Effect of roughage quality and period of day on rumen fill after meal termination, digestion, passage rates, and diurnal feeding behaviour in cattle fed on tropical roughage

By

Bhiya Siyabonga Thapelo

A dissertation submitted in fulfilment of the requirements for the degree of

Masters of Science in Agriculture

In the

Discipline of Animal and Poultry Science

College of Agriculture, Engineering and Science

School of Agriculture, Earth and Environmental Science

University of KwaZulu-Natal

2018

Pietermaritzburg, South Africa

Supervisor: Professor Ignatius Verla Nsahlai

Declaration

I, Siyabonga Thapelo Bhiya, hereby declare that the exploration reported in this thesis is my own work and effort. This thesis has not and will not be submitted to any other institution for an award and does not contain any person's writing and data; where other sources of information have been used, they have been appropriately cited and acknowledged. All the graphics or tables, and pictures presented in this thesis have not been copied and pasted from the internet.

As the Researcher, I hereby submit this dissertation for examination.

Name: Bhiya Siyabonga Thapelo

Signed …………………. Date ………………

As the Research Supervisor, I agree to the submission of this dissertation for examination.

Name: Prof Nsahlai Ignatius Verla

Signed ………………….. Date ……………….

Dedication

This thesis is dedicated to the entire Bhiya family, particularly my mother (Mrs. T.S Bhiya), father (Mr. J.L Bhiya), and my late big brother (V.C Bhiya) who inopportunely couldn’t live lengthy enough to witness the success of his younger brother. Above all, I dedicate this thesis to God almighty.

Now faith is the assurance of the things we hope for, being the proof of things we do not see and the conviction of their reality (Hebrews 11:1).

Acknowledgements

Firstly, I would like to thank the blessings, guidance and support from the Lord God almighty. Secondly, I would like to offer my sincerest gratitude to my supervisor Prof Ignatius Verla Nsahlai for accepting me to do my Master's degree under his supervision and providing guidance during the experimental work and thesis write up. I would also like to thank Prof Michael Chimonyo who made it possible for me to run my trials by assisting during the purchase of experimental animals.

I would also like to offer my heartfelt appreciation to my parents Mr. J.L and Mrs. T.S Bhiya for their continuous support from the very beginning until the completion of the study, for the most part when the going got tough. I would also like to thank my colleague Mehluli Moyo (tooth pick) for helping me throughout the study and sharing ideas which reinforced and sharpened my writing of this thesis and also not forgetting Nkanyiso Majola and Serumula Mahlogonolo (Sthwab'thwab) who assisted with feed preparations and data collection. I would also like to thank Kagiso Mowa, Jubilate Mothotse, Sonto Khumalo, Senzi Nxumalo, and Vuyelelo Mzondi (Vivo) for their reinforcements during the course of my studies.

I would also like to thank my friends Fortune Thabethe (Mbodla), Charity Matikwane (Zamfumfu), Boy Sirenda (Hlokoloza), Theophilus Sibambo (Ndondo), Linda Malindzisa (Ndosi), Sicelo Fundama (Madakwane), and Lawrence Mashele (Master Roshi, Mcayi) for the motivation and courage they gave which made this work a success. I would also like to thank the National Research Fund for their financial assistance.

I also want to sincerely thank the staff of the discipline of Animal and Poultry Science; Miss S Ndlela and Nomandla Baca for their assistance with the required chemicals throughout the experiment and the Ukulinga Research Farm staff (Sam Khumalo, Emmanuel Makhoba, B Ngcobo, and Masefo Mokoma) for data collection and their technical support.

Lastly, I would like to thank every individual who contributed in one way or the other in making this work a success.

List of abbreviations

a	: Rapidly degradable water-soluble fraction
ADF	: Acid detergent fibre
b	: Slowly degradable portion of the insoluble fraction
BM	: Body mass
c or k_d	: Rate of degradation of the "b" fraction
CF	: Crude fibre
Co-EDTA	: Cobalt ethylenediaminetetraacetic acid
CP	: Crude protein
DM	: Dry matter
DMI	: Dry matter intake
DRF	: Dry matter rumen fill
DVR	: Digital video recorder
FB	: Feeding behaviour
FI	: Feed intake
FPR	: Fractional passage rate
GIT	: Gastrointestinal tract
GLM	: General linear model
HEM	: Hemicellulose
HG	: Hindgut
IRQ	: Improve roughage quality
K_l	: Rate of passage of liquid
K_p	: Rate of passage of solid
L	: Time lag

LSD	: least significant difference
MC	: Microbial yield
MC	: Moisture content
MIRQ	: Moderately improved roughage quality
NDF	: Neutral detergent fibre
NDFI	: Neutral detergent fibre intake
NDS	: Neutral detergent solution
PRQ	: Poor roughage quality
PS	: Particle size
RF	: Rumen fill
SF	: Selectivity factor
SIRQ	: Semi-improved roughage quality
VFI	: Voluntary feed intake
WM	: Wet matter fill

Thesis output

Symposium abstracts and poster presentations

S.T. Bhiya and I.V. Nsahlai. Effects of roughage quality and period of day on rumen fill after meal termination, passage rate, and diurnal feeding behaviour of cattle. SASAS 50th Congress, 2017: "Golden Innovations for Sustainable Animal Agriculture". Port Elizabeth, Eastern Cape, South Africa. pp 339.

S.T. Bhiya and I.V. Nsahlai. Effects of roughage quality and period of day on rumen fill after meal termination on rumen fill, passage rate, and diurnal feeding behaviour in cattle fed on tropical roughage. College of Agriculture, Engineering and Science Postgraduate Research and Innovation Day. 26th of October 2017. University of KwaZulu-Natal, Westville Campus. pp 72.

To be submitted

S.T. Bhiya, M. Moyo and I.V. Nsahlai. Effects of roughage quality and period of day on diurnal rhythm of feeding behaviour patterns of cattle.

S.T. Bhiya, M. Moyo and I.V. Nsahlai. Effects of roughage quality and period of day on rumen fill after meal termination, degradation, digestibility, and passage and rates in cattle.

General abstract

In tropical and subtropical regions, ruminant production is prominently dependent on tropical veld grass characterized by low nutritional quality. Feed intake is an essential constituent determining animal performance and the degree at which ruminants utilize feeds of poor quality is reigned by the passage from and degradability rates of digesta in the rumen. Feed intake by ruminants is regulated by rumen fill, which is further influenced by processes occurring in the rumen i.e. degradation, digestion, and passage rates. Furthermore, intake is a result of time spent eating and meal pattern hence, feeding behaviour regulates intake. Therefore, rumen fill, degradation, digestion, passage rates, and feeding behaviour are vital in understanding intake by ruminants. The objectives of the study were to: (i) determine the effect of roughage quality and period of day on diurnal rhythm of feeding behaviour patterns in cattle, (ii) determine the effect of roughage quality and period of day on rumen fill after meal termination, and (iii) confirm the effect of roughage quality on degradation, digestibility, and passage rates. Four ruminally cannulated Jersey heifers were assigned to four dietary treatments comprising improved roughage quality (IRQ), semi-improved roughage quality (SIRQ), moderately improved roughage quality (MIRQ), and poor roughage quality (PRQ). Consequently, heifers were randomly assigned to one of the four roughage diets in a 4 × Latin square design. Data on time spent on each of 11 different behavioural activities (drinking water, eating, idling standing and lying, ruminating whilst standing and lying, hedonic feeding, grooming, licking objects, tongue rolling, and other activities i.e. feed searching) was recorded. Roughage quality had no significant effect on the time spent on each behavioural activity except grooming and tongue rolling. The period-of-day affected time spent on each activity except for idling whilst lying and tongue rolling. Consequently, heifers spent more time eating during the day and ruminating at night. Roughage quality had no effect on fractional passage rates, rumen retention time, and mean retention time. Conversely, the mean retention time of solids in the hindgut was affected by roughage quality. Roughage quality had no effect on total rumen load, rumen DM, and rumen liquor. Total rumen load and rumen liquor were affected by period of day except for rumen DM. Total rumen digesta and rumen liquor were greater at evening than in the morning, afternoon, and late afternoon.

Additional keywords: Intake, rumen fill, digestion, degradation, passage rates, feeding behaviour, roughage quality, heifers.

Table of Contents

List of Tables

List of Figures

Chapter 1

General introduction

1.1 Background

Roughage is a vital dietary component that need to be considered, as it is the primary source of carbohydrate for ruminants and provides energy for body activities, carbon for skeleton for microbial protein synthesis, and microbial activity (Nocek and Tamminga, 1991). Carbohydrates, proteins, and lipids in plants, predominantly forages provide most of the energy for ruminants. About 80% of the ruminant's energy comes from carbohydrates attained during forage consumption and their digestible portion is more important in evaluating the energy available to the animals (Mertens, 1993). Fibre is not a cost-competitive alternative for supplying diets with minerals, energy, protein and vitamin (Nocek and Tamminga, 1991). Feed intake is a crucial component determining animal performance (Illius and Jessop, 1996) and with both protein and energy being the key pivot in most ruminant production. Galyean and Oltjen (1988) reported rumen fill as an important indicator for long-term control of roughage intake in ruminants thus, accurate rumen fill predictions are crucial to enhance ruminant production (Yearsley *et al.,* 2001). The termination of feed by ruminants occurs when the reticulo-rumen is filled hence, feed termination by ruminants occur mainly because of rumen fill (Hofmann, 1989; Forbes, 1995; Nsahlai and Apaloo, 2007). Furthermore, feed bulkiness in relation to reticulo-rumen volume can limit feed intake (Fisher, 2002; Tahir, 2008). Such physical regulations come into play in feed intake of dairy cows fed low caloric and poor quality diets (Van Soest, 1994). Feed intake is also influenced by the diet's energy content (Fisher, 2002) and the metabolic processes occurring within animal's body.

Passage and digestion rates of digesta and fill effects of the diet are the core parameters that determine the physical fill. The rate of passage of digesta from the rumen is predominantly influenced by the quality of forage diets. Forage intake by ruminants vary with the chemical and physical characteristics of the forage and their digestibility can be used as an energy content evaluation. On the other hand, reticulo-rumen capacity is affected by high moisture content in forages as high levels of moisture content increase the diet's bulkiness, which is negatively related to the capacity of the reticulo-rumen (Tahir, 2008). The ceaseless decamp of particles and degradation by rumen microbes cause the rumen fill not to remain constant at peak even in nutritionally restricted diet (Gill and Romney, 1994).

The interaction between rate of DM clearance from the rumen and the availability of useful energy available for the animal also regulates voluntary feed intake by ruminants fed on forage-based diets (Weston, 1996). The retention period of feed in the digestive tract for digestive action is determined by the rate of passage. Therefore, digestion that eventuates during the retention time is a result of the rate and possible extent of degradation hence, the dynamic degradation factors are essential to precisely predict the accessible energy from a feed and protein degradability in the rumen (Dijkstra *et al.,* 2005).

With feed intake basically being regulated by rumen fill, factors such as passage rate, digestibility, degradation rate and feeding behaviour would affect and be affected by rumen fill and thus, feed intake. However, digestibility and passage rate are not the only factors affecting feed intake, feed intake can also be affected by the capacity of the digestive tract (Forbes, 1995). Feed digestibility is reduced with the addition of high fibre diets, which further reduces feed intake due to the feed being poorly digestible in the rumen resulting in slow passage rate creating rumen distension (Dado and Allen, 1995). Rumen fill and feed intake can be inhibited when the forage neutral detergent fibre (NDF) exceeds a maximum threshold (Mertens, 1987). Tahir (2008) reported that diets high in forage content result in cows spending more time ruminating and chewing per unit of dry matter or neutral detergent fibre intake compared to pelleted or concentrate diets. Rumen fill and NDF content of diets have a positive relationship (Dado and Allen, 1996) and there is a variation in passage rate between high and low-quality roughages (Defoor, 2000). Compared to other dietary components, forage NDF is digested more slowly and less dense hence, retained longer in the rumen (Allen, 2000). Although the digestive efficiency of cattle is higher and the retention of forage diets in the rumen vary among ruminant species, cattle retain forage diets longer than in both sheep and goats (Poppi *et al.,* 1981). Poor quality roughages are characterized by longer retention times, delayed clearance from the ruminal compartments, lower ruminal digestion and slow rates of passage, which creates a dietary fill in the reticulo-rumen (Tahir, 2008). Osuji *et al.* (1993) indicated that designing diets that will be utilized more efficiently could be attained through better understanding of the factors affecting rumen degradability of low-quality basal feeds and microbial protein production.

A study by Nsahlai and Apaloo (2007) revealed that the mathematical model developed by Illius and Gordon’s (1991) underrated gut fill levels and roughage intake of ruminants grazing on poor quality roughages in tropical regions. As a result, the model failed to precisely foretell intake due to the erroneous standardizations used to estimate rumen fill and rates of passage influences. Therefore, since ruminants depend on feed intake for growth, production, and to maintain their energy requirements, better understanding of degradability, digestion, passage rates, rumen fill, and feeding behaviour of ruminants fed on poor roughage quality will enable accurate prediction of these variables hence, accurate prediction of voluntary intake.

1.2 Problem statement

Rumen fill and passage rates have direct effects on feed intake by ruminants fed on high forage diet. Only a few studies (Moyo *et al.,* 2018) have been done on the effects of improving low roughage quality through urea treatment and period of day on rumen fill, degradation, digestion, passage rates, and diurnal feeding behaviour in sheep and goats, but not in cattle. Moreover, only a few studies have been done on rumen fill after meal termination of cattle fed on poor quality roughages.

1.3 Justification

At any specific point, reticulo-rumen fill is a result of intake, degradation, digestion, passage rates, and feeding behaviour. Ruminant production is exceedingly dependent on forage quality and the production rate of cattle fed on forage-based diets is determined by the quantity of herbage consumed. Precise assessment of voluntary intake by grazing animals is one of the supreme tools in enhancing production and management. With feed accounting 60-70% of the total cost of livestock production. Improving roughage quality through the use of urea will positively influence dry matter intake and live weight gain thus, improving ruminant production for resource-limited farmers in tropical and sub-tropical regions of Africa. This will also help ruminants to meet the needed nutrients i.e. protein and energy for growth and meat production. It is therefore necessary to study the effects of roughage quality and period of day on intake, degradation, digestion, passage rates, diurnal feeding behaviour, and rumen fill of cattle to develop mathematical models that will accurately predict voluntary feed intake of ruminants grazing on tropical grasses. This will also enable resource-limited farmers in tropical and sub-tropical regions to know the potential herbage intake of ruminants in order to predict their livestock production and to determine how much nutrients ruminants get in a region from the available roughage sources thus, improving food security.

1.4 Objectives

The broad objective of the study was determine the effects of roughage quality and period of day on diurnal feeding behaviour, rumen fill, degradation, and passage rates of cattle. The specific objectives were to:

- Determine the effect of quality of roughage and period of day on diurnal rhythms feeding behaviour of cattle.
- Determine the effect of roughage quality and period of day on rumen fill, degradability and fractional passage rates.

1.5 Research hypothesis

The hypotheses to be tested in the study were:

- Roughage quality has an effect on feeding behaviour of cattle.
- Roughage quality and meal termination time has no effect on rumen fill, passage and degradability rates.

Chapter 2

Literature review

Abstract

Ruminant production depends on roughage based diets, which provides energy for growth, production, and performance. Herbage intake by ruminants is prominently affected by rumen fill. The aim of this review is to discuss factors affecting intake in ruminants, focusing largely on rumen fill, feeding behaviour, and processes occurring in the rumen i.e. degradation, digestion, and passage rates. Rumen fill is a long-term regulator of feed intake in ruminants. However, intake is also affected by roughage quality, particle size and density of the ingested digesta, reproductive state and physiological status of the animal, live body weight, and environmental temperature. In tropical and semi-tropical regions of Africa, ruminant production is largely reliant on grazing animals on grasslands, which are in most parts of poor quality. Logically, poor roughages are slowly degraded by microbes in the rumen due to the strong bond between cellulose, hemicellulose, and lignin. The rate of particle outflow from the rumen is greatly regulated by the functional specific gravity. However, this is not the case with small ruminants; for instance, the outflow rate of particles in sheep is to a lesser extent influenced by particle density not by particle size. Furthermore, large particles form a raft mat and stratification in the dorsal sac in the rumen, decreasing the outflow rates of large particles from the rumen. Intake by ruminants can to a lesser extent be affected by environmental temperature. Ruminants increase their intake to meet the energy demands required to sustain normal body temperature during cold exposure hence, increasing the metabolic rate. The physiological status of the animal greatly influence the digesta passage rate. Generally, the nutrient demand by pregnant animals is greater than by non-pregnant animals. Therefore, pregnant animals tend to increase the outflow rate of liquid to meet their high nutrient demands thus, increasing intake. The role of feeding behaviour in influencing intake is also critical as the voluntary intake by ruminants is a result of time spent eating and meal patterns. Therefore, better understanding of rumen fill, feeding behaviour, and processes occurring in the rumen i.e. degradation, digestion, and passage rates in ruminants feeding on poor quality roughages will pave way in developing mathematical model that will accurately predict feed intake of ruminants in tropical and sub-tropical regions of Africa.

Additional Key words: ruminants, intake, degradation, digestion, passage rates, feeding behaviour

2.1 Introduction

Feed intake is the primary constituent determining animal performance (Illius and Jessop, 1996) and with both protein and energy being the major pivot on most ruminant production. Roughage is a vital dietary component that needs to be considered as it is a primary source of carbohydrate for ruminant species and provides energy for body activities, carbon skeleton, microbial protein synthesis, and microbial activity (Nocek and Tamminga, 1991). The rate of digesta passage from the rumen is predominantly influenced by the quality of forage diets. Furthermore, herbage intake by ruminant species vary with the chemical and physical characteristics of the forage. Forbes and France (1993) reported that the competition between digestion in and passage rates from the rumen is the outcome of the quantity of nutrients consumed, which become available to the animal. The quantity of feed that an animal can consume is modulated by the reticulo-rumen capacity, which is the first chamber of the alimentary tract in ruminants (Forbes, 1995) and such physical regulations come into play on feed intake of dairy cows fed low energy and poor quality diets (Van Soest, 1994). The rate of digestion in the rumen and passage rate of digesta from the rumen are the main determinants of the reticulo-rumen fill. However, the reticulo-rumen volume is not the only factor regulating feed intake, with bulk density of the feed being another factor (Mertens, 1987). Allen (2000) stated that the subsequent influential factor modulating feed intake by ruminants is the energy content of diets that animals consume.

Forbes (1995) indicated that the epithelial linings of the reticulo-rumen has mechanoreceptors, which are concentrated in the interior dorsal portion of the reticulum and rumen. Termination of intake is a result of excitement of these receptors caused by rumen fill, which signal is a message to be sent to the central nervous system (Allen, 200). Several studies have been done on rumen fill, feeding behaviour, passage rates. However, only a few studies have been done on how poor roughage quality influence rumen fill, feeding behaviour, degradation, and passage rates. Moreover, exploration of the dynamics of how improving roughage quality and period of day influence diurnal feeding behaviour patterns and rumen fill after meal termination, degradation, and passage rates with the aim to develop a mathematical model that will accurately predict intake will improve ruminant production in tropical and subtropical regions of Africa. With feed accounting for the highest input cost in livestock production, this model will enable ruminant production planners to know the potential feed intake of ruminants so as to predict the potential of ruminant production in regions from the available forage source. The aim of this review paper was to discuss factors affecting intake by ruminants and focus was largely based on rumen fill, feeding behaviour, and processes occurring in the rumen i.e. degradation, digestion, and passage rates.

2.2 Factors affecting feed intake by ruminants

Feed intake is the amount of feed an animal can consume and is generally exhibited as dry matter intake (DMI), which is the weight of the feed material consumed eliminating the moisture it holds. The interaction between the rate of dry matter (DM) clearance from the rumen and the availability of useful energy to the animal regulate the voluntary feed intake (VFI) of forages (Weston, 1996). Mertens (1994) argued that the physiological factors are the primary control of feed intake, by limiting energy intake until diets contain a sufficient energy concentration through potential fill of the gastrointestinal tract. Forage characteristics in relation to the gut fill capacity are regarded as dominant factors regulating voluntary intake by ruminants. When the peak volume of the digestive tract is attained, feed intake appears to be limited (Allen, 1996), even with modified rumen volumes to increase the transit rate of digesta with decreased forage quality (Van Soest, 1994).

High levels of moisture content in roughages have a secondary role to organic acids and other substances, which influences DMI in some manner thus, high levels of moisture content in roughages reduces voluntary DMI in ruminants (Jackson and Forbes, 1970). The voluntary intake of dairy cows is proportionate to the age, maturity, and lactation state (Faverdin *et al.*, 2006). In addition, variation in physiological requirements of the animal also determine intake. The load of digesta in the reticulo-rumen and other physical conditions within the gut limit voluntary feed intake by ruminants (Allison, 1985). The diet's quality is not the only determinant of intake during grazing, forage availability and distribution are some of other factors related to short-term intake rate (Garcia *et al.*, 2003). Roguet *et al.* (1998) stated that reduced intake rates and biting frequency in tropical rangeland is a result of time spent by the animals searching for feed due to scattered forage resources.

