bite rates, which is supported by the results of this study. Intake rate responds strongly to the bite size because of a trade off between the two competing activities of cropping and chewing (Haschick and Kerley, 1997). Larger bite sizes require more mastication than smaller ones which subsequently increases the time between the bites (Shipley and Spalinger, 1992). Therefore, the significantly strong relationship found between intake rates and bite sizes, and a lack of significant relationship between the intake rates and bite rates in the current study led to a conclusion that bite size is the major variable influencing intake rates (Shipley and Spalinger, 1992; Gordon et al., 1996; Ungar, 1996; Dziba et al., 2003; Shipley, 2007). Because bite size controls intake rate, it also controls the shape of the gain function (cumulative gain of dry matter or energy while an animal resides in a patch) and may influence the amount of time an animal can spend foraging each day (Shipley, 2007).

It was also predicted that animals would obtain higher intake rates from plant species that produce their new leaves on new long shoots (*S. myrtina and G. occidentalis*) as has been observed elsewhere (Dziba et al., 2003). The results only partially supported this prediction because some species with short shoots (*A. natalitia and G. maranguensis*) were also among those from which goats obtained high intake rates and bite sizes.

Inconsistent with Dziba et al. (2003), the effectiveness of spinescence in retarding foraging efficiency was not clearly observed. Goats in this study did not forage less efficiently from species with long straight spines (A. natalitia and G. maranguensis) than from species with no spines (G. occidentalis) or short hooks (S. myrtina). This observation further contradicts other observations that spines restrict the bite size and foraging efficiency of herbivores (Cooper and Owen-Smith, 1986; Wilson and Kerley, 2003). However, studies that demonstrated the effect of spines on foraging have used withinspecies comparisons of spiny vs. spineless branches. Removing spines from a spiny species could allow increased foraging efficiency. Presenting spiny vs spineless species to browsers may yield different results to presenting spiny vs spineless branches within a species if the browsers are specifically conditioned to handling a spiny species (Ortegereves and Provenza, 1993). Furthermore, the study goats may have been better conditioned to thorns because there were more Acacia species and other spiny species in Zululand. Therefore, it is possible that goats foraged as efficiently from A. natalitia and G. maranguensis as from S. myrtina and G. occidentalis because of local adaptation to spinescence.

## Plant fibrousness and foraging efficiency

The relationships observed between the short-term intake rate and plant fibre variables varied inconsistently among seasons and plant species. This made it very difficult to clearly understand the role played by fibrousness in foraging efficiency in controlled experiments. However, these results showed clearly that it was during the dry season that plant fibrousness significantly correlated with foraging efficiency. During the dry season animals could increase their intake rates by increasing the plant fibre intake.

According to Shipley and Spalinger (1992) high fibre content associated with toughness is generally an effective anti-herbivore defense as fibre hinders mastication and ease of cropping, thus resulting in decreased bite rates and consequently a reduced intake However, as this study showed that bite rate did not influence intake rate as rate. effectively as the bite size, it is likely that the negative relationship between bite rates and hemicellulose would have had little or no consequence on the intake rate. Moreover, although NDF increased with increasing bite sizes no significant relationships were reported between intake rate and NDF, ADF, ADL, cellulose or hemicellulose when the data were pooled. This observation is similar to that of Haschick and Kerley (1997) and can be explained simply by the fact that short-term intake rates are not affected by digestion and rumination rates (Shipley and Spalinger, 1992; Illius et al., 1999; Dziba et al., 2003). Therefore, the positive relationship between bite size (a strong determinant of intake rate) and NDF could result from highly fibrous forages fracturing easily when chewed (Haschick and Kerley, 1997), thereby reducing mastication time and hence the time required before taking another bite. Moreover, these results can be attributed to the short-term nature of the experiment because longer term experiments have reported decreasing intake rates and digestibility rates resulting from consuming plant species high in fibre content.

## Nitrogen and foraging efficiency

Intake rate was expected to increase with the increasing nitrogen percentage since animals forage to maximize nutrient intake (Scogings et al., 2004). However, the results from the pooled data set did not support that notion. Nitrogen did not have any significant relationship with intake rate when data were pooled. This observation agrees with that by Scogings et al. (2004), where no correlations were found between the crude protein or phosphorus and dry matter intake rates. Moreover, Cooper and Owen-Smith (1985) found weak and generally non significant correlations between acceptance values and leaf concentrations of nitrogen, phosphorus and mineral nutrients. However, when data were pooled according to seasons and species, it was very clear that correlation between intake rate and nitrogen varies inconsistently with seasons and species.