2.3 The role of roughages on ruminant production in tropical areas

The most significant feed source in ruminant production are roughages (Wilkins, 2000), which are feeds characterised by high fibre contents and low in total digestible nutrients. Ruminant production is exceedingly dependent on forage quality and the production rate of cattle fed forage based diets is determined by the quantity of forage consumed, which is one of the most effortful aspects to predict forage quality (Mertens, 1994). Moreover, the ability of ruminants to produce within their genetic potential is primarily dependent on dietary quality and intake levels (Coleman and Moore, 2003). Forage quality is the amount of plant constituents that have an impact on the animal's use of the feed. Poor quality roughages are usually characterized by longer retention times, delayed clearance from the ruminal compartments, and slower ruminal digestion hence, creating dietary fill of the reticulo-rumen (Tahir, 2008). Allen (1996) reported that ruminant production is highly dependent on energy intake and absorbed protein. Both elements are dependent on various factors including: forage quality, rumen microbial population and forage interaction, animal factors, and other dietary ingredients. Generally, digestibility of forages is used to evaluate the energy content in forages, hence; digestibility is a common measure of forage quality.

Carbohydrates, proteins, and lipids in plants predominantly forages provide most of the energy for ruminants. About 80% of the ruminant's energy comes from carbohydrates attained during forage consumption, and the digestible portion is more important in evaluating the energy available to the animal (Mertens, 1993). However, not all the fibre attained from forage is potentially fermentable. Fibre digestibility is determined by the retention and fermentation time in the rumen (Allen, 1996) and the energy from fibre is available only through microbial fermentation in the rumen. National Research Council (2001) reported that in dairy cattle production, fibre is also required for maximum intake and rumen health maintenance. In tropical Africa, livestock production is essential to support oneself and economic development. Dovie *et al.* (2006) outlined that in tropical Africa, rural households lean on livestock for income, meat, milk, manure for crop production, and provide employment of multitude of people, which makes it basic to the health and subsistence in tropical Africa. However, due to climate change, ruminants production has drastically decrease tropical areas primarily as a result of poor quality forages.

Chenost *et al.* (2001) indicated that poor quality roughages mostly in tropical and subtropical areas in Africa could be improved through urea treatment. Improving the nutritive value of poor quality roughages through urea treatment breaks the bond between cellulose, hemicellulose and lignin, which physically create the fibre to swell (Tesfayohannes *et al.*, 2013). Treating poor quality roughages with urea increases their crude protein (CP) content and improve the nutritive quality of roughages, but reduces the neutral detergent fibre (NDF) cum hemicelluloses of the roughage (Tesfayohannes *et al.*, 2013) hence, increasing the digestion rates (Nsahlai, 1991).

2.4 Effect of rumen fill on feed intake and factors affecting rumen fill in ruminants

Rumen fill is the quantity of digesta inside the rumen calculated by the overall intake and the rate at which the ingested feed vacates from the rumen. Rumen fill is an essential long-term regulator of roughage intake by ruminants (Campling, 1964). Physical control of feed intake and possible variance in the energetic efficiency in ruminants are a result of meal termination due to a filled reticulo-rumen (Waldo, 1986). However, the ceaseless decamp of particles and degradation by the rumen microbes causes rumen digesta levels not to remain constant at peak even in nutritionally restricted diet (Gill and Romney, 1994). Williams *et al.* (2014) reported that at any specific point, the reticulo-rumen fill is a function of intake, digestion rates, and both the outflow and breakdown of particles. Forage characteristics and inherent factors i.e. levels of satiety, are major determinants of intake rates.

Rumen digesta load is a central factor affecting feed intake in ruminant animals (Sauvant *et al.,* 1996), thus rumen digesta load function as a satiety agent (Campling, 1964) and terminate roughage intake (Nsahlai and Apaloo, 2007). The reticulo-rumen is the most important part of the alimentary tract in regulating of feed intake by physical fill (Allen, 2000), and varies the feeding behaviour of grazing cattle (Gregorini *et al.,* 2007) as ad *libitum* feeding increases the rumen volume (Colucci *et al.,* 1984). Hunger is negatively related to rumen fill hence, encourages animals to eat (Newman *et al.,* 1994). The level of hunger influences the grazing dynamics and intake rate (Gregorini *et al.,* 2007). Better understanding of forage utilization can be attained through ruminant anatomy and their rumen ecology concepts (Fisher, 2002).

Allen (2000) stated that the reticulo-rumen capacity restricts feed intake in relation to feed bulkiness. Animal characteristics i.e. passage and digestion rates are related to the volume of the reticulo-rumen. Furthermore, the fill effect of diets on the reticulo-rumen act as a short-term regulator for feed intake (Mertens, 1987). More contractions are produced during reticulo-rumen motility resulting in particle size reduction and increased passage rates. During feeding, the rate of outflow of digesta from the rumen increases due to increased motility, which further increases DMI and decreasing distension (Forbes, 1995). Gregorini *et al.* (2007) indicated that during the progression of a grazing bout, the rumen fill and searching time increases hence, decreasing the bite mass and intake rates maintaining a constant bite rate. The favourable link between degradability and roughage intake support that intake by ruminants is terminated by the reticulo-rumen fill (Nsahlai and Apollo, 2007). Large amounts of non-degradable and progressively degradable materials in the rumen restricts intake of poor quality roughage.

Processes that elevate roughage intake are the alterations in the processes required for digesta clearance and an increase in rumen digesta load (Adebayo, 2015). Nsahlai and Apollo (2007) stated that the stage of maturity and quality of diet could directly influence rumen digesta load. Feed intake rate at any given feed quality and rumen load will increase in direct proposition with passage rate (Allen, 1996). The functional specific gravity of particles in the rumen also regulates the rate at which the digesta pass from the rumen (Lechner-Doll *et al.,* 1991). Reticulo-rumen motility also affects rumen fill as the outflow rate of particles from the rumen is determined by the quantity of material that pass out with liquid digesta at each reticulo-rumen motility (Ulyatt *et al.,* 1986). The rate of rumen digesta clearance from the rumen can also be affected by the rate of particle breakdown and digestion (Williams *et al.,* 2014). However, Aitchison *et al.* (1986) argued stating that the capacity of rumen fill is a result of elements that do not influence passage and digestibility rates. The alteration of meal quality, amount and distribution are a result of limited voluntary intake due to increased rumen fill due to inclusion of material in the rumen (Faverdin, 1999).

2.5 The passage rate of liquid and particulate phases in ruminants

The retention period of feed in the digestive tract for digestive action is determined by the rate of passage. The digestion that eventuates during the retention time is a result of the rate and possible extent of degradation hence, dynamic degradation factors are essential to precisely predict the accessible energy from a feed and protein degradability in the rumen (Dijkstra *et al.,* 2005). The passage rate of digesta from the rumen regulates the degree and manner of fermentation, intake of poor quality roughage (Balch and Campling, 1962), and microbial synthesis efficiency (Harrison and McAllan, 1980). Rumen digesta exist as intermix of solid and liquid. The turnover of both phases is positively associated to increase feed intake and high microbial yield (Sniffen and Robinson, 1987). Stern *et al*. (1994) described microbial protein as the most important source of amino acids for ruminants and their high growth rates as a result of high forage level in the diet (Hansson, 2006) which, increases the outflow of microbial protein causing more amino acids to be available in the intestines. The N-use efficiency (Dewhurst *et al.,* 2003) and microbial efficiency (Sniffen and Robinson, 1987) are both affected by the passage rate of digesta. However, passage rate of digesta from the reticulo-rumen is inversely proportionate to digestibility (Huston *et al.*, 1986).

When fodder is fed *ad libitum*, Poppi *et al.* (1980) observed that cattle digest herbage more efficiently than do sheep and goats (Reid *et al.,* 1990) possibly due to the slow rate of passage of digesta from the rumen in cattle. Hansson (2006) reported an increase in microbial growth from high forage diets. This could possibly be due to increased flow of saliva, which acts as a buffer in maintaining optimal rumen pH. Saliva does not only maintain a stable pH in the rumen but also increase the outflow of liquid digesta, escalating microbial outflow from the rumen. Yansari *et al*. (2007) observed increased DM content and quantity of particulate DM in the rumen as a result of increased intake. Reticulo-omasal orifice (ROO) relaxation during reticulo-rumen (RR) contractions governs the passage rate of digesta from the RR thus, regulating rumen fill and voluntary feed intake by ruminant species (Okine *et al.,* 1998).

2.6 Factors affecting passage rates of digesta in ruminants

2.6.1 The effect of particle size, density, and stratification

The competition between passage rate and digestion determines the quantity of substrate degraded in the rumen (Dijkstra *et al.,* 2005). The forestomach of ruminants is divided by the reticulo-omasal orifice (ROO) into the reticulo-rumen (RR) and the omasum (Sellers and Stevens, 1966). The outflow of particulate and liquid digesta from the rumen is regulated by the ROO which in turn is controlled by reticulo-rumen contractions (Mathison *et al.,* 1994). Kaske and Engelhardt (1990) reported that the mean retention time (MRT) of particles in the RR is governed by particle density and particle size. Poppi *et al.* (1981) reported that two pool systems are used to describe DM present in the rumen namely; large particle and small particle DM pools. The outflow of small particles from the rumen is greater that that of large particles. This could be that large particles must be reduced below a critical extent before passing from the rumen to the abomasum (Poppi *et al.,* 1985). Most of the particle reduction by ruminants is accomplished through chewing in the course of eating and rumination, and to a lesser extent (17%) during digestion (McLeod and Minson, 1988; Kennedy, 2005). The likelihood of particles to escape from the rumen grow with particle size reduction (Rinne *et al.,* 2002).

Therefore, for particles to vacate the reticulo-rumen, particles have to be reduced into a critical size of 1-2 and 2-3 mm in sheep and cattle, respectively (Poppi *et al.,* 1980; Kennedy and Poppi, 1984) thus, rendering particle reduction via rumination, mastication, and to a lesser extent by digestion as a necessity for digesta outflow (Ulyatt, 1983). Particle size reduction not only increases the site of microbial attachment, but also increases the functional specific gravity and particle density, which are essential regulators of digesta outflow (Ehle and Stem, 1986; Lechner-Doll *et al.,* 1990). The functional specific gravity is associated with particle density and buoyancy (Welch, 1990). Rinne *et al.* (2002) reported that even though small particles leave the rumen with the liquid phase, the resistance of large particles to flow from the reticulo-rumen could be due to their low density as of the air-filled interior (Van Soest, 1975; Sutherland, 1988). Furthermore, the slow passage rate of large particles is primary regulated by the floating system of particle separation by density in the reticulo-rumen (Kaske and Midasch, 1997; Clauss *et al.*, 2009; Fritz *et al.,* 2009; Hummel *et al.,* 2009). Due to low initial density and functional specific gravity, large particles are favorably moved into the caudo-dorsal districts of the rumen by reticular contractions hence, extending their mean retention time by inhibiting their escape chances (Ehrlein and Hill, 1969). However, passage rate of particles in sheep is rather, greatly influenced by particle density than particle size. In support to this statement, Katoh *et al.* (1988) observed a greater chance of particles with a density of 1.3-1.4 g/ml to escape from the RR in sheep as a result of their short MRT (Kaske, 1987). The short MRT of these particles compared to freshly ingested particles is due to the reduction of particle size during microbial fermentation and rumination, which increases particle density to approximately 1.4 g/ml (Lechner-Doll et al., 1991). Gas bubbles formed soon after fermentation increases drastically, increasing the floating tendency and prevented passage of these particles (Wattiaux *et al.*, 1992).

As large particles are trapped in the floating ruminal mat/ fibre mat, they are restricted access to the reticulo-omasal orifice (Tschuor and Clauss, 2008), which extend their mean retention time (Faichney, 1986). During their elongated stay in the reticulo-rumen, particle density and functional specific gravity progressively increase due to ion exchange, cellular space destruction, hydration (Hooper and Welch, 1985; Nocek and Kohn, 1987; Yansari *et al.,* 2004). Once the critical particle size is reached or they become denser, these particles sink towards the reticulo-omasal orifice and become accessible to be thrusted out from the reticulo-rumen during the second reticular contraction (Kaske and Midasch, 1997). Moreover, *Seo et al.* (2009) described functional specific gravity as a significant regulator of particle outflow. However, raft mat formation not only entraps and prevent large particles from escaping the rumen; the floating mat also stimulates contractions of the ruminal wall (Varga and Harpster, 1995), which in turn lead to rapid liquid outflow and to a lesser extent solid digesta outflow from the rumen. The stratification of rumen content varies among ruminant species, with grazing species having more stratified rumen contents than browsers (Clauss *et al.*, 2006). High fibre diets aid floating mat formation than concentrate diets. This is due to small particles in concentrate diets, which form a homogenous mixture in the rumen (Moore *et al.,* 1990). Rinne *et al.* (2002) and Lund *et al.* (2007) observed slow passage rate of potentially digestible NDF (pdNDF) than indigestible NDF (iNDF) representing selective retention of digesta particles in the rumen. However, incidences of the transit of more digestible particles being slow enough to allow maximum energy yields by providing enough time for fermentation have also been noticed.

2.6.2 The effect of ambient temperature

Voluntary intake of forage-based diets is positively linked with cold temperature (Kennedy *et al.,* 1976). Christopherson (1976) observed increases in passage rate and gut motility with increased feed intake, and increased thyroid hormone circulations during low temperatures. However, intestinal passage rates were not affect by temperature (Kennedy *et al.,* 1982). The decrease in DM digestibility during cold exposure is associated with short MRT mainly due to escalated passage rate by increased RR contraction frequency, which is closely coordinated with the reticulo-omasal orifice movement. The effect of low temperatures on digestion affect dietary energy accessibility to a greater degree than protein (Christopherson and Kennedy, 1983), increasing the recycling process of urea nitrogen in the rumen. Depressed digestion, increased microbial efficiency and growth during low temperatures are likely to increase the supply of amino acids (Christopherson and Kennedy, 1983), non-ammonia nitrogen and undegraded dietary protein (Weston and Hogan, 1967) to the small intestines and other essential nutrients to the animal (Westra and Christopherson, 1976).

The increased energy demands desired to sustain normal body temperature by ruminants during cold exposure are met through increasing DMI and metabolic rate in association to increases in triiodothyronine (T3) plasma concentrations. Increased metabolic rates during winter compensate the heat losses from metabolism enabling animals to survive (Todini, 2007). Thomson *et al*. (1978) observed modifications in chemoreceptor responses during cold exposure by manipulating rumen blood flow to enhance absorption. Increased blood flow increases volatile fatty acids (VFA) absorption into the portal circulation thus, reducing VFA concentrations in the rumen (Hales, 1973). Kennedy *et al.* (1976) reported a 15% decline in VFA concentration in the rumen of sheep exposed to cold temperature. Such low VFA concentrations in the rumen result in increased RR contractions (Leek and Harding, 1975). Levin (1969) described the thyroid hormone as one of the factors influencing RR contractions, passage rate (Kennedy *et al.*, 1977), appetite, and feed intake (Young, 1981). During cold exposure, thyroid increases, which result in reduced MRT due to increased passage rate (Westra and Christopherson, 1976). During cold exposure, Kennedy and Milligan (1978) reported increased dilution rate of fluid markers and a decline in rumen fluid volume. The decrease of turnover rate and water intake during cold exposure result to the observed declines in rumen fluid volume (Degen and Young, 1980).

2.6.3 The effect of physiological status

The physical and chemical attributes of a feed are not the only determinant of voluntary feed intake (Gill and Romney, 1994). Intake of forage-based diets is also determined by the metabolic and physiological state of the animal. Roughage based diets increase particulate passage rates during the late changeover period of dairy cows to recompense for rumen fill (Dado and Allen, 1995). Pregnancy and lactation are linked with increased digesta outflow (Dijkstra *et al.*, 2005). Coffey *et al.* (1989) observed a noticeable increase of digesta outflow from the RR of pregnant ewes in contrast to non-pregnant ewes fed *ad libitum*. Evans (1981) reported declines in ruminal fluid turnover rates when dietary forage content was decreased. The increase of NDF outflow and ruminal fluid turnover rate in pregnant cows compared to non-pregnant cows is associated with increased DMI during pregnancy (Westo, 1982; Okine and Mathison, 1991). The ruminal MRT decrease as gestation advances (Faichney and White, 1988) by way of reduced DMI as greater digestion and rumen fill restrictions (Dann *et al.*, 1999). The reduction of ruminal volume from the growing foetus applying pressure on the ruminal wall forcing out particulate and liquid (Stanley *et al.*, 1993; Van Weyenberg *et al.*, 2006). Nutrient demand for pregnant animals are greater than for non-pregnant animals (Kennedy and Murphy, 1988) due to high energy and protein demands for foetal growth (Hutjens, 2005). Pregnant animals therefore meet this increased nutrient demands by increasing liquid passage rates (Lunn *et al.*, 2004), which contains short chain fatty acids (Lopez *et al.*, 2003) and liquefied protein (Fox *et al.*, 2004) and these nutrients could be easily absorbed by the animal. Kaske and Groth (1997) observed a 20-30% decline in MRT of particulate and liquid digesta during late pregnancy than at mid-pregnancy. However, Weston (1988) reported a 14-22% decrease in rumen volume of ewes during late pregnancy.

Fuller *et al.* (2004) described the rumen fluid as a water pond comprised of liquefied minerals and soluble proteins, which are absorbed through the foregut and small intestines into the blood stream to the liver. The liver convert the proteins to amino acids (AA), which are transported to the mammary gland for milk synthesis during the lactation period. The high water demand in the lower intestines might source water mobilization reserved in the rumen, hence, increasing ruminal fluid outflow to meet the water and minerals required by the animal for milk synthesis. Higher outflow rates of fluid and particulate digesta from the rumen during lactation than pregnancy is better explained by increases of DMI by 20-30% observed during early lactation (Larsen *et al*., 2009; Helander *et al.,* 2014). Kaske and Groth (1997) reported a greater quantity of large particles in the rumen content during late lactation as a result of reduced rumination activity thus, reducing particle breakdown.

2.7 Mean retention time of digesta in the GIT and passage rate of liquids and solids in ruminants

The passage and digestion kinetics permit better understanding of how much nutrient an animal can absorb from the feed they consume. Better understanding of digestion kinetics and passage provide not only the opportunity to understand limiting factors of the digestive process but also help for optimizing production systems through developing feeding strategies (Tahir, 2008). The rate of passage from the rumen and ruminal digestibility are positively related to improved feed intake but negatively related to the fill effect of the diet. Both the volume and weight of digesta are determinants of the distension in the rumen (Van Soest, 1994). The fractional passage rate (Kp) is the proportion of mass in the pool that leaves per unit of time and is given by dividing ruminal output by the ruminal capacity (Owens and Goetsch, 1988).

The dilution rate (liquid, Kt) is attained from the quantity entering rather than the outflow from the rumen and the digesta load in the rumen. Ruminal stratification can be influenced by the source of roughage (Owens and Goetsch, 1988). The raft formed in the rumen is not only delaying passage rate of trapped particles, but also increase liquid input and fluid passage rate by stimulating rumination. Rates of passage and digestion are important determinants of the physical limitation of voluntary feed intake because they are means by which gut fill is reduced. Kennedy and Murphy (1988) reported that the duration of digesta in the rumen is a function of two processes. One process involves reforming the physical and structural properties of the residue enabling it to escape through fermentation and mastication, while the other involves turning over for a simple passive escape. Grovum (1986) reported that an increase in both frequency of reticular contractions and passage rate is positively linked with increased feed intake. Increased passage rate from the reticulo-rumen is positively related to increased reticulo-rumen contractions frequency (Sissons *et al.*, 1984).

From the rumen to the lower tract, digestible fibre moves by passage or disappear by enzymatic breakdown (Allen and Mertens, 1988). The physical regulation of feed intake is based on the fill effect of the diet thus, the physical distension of the reticulo-rumen is caused by the fill (Mertens, 1987). Forbes (1995) described the reticulo-rumen as the first chamber in the alimentary tract and the quantity that an animal can eat is set by the reticulo-rumen capacity. Forages with high ruminal digestion rates result in increased voluntary feed intake as faster digestion rate and faster passage rate result in quicker reticulo-rumen emptying. Increased passage rates of supplemented low quality forages results in elevated voluntary intake (Ellis, 1978).

Shown in table 1.1 are the mean retention time and passage rate of particulate and liquid matter in ruminants. The passage rate of particulate and liquid vary among ruminant species. Abdullah *et al.* (1991) reported slow outflow of liquid material from the rumen in buffaloes than the outflow of liquid in cattle when fed Guinea grass. Bartocci et al. (1997) obtained similar results where cattle showed faster outflow rates of liquid digesta than in buffaloes fed alfalfa hay. Faster degradation rates in buffaloes than in cattle have been reported (Abdullah *et al.,* 1991; Bartocci *et al.,* 1997); this may be associated with high fermentation activities in buffaloes, which provides a suitable environment for microbial growth that increases microbial protein yield. The fast outflow of digesta in cattle can also be due to slow digestion rates as it is inversely proportional to passage rate of digesta from the rumen. Allen and Mertens (1988) stated that at any given level of feed, passage rate is inversely proportional to rumen volume, hence, the fast passage rate of digesta from the rumen in cattle result in increased intestinal digestion and absorption because of increased nutrient flow. The observed fast passage rate of liquid in cattle are also associated with increased reticulo-rumen motility observed in cattle than in buffaloes, which in turn is associated with increased contractions of reducing particle size, hence, increasing passage rate (Forbes, 1995). The passage rate of particulate matter is proportional to fluid passage rate hence; the passage rate of solid in cattle is more rapid due to fast outflow of small particles from the rumen due to increased removal of liquid phase than in buffaloes (Church, 1988).

With ruminant species classified into three different feeding activities, namely: grazers, intermediate feeders, and browsers. The retention time of digesta in the rumen varies with respect to their feeding activities as browsers i.e. browsers have a shorter retention time than grazers i.e. cattle (Hummel *et al.,* 2006). High amount of indigestible lignin in the cell wall fraction, which cannot be efficiently broken down by extending fermentation of diets consumed by browsers is due to the short retention time in browsers (Spalinger *et al.,* 1993). Huston *et al*. (1986) reported that goats have a fast rate of digesta passage from the rumen than sheep. This could be due to increased daily feed intake by goats, which is relative to their body-weight gut volume than sheep (Parra, 1978; Garcia *et al.,* 1995). Uden *et al.* (1982) reported similar rate of fluid passage from the rumen in both goats and sheep fed on Timothy hay. However, goats appear to be more proficient in digestion than sheep regardless of having similar passage rate (Reid *et al.* 1990).

The rate of passage of solids varies among ruminant species and can be modified by numerous factors, which include particle size (Lechner-Doll *et al.,* 1991), particle specific gravity (Ramanzin *et al.,* 1994), animal species (Colucci *et al.,* 1990), and feeding level. Hume and Sakaguchi (1991) stated that the slow rate of digesta passage from the rumen is accompanied by large body size, hence; large ruminants are likely to have slow digesta passage from the rumen than small ruminants (Furstenburg, 1992). Faichney (1986) observed that less dense particles are accompanied by slower passage rates from the reticulo-rumen as the raft map traps them, or propel away from the reticulo-omasal orifice than denser particles during rumen motility (Lechner-Doll *et al.,* 1991). To escape from the rumen, large particles need to be reduced into a threshold size, primarily through rumination (Kennedy, 1985) to pass through a sieve of 2-4 mm for cattle (Cardoza and Mertens, 1986) and 1-2mm for sheep (Poppi *et al.,* 1980).

Table 2. 1: Mean retention time of digesta in the GIT and passage rate of particulate and liquids from the rumen of cattle, sheep, buffaloes, and goats

Parameters	Species	Diet	Value	Source of data
Passage rate of liquid (h^{-1})	Cattle	Guinea grass	1.55	Abdullah *et al.* (1991)
	Cattle	Perennial grass	0.123	Boudon *et al.* (2009)
	Cattle	Timothy hay	0.066	Uden *et al.* (1982)
	Cattle	Grass	0.123	Estrada *et al.* (2004)
	Cattle	Alfalfa hay	0.066	Bartocci *et al.* (1997)
	Cattle	Blue grama grass	0.105	McCollum and Galyean (1985)
	Sheep	Timothy hay	0.053	Uden *et al*. (1982)
	Sheep	Alfalfa hay	0.069	Bartocci *et al.* (1997)
	Sheep	IRQ	0.035	Moyo *et al.* (2018)
	Sheep	PRQ	0.043	Moyo *et al.* (2018)
	Sheep	Teff straw	0.075	Bonsi *et al.* (1996)
	Buffalo	Alfalfa hay	0.007	Bartocci *et al.* (1997)
	Buffalo	Guinea grass	1.06	Abdullah *et al.* (1991)
	Goat	Timothy hay	0.053	Uden *et al.* (1982)
Passage rate of solid (h^{-1})	Cattle	Alfalfa hay	0.030	Bartocci *et al.* (1997)
	Cattle	Blue green grass	0.035	McCollum and Galyean (1985)
	Cattle	Timothy hay	0.022	Uden *et al.* (1982)
	Cattle	Bush hay	0.033	Schlecht *et al.* (2007)
	Sheep	Alfalfa hay	0.032	Alcaide *et al.* (2000)
	Sheep	Alfalfa hay	0.028	Bartocci *et al.* (1997)
	Sheep	Timothy hay	0.028	Uden *et al.* (1982)
	Sheep	Teff straw	0.019	Bonsi *et al.* (1996)
	Sheep	Bush hay	0.032	Schlecht *et al.* (2007)
	Sheep	IRQ	0.020	Moyo *et al.* (2018)
	Sheep	PRQ	0.016	Moyo *et al.* (2018)
	Buffalo	Alfalfa hay	0.025	Bartocci *et al.* (1997)
	Goat	Timothy hay	0.038	Uden *et al.* (1982)
	Goat	Alfalfa hay	0.034	Alcaide *et al.* (2000)
	Goat	Bush hay	0.042	Schlecht *et al.* (2007)
Mean retention time of digesta in GIT (h^{-1})	Cattle	Alfalfa hay	64.55	Bartocci *et al.* (1997)
	Cattle	Alfalfa hay	45.8	Judkins *et al.* (1987)
	Cattle	Alfalfa hay	41.1	Warren *et al.* (1974)
	Sheep	Alfalfa hay	58.42	Bartocci *et al.* (1997)
	Sheep	Teff straw	54	Bonsi *et al.* (1996)
	Sheep	Barley straw	39.4	Ndlovu and Buchanan-Smith (1985)
	Sheep	Alfalfa hay	44.82	Tsiplakou *et al.* (2011)
	Buffalo	Alfalfa hay	57.73	Bartocci *et al.* (1997)
	Goat	Alfalfa hay	51.8	Coleman *et al.* (2003)
	Goat	Alfalfa hay	31.78	Tsiplakou *et al.* (2011)

GIT: gastrointestinal tract; IRQ: improved roughage quality; PRQ: poor roughage quality.

Bartocci *et al.* (1997) reported a fast passage rate of particulate digesta from the rumen in cattle than in buffaloes fed alfalfa hay. The slow passage rate of solids from the rumen implies that the retention time of digesta in the rumen of buffaloes is greater than in cattle; hence, buffaloes utilize slowly digestible constituents of the diet better than cattle (Lechner-Doll *et al.*, 1991). Uden *et al.* (1982) and Schlecht *et al.* (2007) reported that the passage rate of particles from the rumen is faster in goats than in cattle and sheep. Furthermore, goats and cattle have greater digestibility than sheep (Reid *et al.* 1990). Unlike small particles and fluids, large particles go through diverse treatment in the rumen (Bernard *et al.*, 2000). Bartocci *et al*. (1997) reported prolonged retention time of digesta in the rumen of cattle than in sheep and goats, which could be due to slow passage of digesta from the rumen. This make cattle digest roughage more proficiently than do goats and sheep when fed *ad libitum* (Poppi *et al.,* 1980).

2.8 Fibre digestion and factors affecting digestibility in ruminants

Feed digestibility determines the quantity that is literally absorbed by animals and the nutrient availability for growth and reproduction. Digestibility estimates the energy content of forages and mostly foretell it from forage fibre content making digestibility a common estimate of forage quality (Allen, 1996). Mayes and Dove (2000) reported that digestibility and intake diverge with forage species, thus; accurate measurement of feed digestibility is significant to meet the nutritional demand of animals and enhance production.

In dairy formulations, passage and particle size reduction rate, and nature of fibre are the most dominant restricting aspects due to high forage inclusion rates (Zinn *et al.,* 2004). The extent of ruminal fibre digestion is a result of digestion and passage rate (Zinn *et al.,* 2004). In dairy cattle, energy intake is a result of the energy content and the quantity of DM consumed. Dry matter digestibility is altered by the level of DM consumed thus, the energy content (NRC, 2001). Mertens (1973) reported that up to some extent, fibre digestibility is determined by the duration at which they are retained and how quickly it ferments in the rumen. Fibre digestibility of forages commonly range from 30-50% (Allen, 1993).

The microbial population, chemical and physical attributes of the consumed fibre are the main determinants of fibre digestion in the rumen. In the cattle's hindgut, less than 10% of NDF digestion occurs (Huhtanen *et al.,* 2006). Decreased ruminal digestion is a result of slow digestion or fast passage rate hence, fibre digestion in the rumen is determined by the rate at which feed passes from the rumen and the balance of microbial digestion rate of feed (Huhtanen *et al.,* 2006). Fibre utilization is a result of enzymes produced by protozoa, fungi and anaerobic bacteria in the rumen. Rumen microbes use some of the energy obtained from carbohydrates for their growth. The microbes ferment sugars to produce VFAs, which are then absorbed across the ruminal epithelium and carried by the blood stream to the liver, where some are converted to glucose through gluconeogenesis (Van Soest, 1994) and to other energy sources for growth, body condition, pregnancy, and maintenance.

Digestibility can be easily conceptualizing as a linear function of time rather than a curvilinear function and passage rates are normally expressed as retention times (Allen and Mertens, 1988). Variances in digestibility amongst forage species have led to low intake of semi-natural grassland forages than clover and ryegrass by ruminants (Armstrong *et al.,* 1986). The physico-chemical interaction of lignin, cellulose, and hemicellulose are the central fundamentals influencing ruminal fibre digestion rate in ruminants. These factors are influenced by the stage of maturity, age prior harvesting, and preservation and processing methods of forages (Zinn *et al.,* 2004).

The chemical composition of cell wall is not the only factor affecting forage digestibility in ruminants. Digestibility can also be affected by anti-nutritional factors such as tannins (Moghaddam and Wilman, 1998). Peak grass digestibility occur during the vegetative phase due to low stem: leaf ratio and cell wall content, which are linked to increases in maturity (Groot, 1999). Terry and Tilley (1964) reported that before plants attain an advance phase of maturity, leaf digestibility is higher than stem digestibility but decrease rapidly over time hence, stem leaf ratio increases with increasing maturity. McDonald *et al.* (2002) reported that cattle digest low-quality forages better than sheep. Vast recycling of nutrients in the rumen of cattle makes cattle to digest forages better than sheep (Playne, 1978). As fibre digestion rates decline, the quantity of gradually digestible organic matter (OM) in the rumen elevates (Zinn *et al.,* 2004).

2.9 Feeding behaviour of ruminant herbivores

Feeding behaviour is used to foretell the response of ruminant species to a particular environment (Grant, 2006), morbidity in steers kept in feedlot (Sowell *et al.,* 1999), and aid as a physiological mechanism modulating feed intake. The physiological needs of animals are met through absorption of sufficient amount of nutrient from the gastrointestinal track (Phillips, 2008). Intake is predominantly regulated by both hunger and satiety (Read, 1992) and is often by the ingredient inhibiting the sum total of nutrients that an animal can obtain from its ration (Dulphy and Demarquilly, 1994). In relation to the body homeostatic control, dietary alternatives and feed intake regulation merges short-term regulation of feeding behaviour, and long-term regulation rely greatly on body reserves and nutritional requirements (Faverdin *et al.,* 1995).

Feed gathering is the prime concern of all animals (Albright, 1978). Munro and Walters (1986) stated that the voluntary feed intake contribute closely with the nutritive value in regulating the feeding merit of grazing plants. Voluntary feed intake is the quantity an animal consumes during a period of time at *ad libitum* feeding (Freer, 1981) and comprises of the quantity of meals consumed daily, the degree of eating, and bite and mass rate (Rook, 2000). Feeding behaviour of ruminants in the wild varies from that in captivity. Unlike animals kept in barns, which spend more time lying due to less time spent searching for feed (Phillip, 1993), feeding behaviour in the wild is influenced by feed searching and feed selection behaviour, which results in less time spent resting. However, Phillips (1993) argued that unless they are crowded, the feeding behaviours of cattle in barn environments are similar to grazing cattle. The total voluntary intake of dairy cattle is a result of time spent eating and meal patterns. Precise assessment of voluntary intake by grazing animals is an important factor in ruminant production and management (Grant and Albright, 2000).

Unlike sheep, grazing behaviour of cattle involves less selectivity and gathering of large amounts of ground level shrub material (Ginnett *et al.,* 1999). Cattle prefer to graze darker greener herbage as an indication of higher nitrogen content (Phillips, 2008). Feeding behaviour of cattle on pasture is influenced by sex, age and breed (Aharoni *et al.,* 2009), management (Arachchige *et al.,* 2013), sward composition (Caton and Dhuyvetter, 1997), and environmental conditions (Butt and Batool, 2010). Although it is an energetically costly technique of attaining palatable feed sources, cattle can consume grass heads on tall reproductive stems individually (Ginnett *et al.,* 1999). Feeding behaviour of ruminants is affected by various factors categories as: (i) plant factors: fibre content, sward surface height (SSH), tiller density, and herbage allowance (Gibb *et al.,* 1998; Gregorini, 2011); (ii) environmental factors: rain fall, ambient temperature, photoperiod, and relative humidity (Champion *et al.,* 1994; Gregorini, 2011); and (iii) animal factors: productive capacity and nutritional demand, body weight, lactation stage, rumen fill and function, and physiological status (Gibb *et al.,* 1998; Taweel *et al.,* 2004).

2.10 The meal behaviour of grazing and captive ruminants

When grazing, ruminants exhibit a diurnal form of liking for legumes and grass (Gregorini, 2012), and have two central grazing periods which usually occur at dawn (sunrise) and dusk (sunset) (Jarrige *et al.,* 1995). The two key meals are separated by numerous smaller meals called secondary meals. The preference for grass to legumes during sunset foraging event could be due to the ability of roughage to sustain rumen fill throughout the night thus, gradually supplying nutrients (Rutter, 2006). Jarrige *et al*. (1995) reported that it is during the two main meals that 60 – 80% of the daily intake is attained, hence; voluntary intake is close to the quantity consumed through the main meals. High levels of intake occur during the dusk grazing event. This is an adaptive feeding approach developed by ruminants to maximize diurnal energy attainment, supplying a constant release of nutrients overnight (Gregorini, 2012). Intake rate is peak during the start of main meals representing the stimulus to eat and declines constantly as satiation continues until satiety (Jarrige *et al.,* 1995). Campling and Morgan (1981) reported that housed cattle feed on hay or silage will have 6-12 meals per day.

When animals are grazing on new pasture in the afternoon, Vibart *et al.* (2011) and Gregorini *et al.* (2008) observed that animals exhibit fewer, extended and additional grazing bout in the late afternoon and early evening compared to feed distribution in the morning, therefore, dusk meal dominates voluntary and nutrient intake (Gregorini *et al.*, 2007). The small quantity of ingestive chews of fresh herbage during dawn compared to dusk grazing event is a result of increased herbage intake due to high hunger level during dawn (Gregorini *et al.*, 2009), resulting to ingestion of greater particles with high water content. McLeod and Minson (1988) reported that herbage particle size is reduced through ingestive chewing by 25–30%, which releases approximately 65% of the cell wall content. However, this phenomena inhibit the ability to appropriately pack vast amount of herbage consumed rapidly at dawn event (Chilibroste *et al.*, 2005) due to the created filling phenomena regardless of the slow rumen digesta pool (Taweel *et al.*, 2004). Gregorini *et al.* (2008) and Taweel *et al.* (2004) reported low rumen fill during the dawn because of elongated and supreme intensive rumination bouts taking place at night.

Daylight signal animals to wake up and seek food (Toates, 2002). High herbage intake rates (fresh matter basis) during the day is stimulated by the phenomena of rumen emptying, thus, the main internal stimulus for animals to graze (Gregorini, 2011). Regardless of the animals being motivated to eat during the dawn, bouts are short and segregated by long intervals (Rook and Huckle, 1997). During the dawn, elevated bite mass, herbage intake, and plasma concentration of ghrelin in dairy cattle and beef heifers are a result of declines in rumen fill (Gregorini *et al.,* 2009). Approximately 4 h before sunset, stocked sheep spend 25-48% of total diurnal time grazing (Penning *et al.,* 1991), while Gregorini *et al*. (2008) reported that stocked beef heifers spent 36% and 48% of their over-all grazing time at dawn and dusk, respectively.

When distributing pasture at dusk, Gregorini *et al.* (2008) observed lower rumen digesta retention times, greater glycogenic nutrient supply and rumen fermentation, escalation in true rumen organic matter digestion and microbial protein flow to the intestines in heifers. When fed indoors with two feed distributions daily, Baumont *et al.* (1988) observed that the first rumen fill reaches maximum after the dawn meal and the diurnal maximum after the dawn meal. Thomson *et al.* (1985) reported that after the main grazing event, grazing sheep reach the first and daily maximum at 9h00 and 20h00, respectively. Gregorini *et al*. (2008) reported that sheep and cattle delay rumination following the dawn main meal. Lactating dairy cows on pasture naturally have five meals per day, with each meal categorized by approximately 110 minutes. Dairy cows usually spend 6-10 hours when grazing on pasture and 4-6 hours in a barn (Phillips, 2008).

2.11 Factors affecting diurnal feeding behaviour of ruminant herbivores

2.11.1 The effect of sward height and density

The multiplex interactions amongst sward and animal characteristics are the determinants of grazing dynamics by ruminants. Gregorini *et al*. (2011) reported that intensive stocking rates and herbage characteristics reduce bite rate (BR) and bite mass (BM). Prolonged grazing time results in decreased intake rates due to sward depletion (Baumont *et al.,* 2004). Wade (1991) reported that cattle and sheep (Hodgson, 1966) favour grazing the top fragments of the sward as the nutritive value of grass declines from the upper to the lower parts of the sward (Delagarde *et al.*, 2000). Sward surface height (SSH) management is essential to attain high levels of herbage intake, as SSH is a crucial physical characteristic that greatly influences the bite size (Hodgson, 1990). Sward surface height is the height of sward from ground to the top surface of undisturbed sward (Tharmaraj *et al.*, 2003). The sum intake time increases with a decline in SSH as cattle are incapable of grazing swards shorter than 1cm (Domont, 1995), signifying that dairy cows compensate the low herbage accessibility by elevating the total intake time (Gibb *et al.*, 1999).

During grazing, herbage state such as SSH (Gibb *et al.* 1997; Phillips, 2008) and herbage bulk density (Laca *et al.,* 1992) significantly influence the bite mass, bite rate, ruminating time, and the total eating time which essentially determines dry matter intake and rumen function. Delagarde *et al.* (2000) reported that the sward's bulk density decline from the bottom to the upper strata of the sward canopy. Benvenutti *et al*. (2009) described bite mass as another vital contributing factor to short-term herbage dry matter intake by grazing ruminants.

Gibb *et al.* (1999) observed that an increase of SSH from 5-9 cm resulted in a notable increase in bite mass (BM) due to the ability of tall sward to allow effortless prehension (Phillips, 2008). In continuous grazing, Ernst *et al.* (1980) reported that high intakes are obtained at sward heights of 8-9 cm, and at 9-13 cm in rotationally grazed forages. A sustained bite mass of 640 mg DM/bite when SSH was increased from 25-40 cm (Stakelum *et al.*, 1997). Declines in bite mass were observed when SSH surpassed 55 cm (Stobbs, 1973), this could be associated with herbage depletion, which is attributed by low bulk density in the top strata of the sward. When the animal strives to obtain blades that are more dispersed, the bite mass is reduced increasing time spent on each bite (Palhano *et al.,* 2007) and swards close to 50 cm offer effortless herbage harvest.

2.11.2 The effect of photo-period and time of day

Dairy cows exhibit three main grazing sessions during the dawn, afternoon, and dusk (Rook and Huckle, 1997). Coulon (1984) described cattle as diurnal feeders with an inclination to feed more at dusk. However, nocturnal feeding occur at high intake requirements and short day length. Nocturnal feeding is expected to arise in hot humid environments to limit sun exposure throughout daytime (Coulon, 1984). Albright and Arave (1997) also described cattle as crepuscular as they are mostly lively throughout the dawn and dusk although feeding activities subsequently decline at sunset and overnight. Feeding activities such as grazing, ruminating, walking and resting occupy approximately 95% of cattle's time budget on grassland.

In hot conditions, cattle utilize meal quantity and size to disperse their meals through hours of daylight, with large quantities of short meal durations during daytime in mid-summer (Coulon, 1984). Krysl and Hess (1993) observed regular grazing event at dusk when temperatures were above 25°C during the daytime, and mostly in non-supplemented animals

(Scaglia *et al.*, 2009). Although the number of meals increase with prolonged day length, the total diurnal feeding time does not increase (Phillips, 2008). During the feeding bout occurring at dusk, dairy cows grazed 71 minutes longer than during the dawn meal. Dry matter content of grasses increases at dusk resulting in increased bite mass during this grazing event (Taweel, 2004). The accumulation of essential fatty acids, sugars, and dry matter in herbages as a result of transpiration and photosynthesis during the day enables sward particle breakdown during ingestion (Gregorini, 2012). In contrast, Arachchige *et al.* (2013) reported extended time spent on feeding activities by 152 and 149 minutes per day in the morning than at afternoon, respectively. High herbage intake as a result of high bite mass and bite rate, and prolonged eating period at dusk grazing event resulted in high pool sizes at 23h30 than during daytime (Taweel, 2004).