# Condensed tannin and foraging efficiency

Inconsistent with expectations, bite sizes and intake rates increased with increasing CT content for the pooled data set. Similar results were observed by Scogings et al. (2004) in the semi-arid subtropical savanna of the Eastern Cape. These results imply that chemical defenses that enhance either toughness or astringency of the plant do not limit intake rates under short-term, confined experiments. Moreover, goats can tolerate high intake of defensive chemicals like tannins and can therefore, feasibly increase their nutrient intake

by ingesting chemically defended species for limited time periods (Provenza et al., 1990). The positive relationship observed between intake rate and tannins can be a consequence of goats optimizing their nutrient intake rates, regardless of the prospect of postingestive feedback later (Scogings et al., 2004). Moreover, these relationships were actually more significant during the dry season than other seasons. For some species such as *D. cinerea* the relationship was negative, which shows that the actual effect of plant chemistry on intake rate differs with different plant species and different seasons.

It is clear that even the intake rate of the same plant species relate differently with the same chemical compound during different times of the year. This makes the effect of plant chemistry on foraging efficiency even more cumbersome to comprehend. This observation could result from the interactions between the chemicals themselves or that there are other chemical compounds that actually drive foraging behavior but were not part of this study (Provenza et al., 2003). This research extends our understanding of browsebrowser interactions in subtropical savannas, which support large population of browsers. There is therefore, an opportunity for further investigations of the effects of plant chemical composition that will look at other compounds and interactions thereof on intake rates of individual plant species during different seasons.

#### **CHAPTER 3**

# DIET SELECTION OF NGUNI GOATS IN RELATION TO SEASON AND PLANT SPECIES IN A SUB-HUMID SUBTROPICAL SAVANNA

#### Abstract

Although diet selection is a central process in plant-herbivore interactions, little is known about this important parameter of Nguni goats' foraging behaviour in subtropical savannas. This study was conducted firstly to determine the seasonal and plant species patterns of diet selection by goats and secondly, to investigate if plant chemistry, phenology and morphology would explain diet selection. Six browse species (Acacia natalitia, A. nilotica, Dichrostachys cinerea, Grewia occidentalis, Gymnosporia maranguensis and Scutia myrtina) were used in a cafeteria-style experiment in four seasons. In each season, six 2-year old castrated indigenous goats weighing an average of 26 kg each were individually penned under shelter and maintained on a basal diet of pellets and hay. The design of the experiment was a 6x6 Latin Square in which six branches of each species were offered to goats simultaneously. The plant species by season interactions affected diet selection. S. myrtina and G. occidentalis were the most preferred species while G.maranguensis and A. nilotica were the least preferred species. Broad leaf species were preferred over fine leaf ones only during the dry ( $P \le 0.050$ ) and late wet seasons (P< 0.050). Long shoot species were preferred over short shoot ones (P < 0.001) throughout all seasons. Plant phenology did not influence goats' preference. The negative effect of spinescence on preference was clearly observed only during the dry season. Preference was

positively related with condensed tannins (r = 0.27; P = 0.001). The relationships between the intake and chemical variables were highly variable with seasons, making it difficult to explain the role played by plant chemistry on preference. These results have important implications for vegetation management and goat production in the Zululand Coastal Thornveld.

#### Introduction

Diet selection may be defined as the removal by animals of some sward component(s) or plant parts rather than others (Newman et al., 1995). This process determines both the quantity and the quality of food intake and hence the nutritional status of individual animals, their time and activity budgets, their physiological condition, growth rates, and potential reproductive and survival rates (Hanley, 1997). In simpler terms, diet selection determines which plants are consumed where, when, and to what degree. Moreover, it is a central process in plant-herbivore interactions, with consequences for the structure, species composition, and ecological relations of plant communities and their ecosystems. Therefore, knowledge of the basis of why herbivores select one food item and not the other is necessary for an understanding of their forage needs and is the underlying basis for understanding possible competitive interactions amongst them (Haschick and Kerley, 1997).