2.11.3 The effect of ambient temperature and humidity

Meal patterns and physiological necessities of dry cows are mainly affected by temperature (Sniffen *et al.*, 1993). Phillips (2008) described cattle as thermolabile. During extreme weather conditions cattle seek out thermal cover, remain inactive, lying down and positioning their body in the direction of the sun in attempt to minimize energy losses (Fraser, 2004). Optimal weather circumstances aid optimum feed intake and feeding behaviour, but decline during rain (Charlton *et al.,* 2011) and at high ambient temperature and increased sunlight (Uzal and Ugurlu, 2010). The need to seek shade by cattle in the course of the day is increased by humidity and temperature. In hot dry environments, cattle change their feeding to dusk feeding to lessen heat load (Phillips, 2008).

Although feeding times of cattle increase at low temperatures, healthy cattle can easily adjust to temperatures of -20°C by increasing intake to increase reticulo-rumen motility rates thus, increasing ruminating time and heat increment of digestion (Gonyou *et al.*, 1979). When temperatures exceeded 28°C, all feeding activities by cattle ceased (Langbein and Nichelmann, 1993). Heat stress due to high temperature and humidity changes feed preference as animals will prefer concentrate feeds avoiding fibrous feeds since they yield a greater heat increment of digestion compared to other nutrients. In various tropical regions, fibrous feeds are a source of feed to cattle, and such diets enable cattle to endure extremely low temperatures without declines in productivity (Phillips, 2008). During summer, dusk grazing by cattle increase and account for approximately 80% of the sum grazing time resulting in reduction or elimination of mid-day grazing. Gregorini (2012) also observed that grazing events merge during warm and long days leading to prolonged and fewer grazing occasions focused at dusk.

Feeding behaviour is exceedingly suitable to assess diets as it give feed management of animals to achieve preferable reproduction and production performance since nutrient intake is a key determinant of animal performance (Mertens, 1994). Feeding is the main activity of behaviour, and feeding actions have importance over rumination on every occasion the fundamental influences of the two actions conflict (Metz, 1975) and ruminants adjust feed intake according to their nutritional requirements, primarily energy (Van Soest, 1994). DMI and feeding behaviour in ruminants is regulated by chemostatic mechanisms and reticulo-rumen fill. Peak DMI and high feeding activities can be promoted by enhancing factors that regulate feeding behaviour. Older and high producing cows will consume vast amount of feed and water with long rumination periods, and eat greater meals more rapidly than do younger and low producing cows (Dado and Allen, 1995). Sniffen *et al.* (1993) reported that dietary formulation and feeding system designs should meet the potent nature of cattle nutrient needs and feedstuff configuration variability. In non-rivalry feeding conditions, where animals are confined, feeding and ruminating times are influenced by feed characteristics, primarily the cell wall rate. Digestibility and passage rate through the gastro-intestinal tract are also influenced by intake behaviour (Costa *et al.*, 2011).

2.12 Summary

In ruminant production, roughage is a vital dietary component that need to be considered. Feed intake is the primary constituent determining animal performance with protein and energy being the major pivot in ruminant production. Forages are the primary source of carbohydrate for grazing ruminants with the rumen digesta load being a central factor affecting feed intake by ruminant animals. Rumen fill is a parameter of intake, degradation, digestion, and passage rate, which are in turn affected by the quality of roughages. Poor quality roughages can be improved through urea treatment.

2.13 Conclusion

In conclusion, this review outline the need to explore how improving roughage quality of tropical veld through the use of urea and period of day would affect rumen fill, feeding behaviour, degradation, digestibility, passage rates, and thus, voluntary intake. Since intake is determined by the time spent eating, number of meals, and bite rate, feeding behaviour could be used to predict intake. Furthermore, this study will enable resource-limited farmers in tropical and sub-tropical regions to know the potential herbage intake of ruminants in order to predict their livestock production in a region from the available roughage sources. Improving roughage quality through urea treatment will help sustain production during the winter season in these regions.

Chapter 3

The effect of quality of roughage and period of day on diurnal rhythm of feeding behaviour of cattle

Abstract

The current study explored the effect of roughage quality and period-of-day on feeding behaviour of cattle. Four ruminally cannulated Jersey heifers were used in a 4×4 Latin square design. Hay of poor quality (RPQ) was improved by treating with 4% (w/w) urea for 20 days (IRQ); or by spraying hay with 2.5% (w/w) urea and sun drying before feeding to give semi-improved roughage quality (SIRQ); or by mixing equal proportions of IRQ and PRQ to give moderately improved roughage quality (MIRQ). All four roughage diets were distributed once daily in the morning at 8h45. During the adaptation period, all heifers were supplemented with Lucerne hay (1.7kg/d), which was removed 4 days prior to the end of each adaptation period. Eight CCTV cameras were mounted to observe the behavioural activities exhibited by each animal for three consecutive days (24h per day) in each of the 4 experimental periods. Four heifers were randomly allocated to the roughages in a 4×4 Latin square design. Each experimental period had an adaptation period of 7 days, except in the first period where 14 days of adaptation was allowed. Data on time spent on each of the 11 different behavioural activities (drinking water, eating, idling whilst standing and lying, ruminating whilst standing and lying, grooming, licking objects, tongue rolling, hedonic feeding, and other activities i.e. feed searching) was recorded. Roughage quality had no significant effect (P> 0.05) on the time spent on each behavioural activity except grooming and tongue rolling. The period-of-day affected (P<0.05) time spent on each activity except for idling whilst lying and tongue rolling. Time spent on each activity was significantly affected by period-of-day. Results obtained in this study indicate that heifers spent most of their time eating and ruminating.

Additional keywords*:* roughage quality, diurnal feeding behaviour, period of the day, cattle.

3.1 Introduction

Generally, the animal's behaviour is the first line of defense in response to environmental alteration (Mench, 1998), and human caretakers can attain information regarding the welfare of the animal through the animal's behaviour (Manser, 1992). In ruminant production, feeding behaviour is a significant tool used to assess diets as it renders animal feed management for improving reproduction and production performance (Cavalcanti *et al.,* 2008). Furthermore, feeding behaviour has predominance over rumination at any time when the casual elements of the two actions conflict (Metz, 1975). Le Magnen (1985) described feeding behaviour as the selection and ingestion of feed by the animal, which is required for growth, milk production and maintenance. With firmly grounded knowledge of interpreting behavioural patterns, information about the animal's demand, fondness and dislikes, and internal states can be attained (Mench, 1998) thus, nutrition is a result of feeding behavioural activities (Forbes, 1995). Grant and Albright (2000) reported that the total voluntary intake of dairy cattle is a result of time spent eating and meal patterns. Precise assessment of voluntary intake by grazing animals is one of the supreme tools in enhancing production and management.

Fisher *et al.* (1997) discussed that rumination, idleness, and feeding are three fundamentals of feeding behaviour, which dominate the daily activities of animals and their time span and distribution is influenced by climatic conditions, diet, and animal activities in the herd. However, even if a stimuli is suitable for more than one behavioural activity, animals can perform only one behavioural activity at a time (Toates and Toates, 1980). Baumont *et al.* (2000) described feeding behaviour in terms of the animal's motivation to eat and satiation process, where satiety is the state from the coda of one meal to the initiate of the next. This is during when the animal does not eat, i.e. when it is not stimulated to eat (Le Magnen, 1985), and reflects the physiological and biological status of animals (Adbelsalam and Al-Seaf, 2013). Intake is predominantly regulated by both hunger and satiety (Phillips, 2008) and often by the ingredient inhibiting the sum total of nutrients, mainly, energy that an animal can attain from its ration (Dulphy and Demarquilly, 1994). Ruminants may be motivated or stimulated to eat by sound and sight of others eating, and possibly by fresh feed delivery (Forbes, 1995). Voluntary feed intake is the quantity an animal consumes during a period of time at *ad libitum* feeding (Freer, 1981) and include the number of meals consumed daily, the extent of each meal, the degree of eating (Grant and Albright, 1995), bite and mass rate (Rook, 2000). Feed gathering is a central concern of all animals (Aziz, 2008), and following extended durations of darkness, cows tend to naturally consume vast amounts of meal soon after light availability (Phillips, 2008).

Animals attain the quantity of required nutrients by overcoming the circumstances that limit feed intake by changing their feeding behaviour (Meneses *et al.,* 2014); hence, the rate at which feed is digested and passed through the gastro-intestine tract is influenced by the intake behaviour. While hunger stimulates the animals to eat, the nutritive value of herbage, plant toxicity, and rumen fill regulate feed termination by ruminants. Increased intake rates are stimulated by the decent colour and pleasant aroma of feeds henceforth, making intake pleasurable (Adbelsalam and Al-Seaf, 2013). When animals are confined in conditions of non-competitive feed, the feeding and rumination time is influenced predominately by the feed's cell wall content (Mendonça *et al.,* 2014). Although ruminants regulate feed intake to meet their nutritional needs (Van Soet, 1994), individually penned cattle consume less hay than group fed due to elevated anxiety expressed by temporarily sequestered cows (Metz, 1975). Hafez and Bouissou (1975) reported that due to preclusion of forage selection, cattle would consume great quantities of poorly nutritious feed when on silage than when on pasture. Time spent masticating various diets alters directly with the sum of chews (Hafez and Bouissou, 1975), and non-forage fibre sources and reduced forage particle size decrease both chewing time and production of saliva which plays a significant role in buffering the rumen (Dohme *et al.,* 2008). In ruminants, feeding behaviour and dry matter intake (DMI) are not only regulated by the reticulo-rumen fill, other factors such as housing and feeding facility, social interactions and grouping strategies modulate feed intake to such species (Grant and Albright, 2001).

The lack of freedom to perform foraging and other feeding behaviour components is associated with factors regulating oral stereotypies in animals (Bayne *et al.,* 1991; Rushen and Mason, 2006; Redbo and Norblad, 1997), even though stereotypes can sometimes be associated with physiological alterations of stress, which in turn reduces stress (Mench, 1998). Only a few studies are being done on intrinsic and improved quality of roughage on diurnal patterns of feeding behaviour in cattle in tropical and subtropical Africa. Voluntary feed intake of ruminants is being affected by roughage quality, time spent eating, and meal patterns, thus suggesting that an understanding feeding behaviour of ruminants will will enable resource-limited farmers in tropical regions to know the potential herbage intake of ruminants in order to predict their livestock production in a region from the available roughage sources. Objectives of this study were to: (i) determine the effect of improving roughage quality on diurnal feeding behaviour of cattle, (ii) To determine the effect of period of day on feeding behaviour patterns and how they vary in roughage quality.

3.2 Method and materials

3.2.1 Study site

The experiment was conducted with the approval of the University of KwaZulu-Natal Ethics Committee, the Animal Ethics Sub-Committee (ref. ARE/066/016M). The study was conducted in summer at the Ukulinga Research Farm, University of KwaZulu-Natal (Pietermaritzburg) in South Africa. The daytime temperatures in summer reach highs of around 29°C with night temperatures averaging around 16°C. The rainfall pattern is characterized by an annual rainfall of approximately 730 mm, which falls mostly between October and April. Summer temperatures may reach highs of above 33°C and with minimum temperatures of 7°C at night in winter.

3.2.2 Animals, housing, diets and experimental design and feeding

Four ruminally cannulated Jersey heifers with an average body mass of 288.5 ± 3.69 were used. Heifers were housed in individual pens and given one of four diets. In the first dietary treatment, hay of poor quality (RPQ) was improved by treating with 4% (w/w) urea for 20 days (IRQ); or by spraying hay with 2.5% (w/w) urea and sun drying before feeding to give semi-improved roughage quality (SIRQ); or by mixing equal proportions of IRQ and PRQ to give moderately improved roughage quality (MIRQ). Consequently, heifers were randomly assigned to one of the four roughage diets in a 4 × Latin square design. Animals were given 14-day adaptation period to experimental diets at the beginning of the trial and 7 days for adaptations just before interchanging animals between diets. During the adaptation periods of 14 and 7 days, all animals were supplemented with Lucerne hay (1.70 kg/d) for 10 and 3 days, respectively. Thus, animals completed 4 days of adaptation consuming only one of the four roughages. Water was provided *ad libitum* throughout the experiment. Approximately 10 kg of feed per head was allocated once daily in the morning throughout the experiment.

3.2.3 Behavioural measurements

Feeding behaviour was recorded using 8 closed-circuit television (CCTV) cameras for three consecutive days (24 h per day). Cameras were preferred to allow heifers to exhibit their normal day-to-day behavioural activities without being disturbed. Feeding behavioural activities evaluated were: times spent eating, drinking water, ruminating whilst standing and ruminating whilst lying, idling whilst standing and idling whilst lying, grooming, licking objects, and tongue rolling (Table 1). Daytime was taken to be (6h00 – 18h00) and night time was taken to be (18h00 – 6h00). The hourly time spent on each activity over 24 h was calculated to determine diurnal feeding behaviour patterns of heifers.

Table 3. 1: Ethogram of feeding behaviour activities recorded for heifers in individual pens

Behavior	Description
Eating	When the animal is obtaining feed from the feed trough
Ruminating standing	When the animal is regurgitating the swallowed feed standing
Ruminating lying	When the animal is regurgitating the swallowed feed whilst lying down
Drinking water	When the animal is drinking water from the water trough
Idling standing	When the animal is standing not performing any activity
Idling lying down	When the animal is lying down not performing any activity
Grooming	When the animal is licking its self or other animals
Tongue rolling	When the animal is flicks its tongue outside and rolls it back inside the mouth
Licking objects	When the animal is licking the bar and walls
Hedonic feeding	When the animal is eating to obtain pleasure in the absence of an energy deficit
Other activities	Any other activities not mentioned, e.g. feed searching.

Feed intake was also determined. The number of meals per day were identified (which were separated by periods of heifers showing no feeding activity). Since heifers may leave the feed bunk to visit water trough or move along the feed bunk before their next bite, meals were separated by a break of 5 minutes. When the animal feed for a few seconds then switch to another activity, it was considered as hedonic feeding.

3.3 Chemical analysis

Dry matter, moisture, and ash contents were analyzed using the procedures outlined by the Association of Official Analytical Chemists (AOAC, 2005). Nitrogen content was determined using the LECO machine (LECO FP2000, LECO, Pretoria, South Africa). Crude protein content was calculated by multiplying the nitrogen content by a factor of 6.25. Neutral detergent and acid detergent fibres were analyzed using ANKOM A220 fibre analyzer (ANKOM Technology, New York, USA) (AOAC, 1990). Hemicellulose content was determined by subtracting acid detergent fibre content from neutral detergent fibre content.

Table 3. 2: Chemical composition of experimental diets

	Chemical composition (g/kg DM)					
	DM	CP	NDF	ADF	HEM	ASH
MIRQ	739	62	732	399	333	69
SIRQ	727	63	721	404	316	68
IRQ	727	89	745	415	330	78
PRQ	745	36	711	380	331	78
Lucerne	906	136	524	361	163	89

IRQ; improved roughage quality; PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality, DM: dry matter; CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; HEM: hemicellulose.

3.4 Statistical analysis

The GLM procedure was used to determine the effect of roughage quality and period of the day on behavioural activities. The statistical model was: $FB_{ijl} = \mu + R_i + P_j + (R\times P)_{ij} + \varepsilon_{ijl}$, where: FB= behavioral observation (eating, ruminating, ruminating whilst standing, ruminating whilst lying, drinking water, idling, idling whilst standing, idling whilst lying, grooming, licking objects, and tongue rolling), μ= overall mean, R= effect of roughage quality, P= effect of period of the day (j= Day; Night), (R×P)= interaction of the effect of roughage quality and period of the day, and ε_{ijl}= experimental error. The Student-Newman-Keuls (SNK) test was used to separate means at $P < 0.05$.

Secondly, these data were analyzed using time as a repeated measure. The experimental model for feeding behaviour was as follows: $t_1 – t_{24} = \mu + P_i + D_j + (P\times D)_{ij} + \varepsilon_{ijl}$, where: $t_1 – t_{24}$ = time spent on each activity over 24 h divided into 24 periods of 1 h intervals, μ= overall mean, P= period (i= 1-4), D= diet (j= 1-4), (P×D)= interaction of period and diet, and ε_{ijl}= experimental error.

3.5 Results

3.5.1 Effect of roughage quality on diurnal feeding behavior of heifers

Roughage quality had no effect on all activities except for socializing and tongue rolling (Table 3.4).

3.5.2 The effect of quality of roughage and period of the day on diurnal feeding patterns of heifers

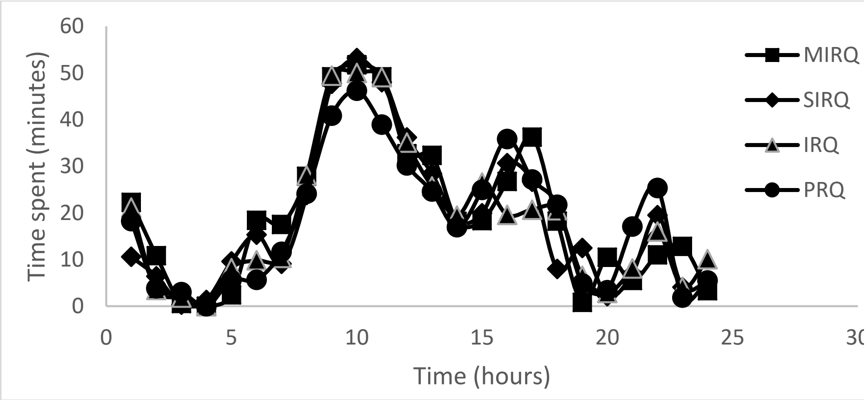

Figure 3. 1 Feeding pattern of heifers fed improved roughage quality.

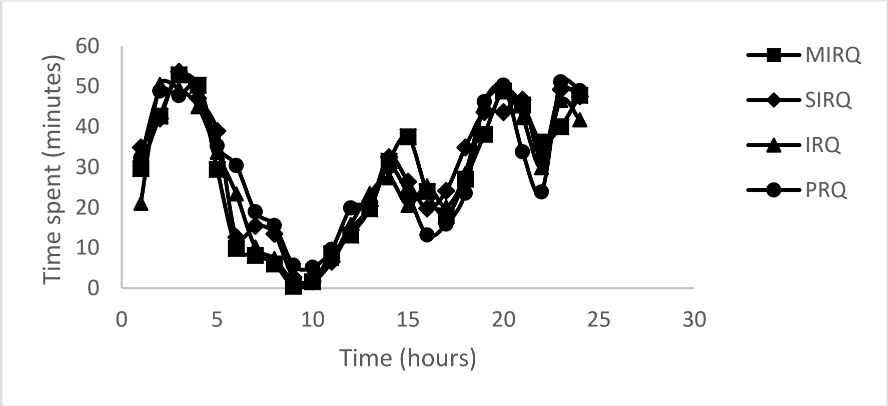

Figure 3. 3 Ruminating pattern of heifers fed improved roughage quality.

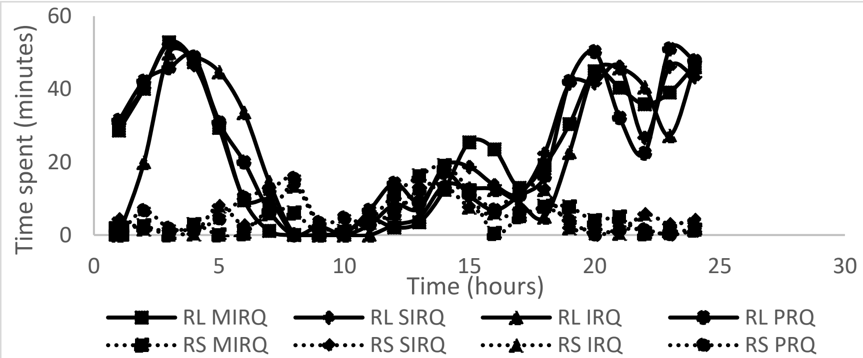

Figure 3. 2 Ruminating whilst standing and lying pattern of heifers fed improved roughage quality.

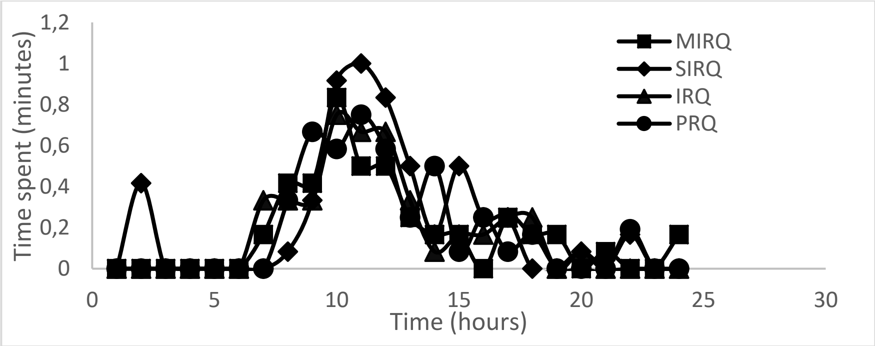

Figure 3. 4 water consumption pattern of heifers fed improved roughage quality.

(PRQ: poor roughage quality; MIRQ: moderate roughage quality; SIRQ: semi-improved roughage quality; and IRQ: improved roughage quality).