Although goats are common domestic browsers in African savannas, factors that affect their diet selection are poorly understood (Dziba et al., 2003). Limited, but insightful knowledge of diet selection of goats in the semi-arid subtropical savannas of the eastern seaboard of South Africa has been developed recently. For example, it is known that within a suite of six woody species commonly found in the semi-arid savannas of the Eastern Cape province, goats prefer species that produce their new leaves on new long shoots (enabling high instantaneous intake rates) if the lignin concentration is < 10% (Dziba et al., 2003; Scogings et al., 2004). However, nothing is known about diet selection of Nguni goats in the sub-humid subtropical savannas of KwaZulu-Natal. This province, with 13% of the national goat population, ranks third after the Eastern Cape (49%) and Limpopo (14%) in terms of goat numbers (Anon, 2004).

This study was conducted (1) to determine the seasonal and plant species patterns of diet selection by Nguni goats among a group of six common browse species, (2) to investigate if plant chemistry, plant phenology and plant morphology can be used to explain the diet selection patterns. It was predicted that the goats would select food species of which morphology offers higher intake rates, as has been observed elsewhere (Dziba et al., 2003; Shipley et al., 1998; Haschick and Kerley, 1997). It was also expected that goats would prefer plant species that allow them to maximize nutrient intake while minimizing the intake of plant secondary compounds (PSC). Finally, it was postulated that the patterns of diet selection would vary among different seasons.

## **Materials and Methods**

## Study Area

The experiment was conducted during the dry season (late July/early August 2006), early wet season (late November/early December 2006), mid wet season (late January/early February 2007), and late wet season (late March/early April 2007) at Owen Sitole College of Agriculture (OSCA) (28°57′ S, 31°55′ E), 20 km inland from the coastline of KwaZulu-Natal province, South Africa. Mean annual rainfall of OSCA is 995 mm, of which 75% falls from October to April. The rainfall data were obtained from OSCA station (03047277) weather records held by the South African Weather Services. Vegetation of OSCA is in a Zululand Coastal Thornveld (Mucina and Rutherford, 2006).

## Study Animals and Plants

Nguni goats are small-framed animals with a characteristic mixture of colour patterns throughout the body and are well suited to harsh environments (Ramsay et al., 2001). Diet selection of these goats was determined using six browse species commonly occurring in the Zululand Coastal Thornveld. The plant species were *Acacia natalitia*, *A. nilotica*, *Dichrostachys cinerea*, *Grewia occidentalis*, *Gymnosporia maranguensis* and *Scutia myrtina*. All but *S. myrtina* and *G. maranguensis* are deciduous. *Acacia natalitia* and *A. nilotica* have long, straight spines, *G. maranguensis* and *D. cinerea* have long, straight "stem-spines" that bear leaves, while *S. myrtina* has irregularly distributed small hooks and *G. occidentalis* is spineless. *Acacia natalitia*, *A. nilotica* and *D. cinerea* are fine-leaved legumes having bi-compound leaves, while *G. maranguensis*. *S. myrtina* and *G. occidentalis* are broad-leaved. *Scutia myrtina* and *G. occidentalis* cannot add new leaf area without extending the internodes of new long-shoots (Scogings et al., 2004). In contrast, *A. natalitia*, *A. nilotica*, *D. cinerea* and *G. maranguensis* can add new leaf area without shoot elongation and thus produce most of their new leaves in clusters on short-shoots (spurs).

#### Conditioning period

During each season, animals were allowed two weeks of conditioning to the experimental procedures, which was divided into two phases of training. In the first phase, six castrated males that were two years old and weighed 26 kg (SEM: ±1.3) were penned individually under a shelter and maintained on hay and "meat goat semi-complete" pellets manufactured by Meadow Feeds (Pty) Ltd. The shelter had a solid roof and two semi-solid sides to protect the goats from rain and wind. Pellets contained (per kg dry matter) 150 g protein, 26 g fat, 150 g fibre, 120g moisture, 10-12 g calcium and 5 g phosphorus. In the second phase, animals were offered fresh branches of browse as part of the diet to familiarize them with the browse species to be used in the experiment. Animals were also run through the experimental procedure in a "foraging arena" in the same shelter where they were housed to condition them to the research protocols.

Baseline dry matter (DM) intake data were collected and calculations made daily to ensure that animals were individually fed sufficient amounts of feed to meet their daily maintenance requirements. Water was provided *ad libitum* to all the animals.