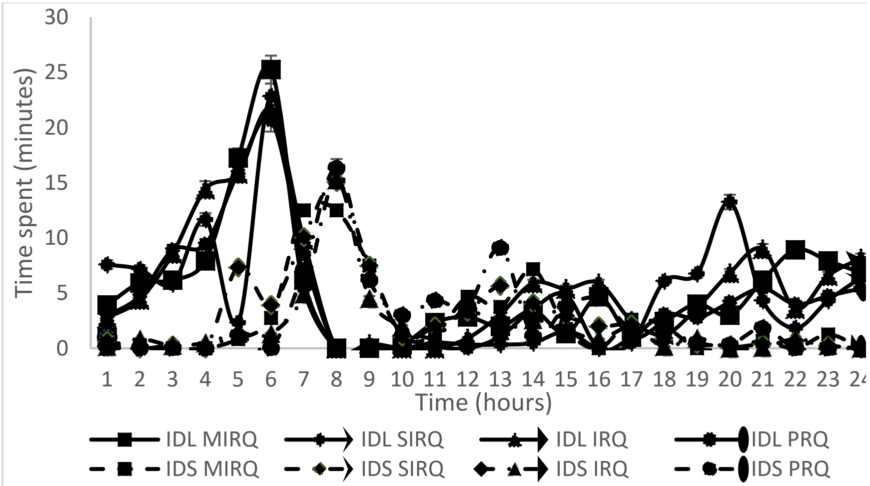

Figure 3. 5 Idling whilst standing and lying pattern of heifers fed improved roughage quality.

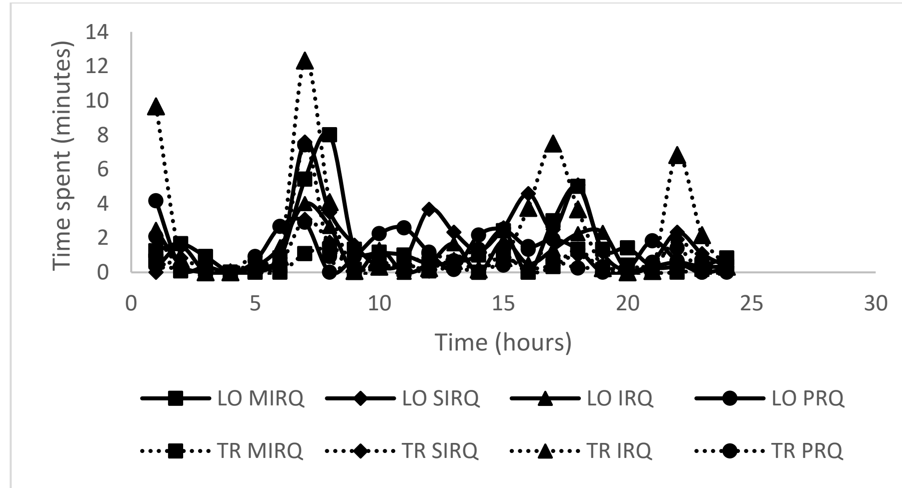

Figure 3. 7 Tongue rolling and licking object of heifers fed improved roughage quality.

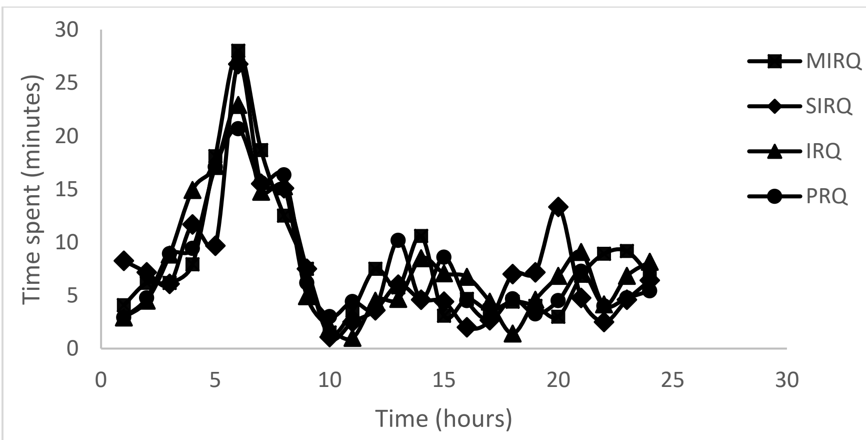

Figure 3. 6 Idling pattern of heifers fed improved roughage quality.

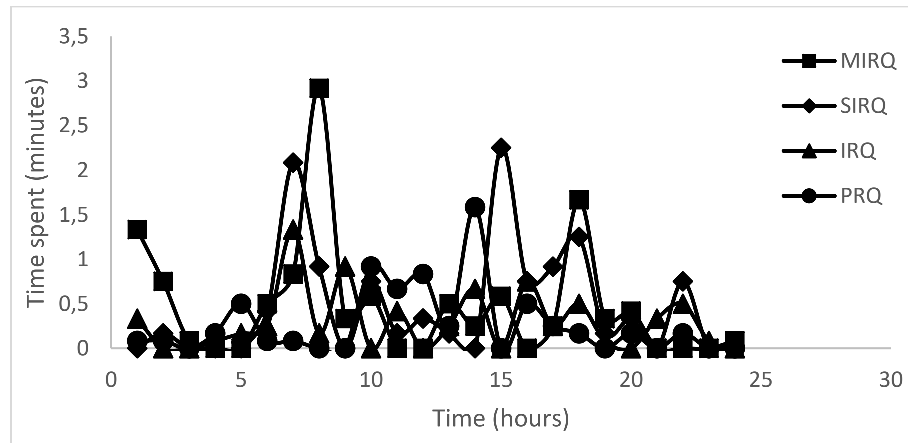

Figure 3. 8 Other activities of heifers fed improved roughage quality.

(PRQ: poor roughage quality; MIRQ: moderate roughage quality; SIRQ: semi-improved roughage quality; and IRQ: improved roughage quality).

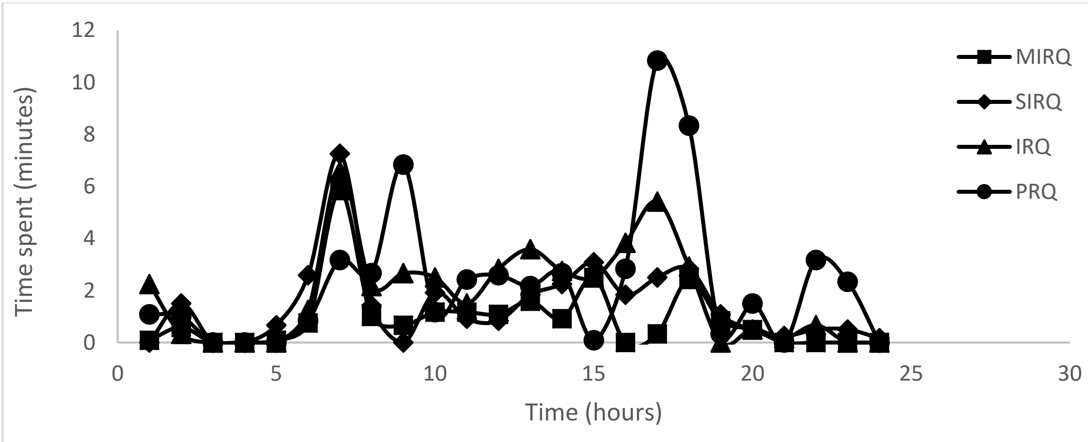

Figure 3. 9 Grooming pattern of heifers fed improved roughage quality.

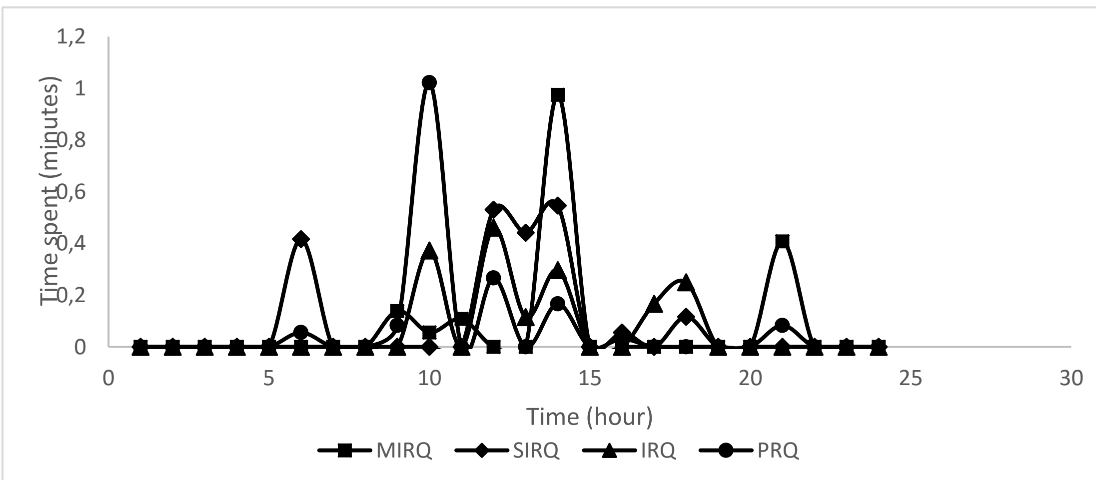

Figure 3. 10 Hedonic feeding pattern of heifers fed improved roughage quality.

(PRQ: poor roughage quality; MIRQ: moderate roughage quality; SIRQ: semi-improved roughage quality; and IRQ: improved roughage quality).

Table 3. 3: Effect of roughage quality and period of day (Daytime and Night-time) on diurnal feeding behaviour rhythms in jersey heifers

	Diet									Significance of influence	
	MIRQ		SIRQ		IRQ		PRQ				
Activities Time spent (Min)	Day	Night	Day	Night	Day	Night	Day	Night	RMSE	D	P
Eating	381	109	367	75	352	97	333	110	26.50	NS	***
Drinking water	4	0.4	5	0.8	4	0.3	4	0.3	1.18	NS	***
Ruminating standing	81	33	96	35	110	17	108	27	36.95	NS	***
Ruminating lying	132	423	132	448	109	431	136	429	36.83	NS	***
Ruminating	213	456	228	483	219	448	244	456	30.77	NS	***
Idling lying	67[a]	64[a]	34	72	72	68	57	51	19.84	NS	NS
Idling standing	59	4	67	4	43	3	62	4	15.46	NS	***
Idling	126	68	101	76	155	71	119	55	29.32	NS	***

IRQ; improved roughage quality; PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; D: diet; P: period; ***P<0.001; NS: not significant; diet and period interaction was not significant for all activities. [a] Means in a row with superscripts are not significantly different ($P < 0.05$).

Table 3. 4: Effect of roughage quality and period of day (Daytime and Night-time) on diurnal feeding behaviour rhythms in jersey heifers

	Diet									Significance of influence	
	MIRQ		SIRQ		IRQ		PRQ				
Activities	Day	Night	Day	Night	Day	Night	Day	Night	RMSE	D	P
	frequency of behaviour (periods per day)										
Number of meals (p/d)	7	3	9	3	9	3	10	4	1.34	NS	***
Number of water trough visits (p/d)	4	1	5	0	3	0	5	0	1.07	NS	***
	Duration of behaviour (Min)										
Grooming	17	4	26	7	38	7	39	20	11.99	*	***
Licking objects	26	14	31	13	16	9	21	14	12.22	NS	*
Hedonic feeding	3	1	4	0.3	2	0	2	0	1.15	NS	***
Tongue rolling	5[a]	4[a]	10	5	32	29	16	5	12.38	***	NS
Other objects	7	5	9	3	5	2	6	0.8	2.86	NS	***

IRQ; improved roughage quality; PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; D: diet; P: period; *P<0.05; ***P<0.001; NS: not significant; diet and period interaction was not significant for all activities. [a,] Means in a row with similar superscripts are not significantly different ($P < 0.05$).

Table 3. 5: Effect of roughage quality on total time spent on feeding behavioural activity per day in jersey heifers

	Diet				Significance of influence
	MIRQ	SIRQ	IRQ	PRQ	RMSE
Time spent (Min)					
Eating	490	442	449	443	43.60
Drinking water	4.4	5.8	4.3	4.3	1.85
Ruminating standing	114	131	127	135	49.63
Ruminating lying	555	580	540	565	50.12
Ruminating	669	771	667	700	45.84
Idling lying	131	106	140	108	30.64
Idling standing	63	71	46	66	23.01
Idling	194	177	186	174	43.35
Number of meals (p/d)	10	12	12	14	1.96
Number of water trough visits (p/d)	5	5	3	5	1.63
Grooming	21^{b}	33^{ba}	45	59^{a}	21.14
Licking objects	40	44	25	35	16.59
Tongue rolling	9	15	61	21	24.46
Hedonic feeding	4	4	2	2	2.03
Other objects	12	12	7	6.8	5.07
Feed intake (kg/d)	8.05^{b}	9.87^{a}	8.35^{b}	7.53^{b}	0.44

IRQ; improved roughage quality; PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; RMSE: root mean square error; $^{a, b}$ Means in a row with different superscripts are significantly different ($P < 0.05$).

3.5.3 Intake and diurnal feeding pattern

The diurnal eating pattern of heifers fed varying roughage quality oscillated through the day (Figure 3.1). Consequently, the time spent eating was not affected by roughage quality (P> 0.05) but by the period of day (P<0.05; Table 3.3). Generally, feeding started between 4h00 and 5h00 AM and there were two distinct feeding peaks in the late morning and at dusk. Time spent eating increased rapidly from 7h00-9h00 AM and peaked between 9h00 and 11h00 AM, at which point heifers fed on PRQ spent less time eating compared to heifers on fed improved hay. Beyond this peak period, time spent eating decreased with other successive peak feeding periods being lower than the preceding one. During these subsequent peaks, heifers fed on PRQ spent more time eating between 16h00 and 17h00, and at 22h00 than others fed on better quality roughage. Regardless of dietary roughage quality, heifers spent more time eating in the morning and during the day than at evening. Surprisingly, heifers fed on PRQ spent more time eating than heifers fed on IRQ for most parts of the day.

3.5.4 Diurnal water consumption pattern

The daily water consumption oscillated throughout the day (Figure 3.4); the time spent drinking water was not affected (P> 0.05) by roughage quality but was affected (P<0.05) period of day (Table 3.3). Drinking periods were low for all roughage diets before 06h00 AM; then increased to peak between 10h00 and 11h00 AM. A drinking session for these heifers was less than a minute; and improved roughage quality tended positively to associate with time spent eating. Peak time spent drinking water coincided with peak times spent eating.

3.5.5 Diurnal idling pattern

Diurnal pattern of heifers idling oscillated throughout the day (Figure 3.6). Consequently, the time spent idling was not affected by roughage quality (P>0.05) but by period of day (P<0.05; Table 3.3). Heifers spent more time idling in the morning and during the day than at evening. Time spent idling increased rapidly from 1h00-5h00 AM and peaked at 6h00 AM, at which point heifers fed on better quality roughage spent more time than others fed on PRQ. Beyond this point, time spent idling decreased rapidly.

3.5.6 Diurnal idling whilst lying and standing pattern

Daily idling whilst lying and standing pattern of heifers fed varying quality roughage fluctuated through the day (Figure 3.5). Time spent idling whilst lying and standing was not affected by roughage quality (P>0.05) but idling whilst standing was affected by the period of day (P<0.05). Surprisingly, time spent idling whilst lying was evenly distributed during the day and at night, while heifers spent more time idling standing during the day than at night. Time spent idling whilst lying was negatively associated with time spent eating and idling whilst standing. Time spent idling whilst lying increased rapidly from 3-5 AM and peaked at 6 AM, at which point heifers fed on better quality roughage spent more time idling whilst lying than other fed on PRQ. Beyond this point, time spent idling whilst lying decreased drastically, at which point time spent idling whilst standing increased rapidly and peaked between 7 and 8 AM. Beyond this point, time spent idling whilst standing decreased drastically.

3.5.7 Diurnal ruminating pattern

Diurnal ruminating pattern of heifers fed on varying roughage quality oscillated through the day (Figure 3.3). Time spent ruminating by heifers was not affected by roughage quality (P>0.05) but by period of day (P<0.05; Table 3.3). Time spent ruminating increased rapidly from 10h00 AM to 1h00 PM and peaked between 2h00 and 3h00 PM, at which point heifers fed on improved quality roughage spent more time ruminating than the others fed on poor quality roughage. Beyond this point, time spent ruminating decreased with other successive peak ruminating periods being greater the preceding one. As expected, heifers spent less time ruminating in the morning and during the day than at evening. Time spent ruminating tended negatively associated with time spent eating.

3.5.8 Diurnal ruminating whilst lying and standing pattern

The daily pattern of ruminating whilst lying and standing by heifers undulated throughout the day (Figure 3.2). Time spent by heifers ruminating whilst lying and standing was not affected by roughage quality (P>0.05) but by period of day (P<0.05; Table 3.3). Regardless of the dietary roughage quality, time spent ruminating whilst lying was negatively associated with time spent eating and ruminating whilst standing. Time spent ruminating whilst lying decreased drastically between 6h00 and 8h00 AM, while time spent ruminating whilst standing increased rapidly.

Beyond this point, time spent ruminating whilst lying and standing decreased rapidly. Surprisingly, time spent ruminating whilst lying simultaneously increased with time spent ruminating whilst standing from 10h00 AM-1h00 PM and peaked between 2h00 and 3h00 PM. Beyond this point, time spent ruminating whilst lying and standing decreased with other successive peak ruminating whilst lying period being greater than the preceding one.

3.5.9 Diurnal grooming pattern

The diurnal grooming pattern of heifers fed varying roughage quality fluctuated through the day (Figure 3.9). As a result, time spent grooming was affected by both roughage quality and the period of day ($P<0.05$; Table 3.4). Time spent grooming increased rapidly from 5h00-6h00 AM and peaked at 7h00 AM except for heifers fed on PRQ at 9h00 AM, at which point heifers fed on improved hay spent more time than heifers fed on PRQ. Beyond this peak, time spent grooming decreased with a peak grooming period of heifers fed on PRQ being higher than the preceding one. Surprisingly, heifers fed on PRQ spent more time grooming than heifers fed on improved roughage diets for most parts of the day. Irrespective of dietary roughage quality, heifers spent more time grooming in the morning and during the day than at evening.

3.5.10 Diurnal licking objects pattern

The daily pattern of heifers licking objects zigzagged through the day (figure 3.7). Time spent by heifers liking objects was not affected by roughage quality ($P>0.05$), but by period of day ($P<0.05$; Table 3.4). Regardless of the dietary roughage quality, heifers spent more time licking objects in the morning and during the day than at evening. Time spent licking objects by heifers increased rapidly from 5h00-6h00 AM and peaked at 7h00 AM, at which point heifers fed on improved roughage spent more time than heifers fed on PRQ. Past this peak, time spent licking objects decrease drastically with other successive peaks on licking objects being lower than the preceding one. During these subsequent peaks, heifers fed on improved roughage spent more time licking objects between 4h00 and 6h00 PM than heifers fed on PRQ.

3.5.11 Diurnal tongue rolling pattern

The diurnal pattern of heifers tongue rolling fed varying roughage quality zigzagged through the day (Figure 3.7). Time spent tongue rolling by heifers was not affected by period of day (P>0.05) but by roughage quality (P<0.05; Table 3.4). Regardless of the dietary roughage quality, time spent tongue rolling during the day was equivalent to the time spent at evening. Time spent tongue rolling increased rapidly from 6h00 AM and peaked at 7h00 AM, at which point heifers fed on improved roughage quality spent more time than heifers fed on PRQ. Beyond this point, time spent tongue rolling decreased with other successive peak tongue rolling periods being lower than the preceding one. During these subsequent peaks, heifers fed on IRQ spent more time tongue rolling between 5h00 and 10h00 PM and between 1h00 AM than heifers fed on PRQ.

3.5.12 Diurnal pattern performing other behavioral activities

The diurnal pattern of heifers performing other activities i.e. feed searching zigzagged through the day (Figure 3.8). Time spent by heifers performing other activities was not affected (P>0.05) by roughage quality but by period of day (P<0.05; Table 3.4). Time spent performing other activities by heifers increased rapidly from 6h00 AM and peaked at 7h00 AM except for heifers fed MIRQ at 8h00 AM. Past this peak, time spent performing other activities decreased with other successive peak performing other activity periods. Regardless of the dietary roughage quality, heifers spent more time performing other activities during the day than at evening. Heifers fed on better quality roughage spent more time performing other activities for most parts of the day than others fed on PRQ.

3.5.13 Diurnal hedonic feeding pattern

The diurnal hedonic feeding pattern of heifers undulated throughout the day (Figure 3.10). Time spent by heifers performing hedonic feeding was not affected (P>0.05) by roughage quality but by period of day (P<0.05; Table 3.4). Time spent performing hedonic feeding by heifers increased rapidly from 9h00 AM and peaked at 10h00 AM, at which point heifers fed PRQ spent more time than heifers fed on IRQ, SIRQ, and MIRQ. Beyond this point, time spent performing hedonic feeding decreased with other successive peak hedonic feeding periods being lower than the preceding one.

3.6 Discussion

3.6.1 The effect of quality of roughage and period of day on diurnal meal and time spent feeding

Animal production is influenced by various factors; one of them being feeding behaviour (Tripon, 2008) and its variation is handy signs of cow health (Proudfoot *et al.*, 2012). Phases of feeding, ruminating, and idling are the ordinary constituents of feeding behaviour patterns in ruminants (Abijaoude *et al.*, 2000). In this study, roughage quality had no effect on diurnal feeding behaviour. However, diurnal feeding behaviour was affected by period of day. In agreement with Krysl and Hess (1993) and Sheahan *et al.* (2013), two main feeding events were observed at dawn and dusk separated by small meals hence, ruminants are crepuscular animal (Phillips, 1993; Herzog and Schwartz, 2002; Shabi *et al.*, 2005). Baumont *et al.* (2000) observed that the two main feeding events accounted for approximately 60-80% of the daily intake consumed by cows. The first meal began soon after sunrise followed by secondary meals. In contrast to studies by (Orr *et al.*, 1997; Taweel *et al.*, 2004; Gregorini *et al.*, 2007), the dawn feeding event dominated the voluntary feed intake of nutrients. This could be due to the distribution of feed per day, as feed was fed only once daily. Our findings concord that, even with only one dissemination of feed daily, cows exhibit two main feeding events and meals either at dawn or at dusk were not shortly followed by rumination (Pearce, 1965). Short periods of meals of approximately 25 minutes i.e. less than 45 minutes were observed at 10h00 PM and 01h00 AM in this study. Phillips and Denne (1988) also reported short period of meals at 01h00 AM which took for approximately 30 minutes followed by periods of ruminating and resting. This could be due to high intake requirements not met during the day as a result of short day-length (Coulon, 1984).

Abijaoude *et al*. (2000) and DeVries *et al*. (2003) reported that the over-all number of meals consumed per day, eating rate during meals, size and length of meals could be used to designate voluntary feed intake. Unfortunately, size and length of meals, and eating rate during meals were not measured in this study. However, the number of meals consumed per day were used to describe daily feed intake in this study. Our results displayed a range of 10 – 14 number of meals were consumed daily. This is in line with Dado and Allen (1994), Miron *et al.* (1996), and Grant and Albright (2001) who reported an average of 11.9, 14, and 9-14 meals per day, respectively. Surprisingly, heifers fed on PRQ had a great number of meals per day without increasing the time spent eating relative to other diets. This could have been an adaptive strategy for these animals to sustain intake levels by increasing the number of meals while maintaining a constant time spent feeding. Heifers fed on MIRQ spent more time feeding than heifers fed SIRQ, IRQ, and PRQ while on the other hand they had less number of meals. Ruminants sustain their desired herbage intake ranks through eating time by reducing intake rates while increasing eating time (Baumont *et al.,* 2004), thus animals with higher herbage intake will have less number of meals (Dado and Allen, 1994).

Contrary to Abijaoude *et al*. (2000) who reported that the time spent eating by ruminants is reliant on quality of feed, our findings show no effect of roughage quality on time spent eating. Voluntary feed intake by dairy cows can be affected by the pattern of meals and time spent eating (Grant and Albright, 2000). As expected, heifers spent more time eating during the day than at night. This is in line with findings by Phillips (2008) who reported that cattle prefer to consume most herbage during hours of the day. Because feed was only distributed once daily in this study, the first peak of time spent eating (during early hours of the day) was achieved soon after fresh herbage was delivered. Therefore, first peak indicated that cattle respond to fresh feed availability at feed trough thus, eating is incited by the delivery of fresh herbage (Forbes, 1995; DeVries *et al.,* 2003). The second peak was attained at dusk in the absence of fresh herbage delivery. Therefore, animals consumed herbage during this time to provide adequate food for maximum ruminal fill in preparing for the dusk (Phillips and Denne, 1998). Furthermore, maximum ruminal fill attained before dusk increase C: N balance and nutrient supply to the rumen hence, improving fermentation and nutrient outflow from the rumen (Gregorini *et al.,* 2008). In addition, Gregorini *et al.* (2008) and Brito *et al.* (2009) observed that beef and dairy heifers consuming more herbage during the afternoon had greater synthesis of rumen microbial protein. Feeding at dusk in the absence of fresh herbage delivery/distribution could be a result of high levels ghrelin hormone in the blood. Roche *et al.* (2009) described ghrelin as an influential hormone-stimulating intake hence, correlated to eating behaviour (Sugino *et al.*, 2004; Gregorini *et al.*, 2009). Ghrelin stimulates feed intake and therefore, acts as a warning sign of hunger as their concentration levels increase in the course of a negative energy balance and decline during a positive energy balance (Ariyasu *et al.,* 2001). Hayashida *et al.* (2001) reported increased intake in cattle and sheep (Sugino *et al.,* 2004) relative to increased plasma ghrelin concentrations. At noon before evening feeding event, dairy cows have the lowermost concentrations of glucose (Kolver and MacMillan, 1993) and peak insulin concentrations (Meier *et al.,* 2010). High levels of insulin at dusk feeding event and to a lesser extent before the dawn feeding event (Roche *et al.,* 2009; Meier *et al.,* 2010). Such high insulin concentrations reduce levels of glucagon reducing gluconeogenesis thus, delaying satiation (Allen *et al.,* 2005). The decline in plasma glucose during glycogenesis stimulates the release of ghrelin (Roche *et al.,* 2008), stimulating intake before dawn and dusk feeding. Furthermore, predation risk in domesticated ruminants is maximum at dusk than during the day. As a result, ruminants tend to spend more time eating than ruminating during the day than at night since predation risk is greater during grazing/eating than during ruminating as their heads are positioned downwards when eating maintaining poor levels of awareness (Rutter *et al.,* 2002). Contrary to findings by Grant and Albright (2000), this study shows that heifers spent 7-8 hours eating per day, which is greater than the time spent eating reported by these authors, 3-5 h/d and 4-6 h/d, respectively. In support of our findings, Abijaoude *et al.* (2000) also reported that cattle spent 6-9 hours eating per day.

3.6.2 The effect of roughage quality and period of the day on stereotypic, social, and water consumption behaviour

The current study also reported stereotypic activities displayed by heifers. Confined cattle like other confined animals might exhibit behavioural activities rarely expressed by wild animals (Shahhosseini, 2013). Thus, stereotypies are only seen or performed by captive animals and are often linked to oral behaviours i.e. tongue rolling and bar biting (Redbo, 1992; Sato *et al.,* 1994; Redbo and Nordblad, 1997). Focus was largely based on two types of stereotypies namely; (i) tongue rolling and (ii) bar biting. In support to our focus to these two stereotypies, Redbo (1990) reported that bar biting and tongue rolling can be performed within 2-4 hour after eating. Tongue rolling was affected by roughage quality while on the other hand bar biting was rather affected by period of day. Grandin and Deesing (1998) reported that stereotypies necessarily need to be performed by animals to please their nature of prehension of roughages during feeding as they are commonly performed prior and post feeding. These stereotypic behaviours could be due to frustration because of feed restriction (Redbo *et al.,* 1996; Redbo and Nordblad, 1997) as feed was only distributed once daily. Heifers fed on IRQ significantly spent a great amount of time tongue rolling than heifers fed on MIRQ, SIRQ, and PRQ. This may be associated with the less amount of time spent eating and ruminating compared to other heifers. In support to our findings, Mason and Rushen (2008) reported that stereotypic behaviour expressed by intensively kept cattle is due to the reduced time spent feeding and ruminating, which accounts up to 9 hours of their daily time budget. (Redbo and Nordblad, 1997) reported a decrease in time spent on stereotypic performance by dairy heifers as they increased their feeding time. Bildsoe *et al*. (1991) and Robert *et al.* (1993) also observed a decrease of stereotypic behaviour with increased level of feeding in mink and pigs, respectively. To a lesser extent, tongue rolling and bar biting may signal a boring environment (Seo *et al.*, 1998). Furthermore, stereotypies are used as a coping mechanism by animals as they beneficially perform a role in helping animals to deal with an uncomfortable environment (Phillips, 2008).

As expected, the water consumption event took place during the day shortly after a feeding event. Water consumption to a certain extent is similar to feed intake and occurs shortly after eating or during eating (Cardot *et al.*, 2008). When water is at liberty accessible, Andersson (1987) reported that cattle drank water 2-5 times a day. Similar results were obtained in this study as heifers drank water more frequently (4-5 times per day). Heifers fed on SIRQ spent lengthy time drinking water than others fed on MIRQ, IRQ, and PRQ. This could have been due to high protein levels in SIRQ compared to the other roughage diets. This is in line with the view that feeding of high protein levels requires high water intake (Phillips, 2008). Dannenmann *et al.* (1985) described grooming as a body care activity. Moreover, grooming has communicative, nutritional, and psychological obligations. Heifers spent more time grooming or allogrooming during the day than at night. In most cases, heifers performed allogrooming than grooming. Wood (1977) described allogrooming as a case where one animal licks the head and to a lesser extent the neck of other animals and signals dominance position.

3.6.3 Effect of roughage quality and period of day on rumination and idling of heifers

Rumination improves attachment of rumen bacteria to ingested feed through fermentation (Russel and Rychlik, 2001). This study observed ruminating as one of the most performed behaviour by heifers without being interrupted by any other activity. In addition, time spent ruminating and idling was not affected by roughage quality, rather, by period of day except that idling whilst lying was not affected. In contrast, Freer *et al.* (1962) reported that time spent ruminating was influenced by roughage quality. However, photoperiod affected time spent ruminating and idling in this study. Heifers spent more time ruminating at night than during the day. These findings are in line with findings by Minervino *et al.* (2014). These authors reported that sheep spent 298 and 370 minutes ruminating during the day and night, respectively. As expected, heifers spent more time ruminating whilst standing during the day than at night. Idling whist lying is essential for recuperation (Metz, 1985). Our findings are in line with Hafez *et al.* (1969) who reported that the diurnal patterning of feeding and ruminating is reliant on light-dark regime. Diurnal variations in time spent ruminating is inversely related to time spent feeding. This is in agreement with findings from this study as heifers spend more time feeding during the day but less time ruminating during the day than at night. Furthermore, time spent ruminating increased with both increased feed intake and feed particle coarseness (Freer *et al.*, 1962; Welch and Smith, 1969; Ruckebusch, 1970). The great amount of time spent ruminating by heifers fed on SIRQ could have been due to their high feed intake than other heifers. Heifers fed on PRQ spent more time ruminating than heifers fed on improved roughage diets. This could be associated with that PRQ is coarser than improved roughage diets, as improving roughage quality through urea-treatment softens the hay making it easy to chew hence, reducing the time spent ruminating (Trach *et al.*, 2001).

Due to predation risks, time spent idling whilst standing during the night was an adaptive way heifers used to stay watchful at night. However, the time spent idling whilst lying was greater at night than during the day. Short and long periods of idling whilst lying at night occurred soon after ruminating thus, ruminating bouts were separated by short and long periods of idling at night. Also, the increased time spent idling whilst lying at night could be due to fatigue as a result of prolonged time spent feeding, ruminating, and idling whilst standing during the day (Fregonesi and Leaver, 2001). In contrast, Phillips and Leaver (1985), and Lindstrom and Redbo (2000), Minervino *et al*. (2014) reported that cows spend 669 min/d, 8-9 hr/d, and 9.4 hr/d ruminating, respectively. Our findings indicate that heifers spent 667–771 min/d ruminating. Such differences could be a result of various factors, including feed distribution, as authors distributed fresh herbage twice daily, whereas feed was distributed only once in this study. This might have affected the time spent eating hence, ruminating time. In agreement with Fraser and Broom (1997), in most cases, heifers ruminated while performing other events such as urinating, defecating, and walking. Heifers spent more time ruminating than feeding in accordance to Phillips (2008).

3.6.4 Effect of period of day on daily feeding and water intake pattern

Metz (1985) and Grant (2006) described feeding response as a prime factor used to assess how cows adapt to a certain environment. Accurate predictions of voluntary feed intake by ruminants requires detailed understanding of eating, ruminating, and idling (Abijaoude *et al.,* 2000; Phillips, 2008). Eating and water intake diurnal patterns of heifers were affected by period of day rather than roughage quality. Ruminants distribute their feeding bouts into two main feeding events (Figure 3.1). Heifers increased time spent eating from 7h00 to 10h00 AM, reaching the first peak intake. This increased feed intake, during the early hours of the morning (7h00-10h00 AM), could be due to high hunger levels (Gregorini *et al.,* 2008), due to extended rumination period at night. This could lower the level of fill in the rumen (Thomson *et al.,* 1985; Woods and Strubbe, 1994; Gregorini *et al.,* 2008), generating space for new herbage (Taweel *et al.,* 2004; Gregorini, 2012), and thereby increasing hunger pangs. Moreover, low levels of ruminal fill are associated with escalating ghrelin concentrations (Sauve *et al.,* 2010) which in turn increase herbage intake (Gregorini *et al.,* 2009). Forbes (1995) described hunger as the steadiness amongst required nutrients and herbage intake (Phillips, 2008), and satiety as the primary stimulus for feed termination. After the first peak, herbage intake drastically declined signaling satiation (Baumont *et al.,* 2000) suppressing herbage intake for an extended period, forming secondary meals before the next peak at dusk. From our findings, it is clear that feeding sessions clustered (at daytime) but were mot evenly distributed throughout the day. Peak eating times mainly occurred in the morning and at dusk, coinciding with low to moderate ambient temperatures compared to the afternoon when ambient temperatures are at their highest. The observed feeding patterns appeared to be more-or-less controlled by ambient temperature.

Heifers fed on improved roughage diet spent more time eating than heifers fed on PRQ. This was in contrast with findings by Trach *et al.* (2001) and Mesfin and Ledin (2004). These authors reported a decrease in feed intake by cattle fed an improved quality roughage compared to those fed on a roughage of low quality. High intake by heifers fed on improved roughage diet is associated with the increased crude protein content through urea treatment since ruminants prefer highly digestible herbage (Provenza, 1996). The second peak was reached at dusk after several short periods of secondary meals during the day. Abijaoude *et al.* (2000) reported that feeding diets of high forage content reduce the number of secondary meals. Unfortunately, the number of secondary meals were not reported in this study and all four experimental diets were of the same forage content. As expected, several short meals of not more than 10 min/h occurred at night. Diurnal patterns of water intake by cows was not affected by roughage quality. As already discussed, water intake is likely to occur shortly after feeding or during feeding. Therefore, the higher levels of water intake during the early hours after sunrise is a result of increased herbage intake. Peak water intake was reached between 10h00 and 11h00 AM (Figure 1.2). Peak water intake was reached simultaneously with feed intake peak; thus, water intake increased with feed intake increases. Although it was expected that time spent drinking water would peak during the afternoon when ambient temperatures are high, water consumption peaked when eating was highest due to the need for water to assist in chewing and solublisation of diets with low water content roughages.

3.6.5 Effect of period of day on diurnal stereotypic behaviour pattern

Performance of stereotypic behaviour by cattle is linked to herbage intake stimulus and time spent feeding (Redbo *et al*. 1996; Redbo and Nordblad, 1997). Stereotypes were most likely performed during the early hours of the morning between 7h00 and 8h00 AM (Figure 3.7) for time spent licking objects and tongue rolling. The greater amount of time spent tongue rolling and bar biting by heifers during the early hours could be due to frustration feeding stimulus (Lindstrom and Redbo, 2000) since new fresh herbage was distributed at 8h45 AM throughout the experiment. When stressed, cattle release cortisol (Redbo, 1993). Lindstrom (2000) reported high levels of cortisol is associated with short periods of feeding. Therefore, the great amount of time spent on stereotypic activities by heifers during the day and early hours in the morning is a result of short feeding periods, which increases cortisol levels, forcing animals to perform stereotypes due to frustration.

3.6.6 Effect period of day on daily ruminating and idling pattern

Ruminants tend to naturally spend less time eating than ruminating. Improving roughage quality through urea treatment and spraying breakdown the lignocellulose bond amongst plant cells softening hay thus, reducing their physical strength (Chenost and Kayouli, 1997) and ruminating time (Chermiti *et al.,* 1994; Jalali *et al.,* 2012). However, in this study, ruminating and idling patterns were not affected by roughage quality. As expected, heifers spent more time ruminating during the late hours of the day, at night, and early morning. Nsahlai *et al*. (1996) reported increased ruminal fill due to increased intake by ruminants after extended exposure to roughage diets. The extended time spent ruminating at night and early hours of the morning occurred shortly after meal termination and could be due to high ruminal fill levels after meal termination (Moyo *et al.*, 2017), resulting in extended time spent ruminating by heifers hence, time spent ruminating is a function of intake. The daily dissimilarities of time spent eating by ruminants is negatively related to time spent ruminating. In agreement to this statement, heifers showed no or little, if any, ruminating activities during the first feeding peak in the morning (Figure 3.1), at 10h00 AM. Therefore, ruminating is more likely to occur after satiety has been reached. In this study heifers spent more time ruminating whilst lying than whilst standing.

As expected, short periods of ruminating whilst standing occurred during the day and little if any at night. This could be due to the fear of predation in domesticated ruminants. Heifers ruminated whilst standing during the day to balance the total time of engaging in behaviours that maintains decent levels of watchfulness throughout the day (Moyo, 2016) as their heads were positioned upwards. Ruminating whilst standing at night occurred shortly after feeding and took not more than 8 min/hr. Daily idling pattern of heifers was not affected by roughage quality. Idling whilst lying occurred towards sunrise. This could be exhaustion during this period after long hours of ruminating at night (Rutter *et al.,* 2002). Time spent idling during the day was lower than expected. This could have been due to that heifers spent much of their time eating and ruminating during the day. The increased time spent idling whilst lying during early hours in the morning (3h00 to 6h00 AM) are associated with lower ruminal fill. This could be due to the rapidly constant emptying of rumen digesta due to extended rumination.

3.7 Conclusion

Improving roughage quality had no effect on time spent and diurnal behavioural patterns except for grooming and tongue rolling. However, improving roughage quality through urea treatment and spraying increased the time spent eating, hence dry matter intake. Our results indicate that, feeding behavioural activities are greatly influenced by period of day and to a lesser extent by roughage quality. Ruminants feeding on poor roughage quality extend their number of meals without increasing the time spent eating as an adaptive strategy to sustain high intakes while maintaining a constant time spent eating. Intake of poor quality roughage is restrained by extended ruminating time.

Chapter 4

Effect of roughage quality and period of day on rumen digesta load after meal termination, degradation, digestion, and passage rates

Abstract

The current study ascertained the effects of roughage quality and period of day on rumen fill after meal termination. The study also explored the effect of roughage quality on passage and degradation rates in the rumen of Jersey heifers. Four ruminally cannulated Jersey heifers were used in a 4×4 Latin square design. Dietary treatments were: (1) poor roughage (veld hay) quality (PRQ), which was either (2) sprayed with 2.5 % (w/w) urea to give a semi-improved roughage quality (SIRQ); or (3) treated with 4% (w/w) urea for 20 days making improved roughage quality (IRQ). (4) A moderate roughage quality (MIRQ) was obtained by mixing equal proportions of IRQ and PRQ. In the first experiment, four cannulated jersey heifers were randomly allocated to these roughages in a 4×4 Latin square design to determine the fractional passage rate of liquid and solid digesta using Cobalt-EDTA and Ytterbium marker, respectively. In the second and third experiment, four ruminally cannulated jersey heifers were used to determine *in-sacco* degradability for PRQ, SIRQ, MIRQ, and IRQ and also, to determine the effects of roughage quality and period of day on rumen dry matter load. In experiments 2 and 3, heifers were randomly assigned to the roughage diets in a 4×4 Latin square design. Rumen fill was determined in the morning, afternoon, late afternoon, and evening. For all three experiments, each experimental period had an adaptation period of 7 days, except in the first period where 14 days of adaptation was allowed. During the adaptation period, heifers were supplemented with Lucerne hay (1.65 kg/d), which was removed 4 days prior to the end of each adaptation period. Roughage quality enhanced the effective degradability (ED) by +76, +40, and +52 g/kg. Fractional passage rates and mean retention time of liquid and solid were not affected by roughage quality ($P>0.05$). Surprisingly, the mean retention time of solid in the hindgut was affected by roughage quality ($P<0.05$). The liquid passage rates was faster than the solid passage rates irrespective of quality of roughage. Total rumen load, rumen liquor, and dry matter were also not affected by the quality of roughage ($P>0.05$), but by period of day ($P<0.05$) except for rumen dry matter. Total rumen load were greater at evening than in the morning, afternoon, and late afternoon. Total rumen load were 22.21, 23.60, 25.51, and 27.73 (kg/ 100 kg BW) at the morning, afternoon, late afternoon, and evening, respectively. Rumen liquor and NDF load increased with increasing total rumen load. Rumen NDF load was affected by both roughage quality and period of day ($P<0.05$). Rumen NDF load was greater in heifers fed on PRQ than those fed on improved roughage quality. Intake and digestion were significantly affected ($P<0.05$) roughage quality. Improving roughage quality increased intake and digestion rates.

Additional keywords: roughage quality, degradation, digestion, fractional passage rates, rumen fill, cattle.