# Diet selection trial

After the conditioning period, diet selection (relative DM intake) was observed over 12 days. At least 21 un-browsed branches of each species were collected in the morning of each experimental day. Based on a sample of 72 branches, mean branch length and diameter were 52.5 cm (SEM:  $\pm 0.76$  cm) and 7.9 cm (SEM:  $\pm 0.98$  cm) respectively. The branches were kept in water to reduce transpiration loss. Eighteen branches of each species were used for the experiment and three of each species were kept as controls to account for transpiration loss (Dziba et al., 2003; Haschicks and Kerley, 1997).

This experiment was run between 13:00 and 15:00 in the afternoon of each experimental day. Individual branches of all six species were offered simultaneously in the foraging board. Branches were distributed so that the animals could take their next bite without spending time on searching. A 6x6 Latin Square was applied and six unique arrangements of the six species were the treatments. The location of each species on the board was controlled to ensure that no species appeared in the same position more than once for each goat, while each species never occurred next to the same species more than twice in all trials (Appendix 1). This design ensured that there was an equal opportunity for goats to select from all options offered with minimum body movement. Animals were allowed to forage from the branches for a maximum period of two minutes (based on preliminary tests) and bites were counted per species. Branches were individually weighed before and after feeding and the weights converted to DM to determine intake (g) which was used as the index for diet selection (Haschick and Kerley, 1997). All branches were later dried in an oven at 60 °C for 24 hrs (preliminary tests had shown that branches completely dried within this period) to determine DM.

## Chemical Sampling and Analysis

Leaf samples from the three completely unbrowsed branches of each species collected concurrently with branches for the trial were oven dried at 60 °C for 24 hours and ground to pass through a 1 mm screen. These samples were then analyzed for nitrogen (N), condensed tannins (CT), neutral detergent fiber (NDF), acid detergent fiber (ADF), acid

detergent lignin (ADL), cellulose and hemicellulose. Chemical composition of all study plants in four seasons appears in appendix 2. All chemical analyses were done at the animal science laboratory of KwaZulu-Natal University, Pietermaritzburg. N was determined by the standard micro-Kjeldahl method while NDF, ADF and ADL were determined as ash-free fractions by the methods described by Van Soest et al. (1991) using the ANKOM<sup>200/220</sup> fiber technology (ANKOM Corporation<sup>®</sup> Technology, Fairport, NY). Cellulose was calculated as the difference between ADF and ADL and hemicellulose as the difference between NDF and ADF. The acid-butanol proanthocyanidin assay (Porter et al., 1986) was used to determine CT (%DM) as leucocyanidin equivalent (Makkar, 1995)

## Data analysis

Data were tested for normality. Intake (diet selection index) and cellulose data were square-root (SQR) transformed, while hemicelllose was log-transformed. General Linear Modelling was used to test the effects of plant species and season on SQR (intake). To test the effects of plant traits such as broad vs fine leaves, or long vs short shoots, on intake, t-tests were done. Pearson's correlation analysis was used to determine the relationships between intake and chemical variables. Significant effects in all tests were declared when P < 0.050. All the analyses were performed using SYSTAT 10® (SPSS, 2000).

## Results

Intake by Nguni goats was significantly influenced by the interactions between the season and browse species ( $F_{15, 118} = 2.73$ ; P = 0.001; Figure 9). S. myrtina and G. occidentalis were consistently among the most preferred species through out all seasons.

while the opposite was true for *G. maranguensis* and *A. nilotica*. During the dry season, *A. natalitia* ranked third among the avoided species and inconsistently featured among the most preferred species later in the wet season. The opposite was observed for *D. cinerea*.



Figure 9. Effects of the interactions between the seasons and plant species on diet selection of Nguni goats (error bars represent the standard errors).

Intake of broad leaf species (only during the dry and late wet season) was significantly greater than that of fine leaf species, which also happened to have long, straight spines (t = -2.20; df = 32.7; P = 0.035) and (t = -2.30; df = 33.3; P = 0.028) respectively (Figure 10). Goats consumed greater amounts from long shoot species (*S. myrtina and G. occidentalis*) than from short shoot species, which were also associated with long, straight or long , stem spines (t = -7.05; df = 99.5; P < 0.001; Figure 11). Plant phenology did not affect intake of Nguni goats.



Figure 10. Seasonal effect of leaf morphology on intake by Nguni goats (error bars represent the standard errors).



Figure 11. Seasonal effect of shoot morphology on intake by Nguni goats (error bars represent the standard errors).

#### Leaf chemistry and diet selection

Only significant relationships are presented in this section. From a pooled data set, N (r = 0.17; n = 144; P = 0.048) and CT (r = 0.27; n = 144; P = 0.001) were positively related with intake. No significant relationships were observed between all other chemical variables and intake. However, when data were analysed within seasons, the relationships tabulated in Table 3 were detected.

Table 3. Significant relationships between intake (g) of Nguni goats and leaf chemicalvariables at different seasons.

Season	Chemical	r	n	Р	<del>~~~</del>
	N	0.40	36	0.017	
Dry	СТ	0.35	36	0.039	
	NDF	0.42	35	0.012	
Early wet	Cellulose	-0.33	35	0.047	
Late wet	CT	0.48	36	0.003	

N= nitrogen, CT= condensed tannins, NDF= neutral detergent fibre

## Discussion

Plant species was a significant factor influencing the diet selection patterns by Nguni goats. Similar results were observed for domestic goats in the Mediterranean mountain forest of Spain (Baraza et al., 2008) and in the semi-arid savannas (Dziba et al., 2003). Diet selection patterns of spinescent species were variable. Similar variability was reported by Owen-Smith and Cooper (1987) who studied the acceptability of different woody plants to kudus. These results show a significant negative effect of long, straight spines on intake and therefore selection especially during the dry season. Woodward and Coppock (1995) also found that physical defenses (thorns, spines and hooks) deterred animals as a function of relative browse dependence. Moreover, Cooper and Owen-Smith (1986) observed kudus to be more deterred by spines and thorns than goats and impalas. However, in the semi-arid savannas, selection was determined more by shoot morphology than spinescence (Dziba et al., 2003). In the current study, *A. natalitia* inconsistently featured on the preferred species list making the effect of spinescence very difficult to explain during the wet seasons. A similar study in a subtropical thicket environment showed that all spinescent species with the exception of *A. karroo* had low preference rankings (Haschick and Kerley, 1997), which agrees well with the current results. Although no measurements of thorns were made, given the fact that the study plants varied in kinds, densities and lengths of thorns, it can therefore, be postulated that spinescence drives foraging behaviour more by such traits than simply the presence or absence of spines (Gowda, 1996).

Deciduous woody species are usually more preferred than evergreen species (Papachristou and Nastis, 1996: Shipley et al., 1998). This study, however, indicated that species preference was generally unrelated to leaf phenology. Both deciduous and evergreen species were among the more preferred species and less preferred species, which supported the observations in the Eastern Cape (Dziba et al., 2003). However, opposite results were observed in the northern Transvaal for free-ranging kudus (Owen-Smith and Cooper, 1987, 1988; Watson and Owen-Smith, 2002). Furthermore, the influence of leaf

and shoot phenology may be largely related to the chemical factors associated with a particular phenophase (Watson and Owen-Smith, 2002).

During dry and late wet seasons goats preferred species with broad leaves over those with fine leaves. However, during the early and mid-wet seasons, leaf type alone did not affect selection. The goats preferred long shoot species that had broad leaves and no/small spines. Although the goats could forage more efficiently from broad leaf than fine leaf species individually, when the broad leaf species was spiny or had most of its leaves on short shoots, then it was less likely to be selected in the presence of other species. Even though the goats could forage as efficiently from fine leaf as from broad leaf species, the former species were less likely to be selected than the latter species because of spines.

## Condensed tannins and goats' preferences

It was predicted that goats would prefer species from which they would minimize the intake of plant secondary compounds. This hypothesis was based on the fact that condensed tannins, for example, have been largely reported to act as anti-feedants to browsing ruminants in African savannas (Cooper and Owen-Smith, 1985; Cooper et al., 1988). However, even though condensed tannin proved to be related to preference, this compound did not limit intake of Nguni goats as would be expected. These results contradict Alonso-Diaz et al. (2008) who observed negative correlations between condensed tannins and goat's preference under cafeteria- type experiments. Jansen et al. (2007) suggested that tannins are not avoided by goats instead they are kept below a certain threshold. According to Cooper and Owen-Smith (1985) browsing ruminants rejected mature leaves of savanna woody species when condensed tannins exceeded 5 % of dry mass. The current study did not however, support this threshold since the most preferred species (*S. myrtina*) possessed high tannin concentration which reached 16 % in some seasons (Appendix 2). It was postulated that in short-term studies, condensed tannins would be a secondary signal for intake regulation (Baraza et al., 2008). Moreover, under controlled environments, it would not be possible for the animals to clearly associate an effect with a particular plant if offered more than one plant containing tannins (Alonso-Diaz et al., 2008). Clearly the current results could better be explained in terms of the above postulates than by the tannin (or PSC) minimization (or keeping below a certain threshold) hypothesis (Jansen et al., 2007). Haschick and Kerley (1997) attributed the inclusion of tannin-rich plants as preferred species to the presence of proline-rich salivary proteins which deactivate the effects of tannins in the tanniniferous forages. The observed failure of tannins as chemical defensive mechanisms has important implications for the conservation and management of the sub-humid subtropical savannas. For example, if goats' tolerance to tannins is sufficient to allow them to survive on poor-quality vegetation, then they can be used to control invasive woody plants (Scogings et al., 2004).