4.1 Introduction

In tropical and semi-tropical regions of Africa, ruminant production is largely dependent on grasslands, which are in most parts of poor quality. During the dry season, most tropical veld grasses are of low nutritional quality (Coleman *et al*., 2003). Rust and Rust (2013) stated that the low production or performance of ruminants in tropical and semi-tropical regions is a result of poor forage quality. The extent to which ruminants would consume these forages depend on both animal and plant characteristics. Rumen fill (RF) is the quantity of digesta within the rumen and is regulated by the overall intake and the rate at which the ingested herbage vacates the rumen (Weston and Hogan, 1967; Ulyatt *et al.,* 1986; Williams *et al.,* 2014) thus, rumen fill is a result of intake, particle breakdown, digestion, and outflow rates. Furthermore, RF is also affected by the quality of diet and tendency of animal to use energy (Nsahlai and Apaloo, 2007). Rumen fill is an essential measure for long-term regulator of intake by ruminants (Campling and Freer, 1966). However, the reticulo-rumen volume is not the only factor regulating feed intake, feed bulkiness is also a limiting factor of intake by ruminants (Mertens, 1994).

Rumen digesta exist as an intermix of solid and liquid, and the turnover of both phases is positively associated to feed intake and microbial yield (Sniffen and Robinson, 1987). Baumont (1996) stated that the great size of gradually degradable and un-degradable digesta in the rumen are the primary factors that terminate intake of poor quality forages by ruminants. Ruminants do not retain a steady level of fill in the rumen regardless that the digesta load in the rumen (Weston, 1985) regulates their voluntary intake. This is due to the ceaseless decamp of particles and degradation by rumen microbes which cause the rumen fill not to remain constant at peak even in nutritionally restricted diet (Gill and Romney, 1994). Furthermore, reticulo omasal orifice (ROO) relaxation during reticulo-rumen (RR) contractions governs the passage rate of digesta from the RR thus, regulating rumen fill and voluntary feed intake in ruminants (Okine *et al.,* 1998). The animal also ceases to consume as a consequence of changes in ruminal pH and nutrient flow to it's organs, particularly the brain. Special receptors and senses situated in the walls of the digestive tract and metabolizing tissues give signal to the brain through vagal afferents (Crichlow and Leek, 1986) to determine when to initiate or terminate intake (Forbes, 2000). Various anoretic hormones are released when digested nutrients consecutively pass through the small intestine, stimulating satiety (Allen, 2014). Volatile fatty acids, end product of microbial fermentation primarily regulate feed intake in ruminants, particularly propionate. Ruminants fed high grain based diets certainly produce and absorb propionate acid at high rates. This leads to a rapid deposition of propionate to the liver where it is converted to glucose and oxidized to Adenosine triphosphate (ATP) giving a satiety signal to the brain (Allen, 2014), hence, terminating intake. Therefore, the brain monitors the concentration of blood glucose and terminate intake when the concentration is over a certain threshold. However, nutrients have a minor effect in controlling herbage intake and they only have a direct effect on intake primarily when they interrupt the homeostasis of the animal (Allen, 2014).

Taweel *et al.* (2004) urged that fluctuations of rumen fill in grazing cows revealed that high rumen digesta is attained at the end of the day than at any time of the day thus, suggesting that maximum ruminal digesta capacity have been reached. Naturally, rumen fill increase across the day (Thiago, 1988) and this is due to the grazing bout-ingestive behaviour (Gregorini *et al.,* 2007). The dry matter (DM) and rumen liquor (RL) pool sizes in the rumen increase after grazing the morning and afternoon pasture allowance (Williams *et al.,* 2014). However, Baumont (1996) reported that the rumen fill of sheep in the morning and evening showed no significant dissimilarities after a 12 hour cycled ruminating and eating patterns. A lot of studies have been done on rumen fill, passage rate and degradability rate. However, only a few studies have been done on the effects of improving the quality of tropical roughage on rates of passage and degradation. In addition, only a few studies have been done on the effects of roughage quality and period of day on rumen digesta load after meal termination. Hence, objectives of this study were to: (i) determine the effect of roughage quality and period of day on rumen fill after meal termination. (ii) confirm the effect of roughage quality on passage and degradation rates, and digestibility.

4.2 Materials and Methods

4.2.1 Study site

The experiment was conducted with the approval of the University of KwaZulu-Natal Ethics Committee, the Animal Ethics Sub-Committee (ref. ARE/066/016M). The study was conducted at Ukulinga Research Farm, University of KwaZulu-Natal (Pietermaritzburg) in South Africa. The daytime temperatures in summer reach highs of around 29°C with night temperatures averaging around 16°C. The rainfall patterns are characterized by an annual rainfall of approximately 730 mm, which falls mostly between October and April. Summer temperatures may reach highs of above 33°C and with minimum temperatures of 7°C at night in winter.

4.2.2 Animals, housing, feed, and feeding

Four ruminally cannulated Jersey heifers with an average body mass of 288.5 ± 3.69 (trial 1: passage rate only) and 330 ± 19.97 (trial 2 and 3: rumen fill and degradability) were used. Heifers were housed in individual pens and randomly assigned to one of four roughage diets in a 4×4 Latin square design. Dietary treatments were: (1) poor roughage (veld hay) quality (PRQ), which was either (2) sprayed with 2.5 % (w/w) urea to give a semi-improved roughage quality (SIRQ); or (3) treated with 4% (w/w) urea for 20 days making improved roughage quality (IRQ). (4) A moderate roughage quality (MIRQ) was obtained by mixing equal proportions of IRQ and PRQ. Heifers were given 14-day adaptation period to experimental diets at the beginning of the trial and 7 days of adaptations just before interchanging animals between diets. During the adaptation periods of 14 and 7 days, animals were supplemented with Lucerne hay (1.65 kg/d) for 10 and 3 days, respectively. Lucerne was removed 4 days prior to data collection hence; animals completed 4 days of adaptation consuming only one of the four roughages. Water was provided *ad libitum* throughout the experiments. The experimental diets were milled to pass through a 12mm screen using a hammer mill (Science Tec hammer mill 400, Lab World Pty Ltd, Johannesburg, RSA). Approximately 15 kg of feed per head was allocated once daily in the morning throughout the experiment. Residual hay in feeding troughs was weighed daily before allocating new hay. Daily feed intake was measured by subtracting feed left from the allocated (Intake = feed in – feed left). For all four experimental periods, trial 1 lasted for 63 days, comprising of 35 days of adaptation period and 28 days of fecal sample collection. Trial 2 and 3 lasted for 76 days, comprising of 35 days of adaptation period and 48 and 28 days of rumen fill and feed degradation measurements, respectively.

4.2.3 Trial 1: passage rate experimentation

4.3.3.1 Preparation of Co-EDTA

Cobalt-EDTA was used as a fluid marker. The fluid marker was prepared according to Uden *et al*. (1980) as clearly highlighted by (Osuji *et al.*, 1993). Procedurally: 297.2g Na-EDTA, 190.4g $CoCl_2.6H_2O$ and 32g NaOH were dissolved in 1600 ml of distilled water in a 5 litre beaker. To ensure that all the reagents dissolved, an additional 5g NaOH was added. The solution was allowed to cool to room temperature, and 160 ml H_2O_2 was added thereafter. The mixture was allowed to stand at room temperature for 4 hours, and 2400 ml of 95% (v/v) ethanol was added. The mixture was placed in a refrigerator for approximately 120 hours for crystallization. The pH of the solution was 9.95. The crystals formed were filtered and washed 3 times using 330 ml of 80% (v/v) ethanol for each cycle. The resulting crystals were oven dried at 90°C for 24 hours and stored in plastic bottles pending administration.

4.3.3.2 Preparation of Ytterbium labelled roughages

Ytterbium was used as a solid marker. Ytterbium marked roughages were prepared according to Hatfield *et al*. (1990). Roughage samples were ground to pass through a 12 mm screen prior being marked with Ytterbium. 100 g each of PRQ, SIRQ, MIRQ, and IRQ were soaked in distilled water overnight to remove soluble material and subsequently dried at a temperature of 80˚C overnight. 7.5 g of $YbCl_3.6H_2O$ was dissolved in 3 L of distilled water. Ytterbium labelled roughages were prepared by soaking roughages in 5 g/l $YbCl_3.6H_2O$ solution at a rate of 100 g of roughage per litre solution for 120 hours. The residue was washed using distilled water until the colour of water turned clear to remove any unbound ytterbium. The residue was oven dried at 50°C for 48 hours. Labelled roughage was kept in plastic bottles pending administration.

4.3.3.3 Administration of markers

In a study by Moyo (2016) who starved sheep overnight prior marker administration to ensure that sheep eat roughages marked with Ytterbium during marker administration. Unlike him, a small quantity (50 ml) of molasses was mixed with the marked roughages to ensure that heifers were enticed to eat. Approximately, 80g of Ytterbium labelled roughages were offered to each heifer. Approximately, 160g of Co-EDTA crystals were dissolved in 960 ml water and each heifers was drenched 240 ml of solution containing Co-EDTA.

4.3.3.4 Trial 2: Rumen fill measurement after meal termination

Rumen fill was measured using the rumen evacuation technique. Rumen digesta was measured after meal termination in the morning (09h00–10h00 AM), afternoon (14h00–15h00 PM), late afternoon (18h00–19h00 PM), and evening (21h00–22h00 PM) over 4 experimental periods. A break of more than 5 minutes after an eating event by an animal was regarded to have terminated eating. The time spent eating and quantity of feed consumed before measuring rumen digesta were recorded. Heifers were allowed to rest for 48 hours before the next evacuation. In each period, one animal was measured for each sampling time, that is, each animal was evacuated four times per period (Table 4.1).

Table 4. 1: Rumen evacuation design over four experimental periods in Jersey heifers

Diet	Morning	Afternoon	Late afternoon	Evening
		First period		
PRQ	1	2	3	4
SIRQ	2	1	4	3
MIRQ	3	4	1	2
IRQ	4	3	2	1
		Second period		
PRQ	2	1	4	3
SIRQ	1	2	3	4
MIRQ	4	3	2	1
IRQ	3	4	1	2
		Third period		
PRQ	3	4	2	1
SIRQ	4	3	1	2
MIRQ	1	2	4	3
IRQ	2	1	3	4
		Fourth period		
PRQ	4	3	1	2
SIRQ	3	4	2	1
MIRQ	2	1	3	4
IRQ	1	2	4	3

PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ: moderately improved roughage quality; IRQ: improved roughage quality; 1-4: animal identification.

4.3.3.6 Rumen and faecal sample collection, preparation and analysis (all experiments)

In trial 1, before administration of markers, faecal samples were taken to determine the initial presence or absence of cobalt and ytterbium. Faecal sample collection was done over a period of 7 days after administration of markers by rectal palpation and extraction of sizeable rectal faecal samples by hand on each heifer. Faecal sampling times were 0, 3, 6, 9, 12, 24, 27, 30, 48, 53, 72, 77, 96, 101, 120,144 and 168 hours post marker administration. Faecal samples from each heifer were oven dried at 60°C for 96 hours soon after collection. Samples were ground to pass through a 2 mm sieve using a hammer mill and stored in sealed plastic bags awaiting analysis. Air dried faecal samples were weighed (2 g), placed in porcelain crucible and ashed at 550ºC overnight. Ashed samples were cooled and dissolved in 5 cm^3 of HCl. The solution was evaporated to dryness using a water bathe. The residue was cooled and 5 cm^3 of HNO3 was added. The solution was heated on a water bathe to boiling point. The resulting solution was passed through filter paper into a 100 cm^3 volumetric flask. The filter paper was washed with warm deionized water. The solution was diluted to volume with deionized water and thoroughly mixed. Ytterbium and cobalt concentrations were determined using an Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) (Perkin Elmer, Precisely, Optima 5300 DV Spectrometer, Shelton, CT 06484, USA).

In trial 2, total rumen contents were estimated by manually emptying the rumen through a fistula. To prevent rapid cooling, solid contents were removed by hand and placed in an insulated container. The liquid material was removed using a plastic container and sieved. After collection, the rumen digesta was weighed and the rumen was allowed to remain empty for at most, 3 minutes and the entire rumen evacuation procedure was done within a period of 20 minutes. After weighing, a sample of about 2 kg was taken and oven dried for 48 hours at 60℃ to determine dry matter content. The dry rumen digesta were analyzed for neutral detergent fibre using the ANKOM A220 fibre analyzer (ANKOM Technology, New York, USA).

4.3.3.7 Chemical analysis of experimental diets

Dry matter, moisture, and ash contents were analyzed using the procedures outlined by the Association of Official Analytical Chemists (AOAC 1999). Nitrogen content was determined using the LECO machine (LECO FP2000, LECO, Pretoria, South Africa). Crude protein content was calculated by multiplying the nitrogen content by a factor of 6.25. Neutral detergent and acid detergent fibres were analyzed using ANKOM A220 fibre analyzer (ANKOM Technology, New York, USA) (AOAC 1990). Hemicellulose content as determined by subtracting acid detergent fibre content from neutral detergent fibre content.

Table 4. 2 Chemical composition of experimental diets

Diet	Chemical composition (g/kg DM)					
	DM	CP	NDF	ADF	HEM	ASH
PRQ	745	36	711	380	331	78
SIRQ	727	63	721	404	316	68
MIRQ	739	62	732	399	333	69
IRQ	727	89	745	415	330	78
Lucerne	906	136	524	361	163	89

PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; IRQ; improved roughage quality; DM: dry matter; CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; HEM: hemicellulose.

4.3.3.8 Mathematical procedures

4.3.3.8.1 Passage rate experimentation

Faecal excretion data were described using a model developed by Grovum and Williams (1973). The model was: Y = 0, when t < TT, Y = Ae-k1(t–TT) – Ae-k2(t–TT), when t ≥ TT, where: Y and A are the adjusted marker concentration in the faecal DM, k1 and k2 – rate constants, TT – calculated time from the first appearance of marker in the faeces and t – sampling time in hours after single dosage.

For graphical presentation, the natural logarithm of faecal DM marker concentration was plotted against time. Linear regression of the linear portion on the descending slope was done using Microsoft Excel. The regression coefficient (k1) gave the slowest rate constants that correspond to the rate of passage in the rumen and y-intercept as A1. The regression coeffient was used to calculate the rumen retention time of solid and liquid (1/k1). Residual (predicted – observed) concentrations for the ascending slope were calculated as: Fitted values minus actual measured marker concentrations. Antilogarithms of the residual concentrations were generated. Regression of the natural logarithm of the log-transformed residual concentrations was done to give a regression coefficient (k2) that corresponds to the rate of passage in the hindgut and y-intercept as

A2. The regression coefficient that corresponds to the rate of passage in the hindgut was used to calculate the hindgut retention time of solid and liquid (1/k2). Regression analysis of the natural logarithm of the residual concentrations and collection time gave the Y-intercept (A2) and the second slowest rate constant, k2. The two lines intersect at the point (TT,A). Where TT is the transit time for the first appearance of marker in the faecal DM and was calculated as: TT = (A2 - A1) / (k2 - k1). Thus, A1 and A2 are natural logarithmic derivatives. The mean retention time (MRT) was calculated as follows: MRT = 1/k1 + 1/k2 + TT. The selectivity factor (SF) was calculated as SF = MRTparticles ÷ MRTliquid (Clauss and Lechner-Doll, 2001).

4.3.3.8.2 In-sacco degradability experimentation

Degradability of roughage samples was determined using dry matter loss in nylon bags (Orskov *et al*. 1980). Dry matter loss was plotted against incubation time. A model developed by McDonald (1981) was fitted on Statistical Analysis System 9.3 (SAS Institute Inc., Cary, NC, USA) and degradation parameters generated. The model used was: $Y = a + b\,(1 – e^{-c\,(t – L)})$ (McDonald 1981), where: Y – degradability at time (t), a – intercept, b – potentially degradable fraction, c – rate of degradation of b, L – lag time. Effectively degradable (ED) was calculated using a passage rate of 0.03 per h (Nsahlai *et al.*, 1998). The ED was calculated as: ED = 0.8 (a+b)*c / (c+0.03).

4.4 Statistical analysis

All data were statistically analyzed using the General Linear Model (GLM) procedure to determine the effect of roughage quality on passage rate, degradability, wet matter, dry matter, and NDF load in the foregut. The experimental model for trail 1 and 3 was: Yijk = μ + Ri + BMj + eijk, where: Y = passage rate and degradability, μ – overall mean, Ri – roughage quality effect (i = 1-4), BM – body mass, eijk – experimental error. The effect of time after meal termination on total rumen load, dry matter, liquor, and NDF load in the foregut were also determined. The experimental model for trail 2 was: $RF_{ijkl} = \mu + R_i + P_j + BM_k + eijkl$, where RF = rumen fill (total rumen load, NDF, liquor, dry matter), μ = overall mean, R_i = effect of roughage quality (i = 1-4), P = effect of sampling time (j = morning, afternoon, late afternoon, and evening), BM = body mass, eijk = experimental error. The Student-Newman-Keuls (SNK) test was used to separate means at P<0.05.

4.5 Results

4.5.1 Effects of roughage quality on degradation and passage rates of solid and liquid digesta, and digestibility in jersey heifers

Roughage quality had a significant effect ($P<0.05$; Table 4.3) on degradability rates. Improving roughage quality enhanced effective degradability (ED) by +76, +40, and +52 g/kg (at $k_p = 0.03$ per h) and increased rate of degradation by +0.022 (per h) for MIRQ, SIRQ, and PR, respectively. Surprisingly, fractional passage rate, rumen retention time, and mean retention time of fluid and solid digesta were not affected ($P>0.05$; Table 4.4) by roughage quality. As expected, fractional passage rates of fluid was greater than fractional passage of solid from the rumen. Unexpectedly, the retention time of solid digesta in the hindgut was affected ($P<0.05$) by roughage quality, with improved roughage quality retained longer than PRQ. The retention time of solid in the hindgut of heifers on fed IRQ was +10, +12, +23 hours greater than in heifers fed on SIRQ, PRQ, and MIRQ, respectively.

4.5.2 Effects of roughage quality and period of day on rumen load after meal termination in jersey heifers

Rumen load was not significantly affected ($P>0.05$; Table 4.5) by roughage quality, but by the period of day. Rumen NDF content was affected by both roughage quality and period of day ($P<0.05$; Table 4.5). As expected, total rumen loads were +5.52, +4.13, +2.22 kg/ 100 kg BW lighter in the morning than in the afternoon, late afternoon, and evening, respectively. Consequently, rumen dry matter did not vary whereas rumen liquor and rumen NDF content increased with increasing total rumen load. Heifers fed on PRQ quality had high rumen NDF load (kg fibre / 100 kg BW) than those fed improved roughage quality.

Table 4. 3 Effect of roughage quality on in-sacco degradability in jersey heifers

	Diet				Significance	
Degradability (g/kg DM)	PRQ	SIRQ	MIRQ	IRQ	RMSE	P value
a	233	249	243	256	36.7	NS
b	475	706	565	530	140	NS
PD (a+b)	708	954	808	786	158	NS
c (per h)	0.042	0.022	0.024	0.041	0.012	NS
L (h)	8.9	11.4	6.9	6.1	3.557	NS
ED (at k_p = 0.03 per h)	456^{b}	468^{ba}	433^{b}	509^{a}	25.8	*

PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; IRQ: improved roughage quality; RMSE: root mean standard error; a: rapidly degradable water soluble fraction; b: slowly degradable portion of the insoluble fraction; PD: potentially degradable fraction; c: rate of degradation of the "b" fraction; L: time lag; ED: effectively degradable fraction; * P<0.05; *** P<0.001; a,b, Means in a column with different superscripts are significantly different (P <0.05).

Table 4. 4: Effect of roughage quality on fraction passage rate and mean retention time of solid and fluid phase digesta in the rumen and hindgut of heifers

	Diets				Significance	
	PRQ	SIRQ	MIRQ	IRQ	RMSE	P value
Fractional passage rate (per/h)						
RR (k_p)	0.028	0.038	0.038	0.035	0.009	NS
HG (k_p)	0.023	0.020	0.035	0.020	0.009	NS
RR (k_l)	0.048	0.048	0.043	0.055	0.013	NS
HG (k_l)	0.028	0.050	0.025	0.023	0.0172	NS
Retention time (h)						
RR_p	40.6	27.8	28.1	28.6	9.97	NS
HG_p	43.5^{ab}	45.6^{ab}	32.3^{b}	55.5^{a}	80.47	*
RR_l	22.5	22.3	24.7	18.4	5.81	NS
HG_l	43.5	25.5	38.3	45.0	11.56	NS
Mean retention time (h)						
$GITRT_S$	85.4	75.2	61.7	86.2	13.90	NS
$GITRT_L$	68.9	49.3	64.8	66.4	9.23	NS

PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; IRQ: improved roughage quality; RR: reticulorumen; HG: hindgut; kp: fractional passage rate of particulate particles; kl: fractional passage rate of fluid; RRp: rumen particulate particles; HGp: hindgut particulate particles; RRl: rumen fluid; HGl: hindgut fluid. GITRTs: retention time of solids in the gastrointestinal tract; GITRTl: retention time of liquid in the gastrointestinal tract [a,b] Means in a row with different superscripts are significantly different (*P* <0.05); NS: not significant; * P<0.05).