## Plant fibre and preference

No statistically significant correlations were found between feed preference and ADF, ADL and hemicellulose in all four seasons. Contrary to expectation, during the dry season NDF was positively related with goat's preference, even though the relationship was not a strong one. This observation was against the prediction that fibres would reduce intake. This prediction was based on the fact that fibre reduces forage quality through its physical toughness as well as poor digestibility. Alonso-Diaz et al. (2008) and Baraze et al.

(2008) also found positive correlations between intake and fibre components. This observation also contradicts the hypothesis that goats select foods to minimize the intake of plant secondary compounds. However, during the early wet season a negative relationship was observed, which suggests that the effect of fibre on foraging behaviour varies with seasons. During this season, fibre (or PSC) minimization (Jansen et al., 2007) could be used to explain the preference of goats since tannin levels did not change (appendix 2). Alonso-Diaz et al. (2008) suggested that in short-term studies, fibre components were better predictors of DM intake than the polyphenolic compounds. However, in this study neither tannins nor fibres could clearly explain the diet choices made by goats. It can however, be argued that during the dry season animals preferred browse species from which they could maximize the bite sizes and subsequently intake rates, since fibres tended to positively relate with the bite sizes and intake rates (Chapter 2). It could also be argued that since these results varied with seasons and it was only in two seasons that preference significantly and weakly related with fibres, preferences showed by goats were unrelated with fibres. The latter argument supports finding from other studies (Ganga et al., 2005; Woodward and Coppock, 1995).

## Nitrogen and preferences

A very weak positive relationship was observed between preference and nitrogen during the dry season. This shows that during this season animals would select species that allow them to maximize nutrient intake so as to meet their requirements for N. However, Danell et al. (1994) did not find any significant relationship between reindeer preference and nitrogen during winter. The latter could be attributed to differences in plant and animal species and climatic conditions between the current study and earlier study area. Moreover, many studies have reported a positive relationship between intake and nitrogen or crude protein levels (Odeyinka, 2000; Dziba et al. 2003; Baraza et al., 2008; Ganqa et al., 2005). However, no evidence was found for the hypothesis of nutrient intake maximization during the wet seasons in this study, which agrees with Jansen et al. (2007).

## Conclusion

This study shows that diet selection by Nguni goats varies significantly with plant species and seasons. Factors such as the plant spinescence, leaf and shoot morphology and their interactions markedly influence diet selection, with the patterns varying with seasons. Condensed tannins and fibres did not restrict preference by goats, which give a promise that Nguni goats can be used to control invasive woody plants in the Zululand Coastal Thornveld, especially during the dry season. The influences of both nitrogen and fibers on preference differed significantly with seasons, showing that these compounds are less important in diet section during the wet season.

#### **CHAPTER 4**

#### GENERAL DISCUSSION

#### Summary of aims and results

This study was conducted to determine the seasonal patterns of foraging efficiency and diet selection of Nguni goats on a group of six woody species commonly found in Zululand Coastal Thornveld. It was a secondary aim to investigate how plant morphology, phenology and chemistry can possibly explain the observed patterns. Short-term intake rate and intake were used as indexes for foraging efficiency and diet selection respectively in two cafeteria- style experiments.

The plant species from the first experiment (foraging efficiency) followed the order: *S. myrtina* > *G. maranguensis* > *G. occidentalis* > *A. natalitia* > *D. cinerea* > *A. nilotica.* The seasons followed the following pattern: dry > mid-wet > early wet > late wet in terms of intake rate. A strong positive relationship was detected between the bite size and intake rate, while a negative relationship was observed between the bite rate and bite size. Although this experiment was specifically designed to test only the patterns above, it appeared that goats achieved higher intake rates from broad leaved species and species with long shoots than their counterparts, especially when the latter plant species had thorns. However, the inclusion of *G. maranguensis* (a species with short shoots) as the second species on a foraging efficiency list is an exception. Goats did not forage less efficiently from spinescent species as would be expected. Correlations between plant chemical and foraging efficiency variables suggested that condensed tannins were positively related with both intake rate and bite size. Plant fibre variables were related with foraging efficiency only during the dry season.

On the basis of intake, *S. myrtina* and *G. occidentalis* were consistently the most preferred species through out all seasons, while the opposite was true for *G. maranguensis* and *A. nilotica. A. natalitia* and *D. cinerea* featured inconsistently among both the most and least preferred species through out seasons. Plant phenology did not seem to affect the goat preference, while broad leaved species appeared to have higher intake than fine leaved ones. Preference also tended to be higher for long shoot species than short-shoot ones. Spinescence alone did not seem to reduce intake. Intake was positively related with condensed tannin. A weak relationship was observed between intake and nitrogen. Inconsistent relationships were also detected during different seasons between chemical variables and intake.

#### Interpretation and implications

While I understand the need to be cautious when extrapolating the results obtained in arena experiments to natural pasture conditions, these results have very important implications for both vegetation management and animal production. The use of cafeteriastyle trials for determining dietary preference and foraging efficiency provides a relatively simple foraging environment in which foraging constrains involved with searching time, availability, accessibility and detectability of plants are avoided (Haschick and Kerley, 1997).

The high intake rates observed during the dry season suggest that the woody plants, especially *S. martina* and *G. occidentalis* can provide forage (as supplements) for goats especially during the dry season, when forage (especially grasses) quality and quantity are low. Although *G. maranguensis* is one of those from which animals can achieve high

intake rates, goats avoided this species. On the other hand, *A. natalitia* ranked fourth in terms of foraging efficiency (probably because of long straight spines), but was one of the most preferred species in some seasons. The goats in this study may have been conditioned to thorns because there were many *Acacia* species and other spiny species in Zululand. Therefore, it can be postulated that the study goats foraged as efficiently from spiny as from spineless species because of local adaptation to spinescence. From the above observation, it is very clear that selection by the study goats was not dependent on their foraging efficiency of plants.

The relationship observed between intake rate and a bite size suggests that: 1) bite size controls intake rate, and 2) bite size controls the shape of the gain function and may influence the amount of time an animal can spend foraging each day. Bite rates are relatively easy to estimate in the field on free ranging animals. However, it is often difficult to determine bite sizes under field conditions and thus often difficult to calculate intake rates (Dziba, 2000). Both the negative relationship observed between bite size and bite rate and the relationship between the intake rate and bite size discussed above can be used to establish a more accurate measure of the stocking rate that considers intake rate, plant palatability, preferred species abundance or forage availability.

The inclusion of *S. myrtina* and *G. occidentalis* as the most preferred species poses a concern that these species are at risk of decreasing in abundance, which if not controlled can reduce plant species biodiversity in the study area.

The positive relationships between condensed tannin and both foraging efficiency and diet selection can be explained in either of the following ways. Firstly, given the shortterm nature of the experiments, the tannin quantities encountered by goats were not sufficient to deter their foraging and selection. Secondly, the presence of proline-rich salivary protein could have deactivated the negative effects of tannins on intake rate and intake and assisted goats to tolerate tannins. This observation means that goats did not consider tannins or nitrogen in their foraging. They could be foraging to maximize or minimize the intake or intake rate of chemicals other than the ones studied. If goat's tolerance to tannins (observed) is sufficient to allow them to survive on poor-quality vegetation, then they can be used to control invasive woody plants.

This research extends our understanding of browse-browser interactions in the subhumid subtropical savannas.

## **Future Research**

More work is proposed on the direct effects of plant chemistry, phenology and morphology on foraging behaviour of Nguni goats in Zululand Coastal Thornveld. The current study only indirectly investigated these effects. For example, designing an experiment to test the effect of nitrogen concentration where branches of one species taken from populations along a gradient of nitrogen, could yield different results.

Studies that show effects of spines on foraging have used within-species comparisons of spiny vs spineless branches. Removing spines from a spiny species would allow increased foraging efficiency above the "normal" level. Presenting spiny vs spineless species to browsers may be different to presenting spiny vs spineless branches within a species if the browsers are specifically conditioned to handling spiny species. Local conditioning should be controlled by using equally naïve or experienced animals at all sites. It would be interesting to compare the inexperienced (or naïve) and experienced animals' foraging behaviour.

It appears that some species, especially long-shoot deciduous ones (e.g., *G. occidentalis*) are highly preferred by goats in subtropical savannas and, therefore, may be at risk of decreasing in abundance. Research should be done to check the magnitude of this decrease and propose some ways of protecting the biodiversity.

Similar research is required on free ranging animals so that the results obtained in the current study can be compared with those from free ranging animals and management decisions can be more informed.

Studying the digestibility of the selected species in this study after confirming the results on free ranging animals would allow a more direct measure of the contribution of these plant species on animal productivity in Zululand.

Bush encroachment is a serious problem in the African savannas. The fact that chemical and mechanical control methods of invasive woody plants are becoming more expensive and politically unpopular provides greater opportunities to utilize goats as a biological control method. More research is needed to explore many avenues for biological control. Both research and extension activities are needed to develop and transfer the technology for improving the effectiveness and profitability of goats for vegetation management.

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## Appendix 1 (Experimental Designs)

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	6 goats	-	-	6 tree spp						6 arran	gements							
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	2			b	Grewia	occidentalis				В	caebfd							
	3			с	Gymnos	poria marang	uensis			С	bdafce							
	4			đ	Dichros	tachys cinerea	1			D	ecfadb							
	5			e	Acacia r	natalitia				Е	dfbeac							
	6			f	Scutia m	vrtina				F	fedcba							
				08:00-11:	08:00-11:30 Intake rate experiments							13:00-15:00 Diet selection experiments						
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	6	12	5	а	f	e	d	с	b	А	F	E	D	С	В

## Appendix 2 Continues.

Season	Species	N	NDF	ADF	ADL	СТ	CELLULOSE	HEMICELLULO
		% DM	% as <u>received</u>	% as <u>received</u>	% as received	<u>% DM</u>	<u>% as received</u>	% as received
Mid-Wet	A, nilotica	2,09	28.94	15.83	9.66	1.21	6.17	13.12
		(0.080)	(1.238)	(0.384)	(0.794)	(0.389)	(0.744)	(1.467)
	G. occidentalis	1.93	59.47	22.13	11.42	3.38	10.72	37.34
		(0.065)	(2.003)	(1.289)	(1.901)	(0.884)	(1.790)	(2.323)
	G. maranguensis	1.21	48.57	33.20	23.69	6.10	9.52	15.37
		(0.061)	(2.587)	(2.630)	(2.630)	(0.885)	(0.276)	(0.848)
	D. cinerea	2.26	55.74	32.98	18.66	6.00	14.32	22.76
		(0.055)	(1.146)	(2.428)	(1.048)	(0.304)	(2.639)	(2.63)
	A. natalitia	2.07	43.67	31.62	24.28	9.65	7.35	12.04
		(0.031)	(1.055)	(1.806)	(2.165)	(1.871)	(0.495)	(1.343)
	S. myrtina	1.77	47.15	26.36	17.86	15.90	8.50	20.79
		(0.084)	(1.027)	(1.262)	(1.573)	(2.561)	(0.518)	(1.623)
Late Wet	A. nilotica	1.73	24.97	10.74	5.44	2.31	5.30	14.23
		(0.049)	(1.780)	(0.634)	(0.515)	(0.425)	(0.141)	(1.752)
	G. occidentalis	2.06	58.87	15.74	4.84	2.61	10.91	43.13
		(0.075)	(1.116)	(1.381)	(0.933)	(1.016)	(0.541)	(1.675)
	G. maranguensis	1.27	43.13	21.95	13.49	5.44	8.46	21.18
		(0.119)	(0.739)	(0.729)	(1.415)	(0.839)	(1.145)	(1.101)
	D. cinerea	1.72	53.64	28.95	17.10	5.36	11.86	24.69
		(0.031)	(2.687)	(1.551)	(1.410)	(0.541)	(0.248)	(1.510)
	A. natalitia	1.88	40.37	25.91	19.15	9.45	6.76	14.46
		(0.036)	(1.763)	(2.065)	(1.784)	(0,579)	(0.561)	(0.523)
	S. myrtina	1.73	43.43	21.02	13.24	9,60	7.78	22.41
		(0.041)	(0.654)	(0.830)	(0.801)	(2.276)	(0.200)	(0.796)

Mean values (±SEM) of chemical components of the six browse species during the mid and late wet seasons