Table 4. 5: Effects of roughage quality and period of day on rumen digesta load in jersey heifers

Rumen load (kg/100 kg BW)	Diet				Period of day				Significance		
	PRQ	SIRQ	MIRQ	IRQ	M	A	LA	E	RSME	D	P
Total rumen load	24.08	25.34	25.34	24.30	22.21^{c}	23.60^{bc}	25.51^{b}	27.73^{a}	2.083	NS	***
Rumen liquor	20.71	21.70	21.83	20.69	19.08^{a}	20.28^{a}	21.87^{a}	23.70^{a}	1.013	NS	NS
Rumen DM	3.37	3.63	3.52	3.61	3.13^{c}	3.32^{bc}	3.64^{b}	4.03^{a}	2.335	NS	***
Rumen NDF	2.64^{a}	2.35^{b}	2.56^{a}	2.33^{b}	2.00^{d}	2.19^{c}	2.47^{b}	3.23^{a}	0.369	***	***

IRQ; improved roughage quality; PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ: moderately improved roughage quality; M: morning; A: afternoon; LA: late afternoon; E: evening; RMSE: root mean standard error; D: diet; P: period of day; DM: dry matter; NDF: neutral detergent fibre; a,b,c Means in a row with different superscripts are significantly different (P <0.05); NS: not significant; *** P<0.0001; * P<0.05.

Table 4. 6: Effects of roughage quality on intake, digestibility, and live weight change in Jersey heifers

	Diet				Significance	
	PRQ	SIRQ	MIRQ	IRQ	RSME	D
Feed intake (kg/d) trial 2 & 3	12.03^{b}	13.60^{a}	12.60^{b}	12.30^{b}	0.442	***
Feed intake (kg/d) trial 1	7.53^{b}	9.87^{a}	8.05^{b}	8.35^{b}	0.441	***
Selective factor						
RR	1.9	1.4	1.2	1.6	0.47	NS
HG	1.2	2.3	0.8	1.3	0.94	NS
Initial weight (kg)	331	311	345	298	-	-
Final weight (kg)	331	309	345	297	-	-
Live weight change (kg/week)	-0.25	1.51	0.25	1.01	1.939	NS

PRQ: poor roughage quality; SIRQ: semi improved roughage quality; MIRQ; moderately improved roughage quality; IRQ: improved roughage quality; RMSE: root mean standard error; D: diet; a,b,c,d Means in a row with different superscripts are significantly different (P <0.05); NS: not significant; *** P<0.0001.

4.6 Discussion

4.6.1 Degradation and passage rate in Jersey heifers

Nsahlai and Apaloo (2007) described protein as the primary nutrient restricting the influence of rumen microbial fermentative activity of poor quality forages. Particle breakdown and digestion rate is critically affected by the chemical and physical properties of the plant material. These factors influence the rate at which rumen microbes access and degrade particle ingredients (Wilson, 1993). Improving roughage quality through the use of urea could have detached linkages between hemicellulose and lignin, enhancing their solubility (Preston, 1995; Tesfayohannes *et al.*, 2003), and substrates for microbial metabolism (Detmann *et al.*, 2009). The greater degradation rates in heifers fed on improved roughages as witnessed by high ED implies that the cellulolytic bacterial mass and activity were greater in the rumen of heifers fed on improved roughage quality. Mean retention time of particulate digesta in the hindgut was affected by quality of roughage. Faichney (1993) and Firkins (1997) reported that in some circumstances, mean retention time in the rumen might be shorter than in hindgut. The prolonged retention time of solids in the hindgut in heifers fed on IRQ may be an adaptation to increase extract from high roughage given a tendency to flow out of the rumen faster, thus retaining particles longer. Generally, selective factors (SF) are used to define ruminant ecological differences and find application in grouping of ruminants into their respectively diverse feeding natures (Clauss and Lechner-Doll, 2001). Heifers fed on PRQ had high SF than those fed on improved roughage quality. This indicate that grazing ruminants adapt to poor quality roughages by extending the retention time of solid digesta.

The low intake levels by ruminants grazing on tropical grasses is primarily due to the slow degradation and passage rates of particulate digesta from the rumen caused by the increased indigestible lignin contents of plant cell wall as a result of global warming. The retention of digesta in the alimentary tract of ruminants for degradation and digestive action is determined by the rate of passage (Dijkstra *et al.*, 2005). Hidari (1984) described passage rate of digesta from the reticulo-rumen as one of the essential factors regulating feed intake by ruminants fed on roughage diets. Results from this study indicate that roughage quality had no effect ($P>0.05$) on digesta passage rate and degradability. This is in contrast with findings by Moyo *et al.* (2018). These authors reported increased passage rates in sheep and goats due to improved roughage quality. This conflict idea could be due to the selective retention of particles in the reticulo-rumen, since it is more prominent in cattle than in goats and sheep (Lechner-Doll *et al.,* 1991) and less selective feeding by cattle. In contrast to these findings, Adebayo (2015) observed differences in rumen fill of goats fed on roughages of different qualities with the highest being in goats fed on urea treated hay. Passage rate is affected by a wide range of factors and results obtained in this study could have been affected also by salivary buffer contents (Cappellozza *et al.,* 2013), particle size, and functional specific gravity (King and Moore, 1957; Poppi *et al.,* 1980; Lechner-Doll *et al.*, 1991; Clauss *et al.,* 2010) as they influence particle dynamics in the gastrointestinal tract. As expected, the mean retention time of liquid phase was shorter in heifers fed on improved roughage quality than those fed PRQ. Extending the retention time of in heifers fed on PRQ could be an adaptive way used to achieve an effective microbial degradation (Lechner- Doll *et al.,* 1991; Grimaud *et al.,* 1998; Schlecht *et al.,* 2002) allowing furthermost nutrient extraction and energy retention from the slowly degradable fibre fractions (Poncet, 1991). Furthermore, the short retention time of liquid in heifers fed improved roughage quality could also be due to large particles compelling liquid phase as pressure builds up in the rumen due to high intake levels by heifers fed on improved roughage quality (Hummel *et al.*, 2009).

4.6.2 Effect of roughage quality and period of day on rumen fill in jersey heifers

Balch and Campling (1962); Mertens (1994); and Dove (1996) described rumen fill as an essential regulator for long-term herbage intake by ruminants. At any particular period, reticulo-rumen fill level is a result of passage rates, degradation, and feed intake rates (Williams *et al.,* 2014) and is greatly affected by the quality of diet and tendency of animal to use energy (Nsahlai and Apaloo, 2007). Rumen digesta load was not affected by roughage quality ($P>0.05$) but by period of day ($P<0.05$). Logically, liquid digesta in the rumen account for approximately 80-90% to total rumen digesta (Fuller *et al.*, 2004), similar to results reported in this study. Regardless of roughage quality and period of day, the rumen liquid was always greater than rumen dry matter content, 21.23 and 3.53 (kg /100 kg/BW), respectively. The small variation in reticulo-rumen digesta load amongst heifers fed on PRQ and improved roughage quality suggest that ruminants have the ability to increase rates of passage and modify rumen volume when fed on poor quality roughages (Johnson and Combs, 1991). In this study, rumen fill levels varied throughout the day with high levels observed at dusk than in the morning, afternoon, and late afternoon. In contrast to our findings, Baumont *et al.* (1997) observed no difference in rumen digesta load of sheep in the morning and evening. This suggests that rumen fill is not maximized after meal termination at dawn, afternoon, and late afternoon but rather maximal after meal termination at dusk (Gregorini *et al.,* 2007).

The rumen fill levels increased constantly with period of day (evening > late afternoon > afternoon > morning). Studies by Adebayo (2015) and Moyo *et al.* (2018) also reported high rumen loads after termination of the evening grazing bout in goats and sheep, respectively. Such high rumen fill at dusk may perhaps point out the existence of feeding behavioural and physiological regulating mechanisms on rumen fill. The short eating period at night could possibly be likened to a mini-fast period. Therefore, the heifers had to maintain high rumen fill levels through high intake levels during the evening eating bout (Moyo *et al.*, 2018). Generally, ruminants are expected to consume more herbage at cool temperatures. Therefore, assuming that temperatures can be extremely high during late morning and afternoon in summer in tropical and sub-tropical regions, these heifers consumed more herbage during the late afternoon and evening when the temperatures are cool hence, heifers attained high rumen fill in the evening. Although maximal rumen fill was attained at dusk, the first maximal levels of rumen fill at dawn could have been due to the available space in the rumen after prolonged ruminating periods at night.

Due to high predator risk at night than during the day, heifers spent more time eating during the day. A high rumen fill levels after evening meal could have been an adaptive way heifers used to attain adequate food to increase nutrient supply and balance carbon: nitrogen ratio in the rumen, which in turn improves fermentation and nutrient outflow from the rumen (Gregorini *et al.,* 2008). Low ruminal fill during parts of the day could be due to high intake rates. Fuller *et al.* (2004) reported an approximate rumen fill to be 13 and 9% of body weight for grazers and browsers, respectively. However, our finding indicate that rumen load is similar across ruminant species when measured according to the animal's body weight. Moyo *et al.* (2018) reported that Nguni goats had a rumen load of 21.16, 25.07, and 30.80 (kg/100 kg BW) in the morning, afternoon, and evening, respectively. Similar results were obtained using heifers in this study. Surprisingly, dry matter content of the rumen digesta was constant at different periods of the day while the wet matter content increased with increasing rumen load. Wet rumen load measured in the morning, which was similar to that of the afternoon was lower than in the late afternoon and evening. With goats, Adebayo (2015) also observed great levels of liquid ruminal fill at evening than in the morning and afternoon. High NDF contents were observed in the evening than in the morning, afternoon, and late afternoon. This could be due to the high herbage intake and rumen load during the evening. Therefore, the low NDF content during the morning and afternoon is associated with low rumen load. Furthermore, NDF content in the rumen can not only be used as a rumen fill indicator (Van Soest, 1994) but also as a determining factor for the high rumen load at evening (Tedeschi *et al.,* 2012). Mertens (1973) reported an average rumen load for NDF of 1.7 (kg fibre/100kg live weight) in ruminants feeding on temperate roughages. Contrary to findings in this study, the average rumen NDF load was greater than the 1.7 for all dietary treatments (2.33 to 3.23 kg fibre/100 kg live weight). A study by Moyo *et al.* (2018) also reported an average rumen load for NDF greater than 1.7 (kg fibre/ 100 kg live weight). These authors reported an average rumen load for NDF of 1.8 to 2.3 (kg fibre/ 100 kg live weight) and 1.9 to 3.0 (kg fibre/ 100 kg live weight) in goats and sheep, respectively. These results suggest that ruminants adapt differently to roughages thus, ruminants fed on tropical veld are expected to have higher rumen load for NDF (Nsahlai *et al.,* 1996) compared to those feeding on temperate roughages. Furthermore, this suggest that the rumen load for NDF range from 1.8 to 3.2 (kg fibre/ 100 kg BW) in ruminants feeding on tropical roughages.

4.6.3 Effect of roughage quality on intake, rumen digestion, and live weight change in jersey heifers

The high feed intake by heifers fed on improved roughage quality could be due the improved digestion rate in the rumen and improved digestibility. Generally, improving the quality of roughage through the use of urea and other non-protein nitrogen compounds improves intake (Archibeque, 2001; Solaiman *et al.,* 2006; Chanjula and Ngampongsai, 2008). Based on hand feeling, IRQ feels smoother, suppler, break easily and much finer the PRQ. Consequently, urea-ammonization increased the crude protein content while reducing the NDF and hemicellulose contents of veld hay. These could have led to high intake by heifers fed on improved roughage quality than heifers fed on PRQ, as crude protein content is positively correlated to intake (Delcurto *et al.,* 1990; Ghana *et al*., 1993; Mathis *et al.,* 2000; Bohnert *et al*., 2011). Ortiz-Rubio et al. (2007); Adebayo (2015); and Moyo et al. (2018) reported similar results. These authors observed high intake in goats, sheep, and cattle fed improved roughage quality than those fed on PRQ. As expected, the digestion of improved roughage quality in the rumen was fairly higher than that of

PRQ. Lengarite *et al*. (2014); Adebayo (2015); and Moyo *et al.* (2018) also reported high digestibilities in sheep and goats fed on improved roughage quality than those fed PRQ. This could have been due to increased number of accessible microbial attachment sites on the surface of particles (Satter and Slyter, 1974; Chen *et al.*, 2008; Lazzarini *et al.*, 2009). This increases the fibrolytic bacteria population in the rumen and hence the, digestion rate. Urea-ammonization breaks the ester bonds between lignin, hemicellulose, and cellulose enabling rumen microbes to easily attack the cellulose (Goto *et al.* 1993; Wanapat and Cherdthong, 2009). Thus, the low digestion rates of PRQ could be due to deficient substrates for fermentation by microbes.

4.7 Conclusion

Improving roughage quality did not affect rumen fill levels nor increased the fractional passage rates of solid and liquid digesta. However, improving roughage quality increased the degradation and digestion rates of the diets. Our results indicate that rumen fill level and rumen dry matter are greatly influenced by period of day. Rumen load increase progressively across the day, with high levels attained at evening. Furthermore, low NDF contents are associated with low rumen load, suggesting a positive linear relationship between rumen digesta load and NDF contents. The use of urea to improve roughage quality increased intake and digestibility, thus; animal would tend to perform better.

Chapter 5

General discussion, conclusion, and recommendations

5.1 General discussion

Ruminants depend on roughages as their main source of carbohydrate thus, energy source. Feed intake is the primary constituent determining animal performance i.e. growth, production, and reproduction. Rumen fill (RF) is a long-term regulator of intake by ruminants. The purpose of this study was to measure factors affecting intake and focus was based on rumen fill, feeding behaviour, and internal and external factors affecting rumen fill i.e. roughage quality, degradation, digestion, and passage rates. The objectives of this study were to: (i) determine the effect of roughage quality and period of day on diurnal feeding behaviour patterns, (ii) ascertain the effect of roughage quality and period of day on rumen fill, and (iii) confirm the effect of roughage quality on intake, degradation, digestion, and passage rates. A state of knowledge in this area brief review in chapter 2.

In chapter 3, the study tested the hypothesis that diurnal feeding behaviour pattern of heifers is affected by roughage quality and period of day. Diurnal feeding behaviour patterns of heifers fed varying roughage quality oscillated through the day and were not affected by roughage quality but by period of day, except for time spent grooming which was affected by both roughage quality and period of day. Two main feeding events were observed in the morning and late afternoon before dusk, which were separated by short feeding events throughout the day. Heifers fed on PRQ had great number of meals than those fed on improved roughage quality. Using a great number of meals per day without increasing the time spent eating could be an adaptive strategy these animals used to sustain intake levels. The first peak intake from this study could have been a respond to fresh feed availability at feed trough by these heifers after constant emptying during the night due to extended rumination, thus, eating was incited by the delivery of fresh herbage. However, the second peak occurred in the absence of fresh herbage delivery at late afternoon. This could be an adaptive way these animals use to consume more herbage at this time to provide adequate food for maximum ruminal fill in preparing for the dusk. Time spent ruminating tended to be negatively associated with time spent eating and heifers spent more time eating during the day and ruminating at night. Heifers spent more time idling whilst lying at night. This could be due to fatigue as a result of prolonged standing time spent eating, and ruminating. Occasions where heifers spent idling whilst standing at night could have been an adaptive way these animals used to stay watchful at night as a result of high predation risks at dusk. Acceptance of the hypothesis suggest that diurnal feeding behaviour patterns of heifers is greatly affected by period of day and to a lesser extent by roughage quality.

Chapter 4 ascertained the: (i) influence of roughage quality and period of day on rumen fill after meal termination, and (ii) to confirm the influence of roughage quality on intake, degradation, digestibility, and passage rates. It was hypothesized that: (i) roughage quality and period of day have no effect on rumen fill after meal termination; and (ii) roughage quality has effect on intake, degradation, digestibility, and passage rates. Roughage quality had no effect on rumen fill after meal termination. However, period of day effected rumen fill after meal termination. Improving roughage quality increased intake, degradation, and digestibility. Rumen digesta loads were greater at the evening than in the morning, afternoon, and late afternoon. Rumen fill loads followed an increasing trend in this order evening > late afternoon > afternoon > morning. Rumen liquor and rumen NDF (kg/100 kg live body weight) increased with increasing rumen digesta.

Literature suggest that the average rumen load for NDF is 1.7 (kg fibre/ 100 kg live weight) (Mertens, 1973). This is in contrary to our findings. Our findings reported a range of 1.8 to 3.2 (kg fibre/ 100 kg live weight) rumen load for NDF for all dietary treatments. This suggest that the 1.7 reported applies only in ruminants grazing or fed on temperate roughages. Based on results from this study, ruminants adapt differently to roughages thus, ruminants fed on tropical veld are expected to have high rumen load for NDF compared to those grazing or fed on temperate roughages. The high selective factor in heifers fed on PRQ than those fed on improved roughage quality further suggest that grazing ruminants tend to adapt to poor roughages by extending the retention time of solids, hence, achieving an effective microbial degradation.

Improving roughage quality had no effect on digesta outflow from the rumen. However, solid particles were retained longer in the hindgut of heifers fed on IRQ than in those fed on other roughage diets. The prolonged retention time of solids in the hindgut may have be an adaptation to increase extract from high roughage given a tendency to flow out of the rumen faster. Improving roughage quality slightly increased the potentially degradable fraction (PD) and improved the effective degradability (ED). Heifers fed on improved roughage quality had high digestibility than those fed on PRQ. Improving roughage quality also increased intake. The first hypothesis was rejected based on that rumen fill was not affected by roughage quality but by period of day. The second hypothesis was accepted based on the view that improving roughage quality increased intake, digestibility, and rate of degradation.

The high rumen digesta at dusk (chapter 4) could be linked to the great amount of time spent eating by heifers at dusk (chapter 3). This suggest that rumen fill may perhaps point out the existence of feeding behaviour regulating mechanisms on rumen fill, which in turn diurnal feeding behaviour is affected by period of day and to a lesser extent by roughage quality. Therefore, high rumen digesta load at evening could be due to high intake at dusk than in any part of the day. Due to high predation risks during evenings, heifers consumed more at dusk, which could have been an adaptive way heifers used to stay watchful at night. Furthermore, with the exception that summer temperatures in tropical and sub-tropical regions can be extremely high during late morning and afternoon, these heifers consumed more feed during the dusk when temperatures are cool, hence, attaining high rumen digesta load. Heifers increased herbage at dusk to attain maximum rumen fill and sustain nutrient supply during none feeding event at night. Low rumen fill in the morning in this study could have been due to extended rumination periods at night. As a result, hunger pangs were increased thereby generating space for new herbage at dawn feeding event. Similar rumen digesta load were observed across varying roughage qualities at various times of the day. This could be due to the similar rate of passage and degradability across the diets.

5.2 Conclusion

Improving roughage quality had no effect on rumen fill levels and on diurnal behaviour patterns. Based on results from this study, rumen fill and diurnal feeding behaviour is greatly influenced by period of day and to a lesser extent by roughage quality. Furthermore, improving roughage quality had no effect on digesta clearance from and retention time in the rumen. However, improving roughage quality enhanced intake, degradation, and digestion rates, thus; animal would tend to perform better.

5.3 Recommendations for further research

With an ultimate aim to determine the effect of improving roughage quality of tropical veld to increase feed intake thus, improve ruminant production in tropical and sub-tropical regions of Africa. Since ruminants depend on feed intake for growth, production, and to maintain their energy requirements, better understanding of degradability, digestion, passage rates, rumen fill, and feeding behaviour of ruminants fed on poor roughage quality will help to develop mathematical models that will accurately predict voluntary feed intake of ruminants grazing on tropical roughages. Based on use of urea to improve roughage quality, it has the potential to improve intake, digestibility, and rate of degradation. It is therefore, recommended that further research should be carried out on:

- Effect of improving roughage quality on ruminal pH, microbial protein yield, volatile fatty acid production, and nutrient outflow to various organs.
- Effect of roughage quality and period of day on duration and number of eating, ruminating, idling, and water consumption bout in cattle.
- Effect roughage quality on rumen fill and passage rates at various times post-feeding termination in cattle.
- Influence of improving roughage quality on passage rates and mean retention time in the hindgut in cattle.
- Effect of diurnal feeding behaviour and period of day on degradation and passage rates in cattle.

References

Abdullah, N., Ho, Y.W., Mahyuddin, M. and Jalaludin, S., 1991. Studies in fibre digestion and passage rate of liquid and solid in cattle and buffaloes. *Asian-Australasian Journal of Animal Sciences*, *4*(2), pp.137-141.

Abijaoude, J.A., Morand-Fehr, P., Tessier, J., Schmidely, P. and Sauvant, D., 2000. Diet effect on the daily feeding behaviour, frequency and characteristics of meals in dairy goats. *Livestock Production Science*, *64*(1), pp.29-37.

Adbelsalam, M.M., and AL-Seaf A.M., 2013. Behavioral Aspects of Aradi and Its First Cross-with Damascus Goats throughout Vital Stages of Their Lives. *Journal of Agricultural and Veterinary Sciences*, *6*(1), pp.3-16.

Adebayo, R.A., 2015. *Effect of roughage quality and period of meal termination on rumen fill* (Masters dissertation, University of KwaZulu-Natal, Pietermaritzburg).

Aharoni, Y., Henkin, Z., Ezra, A., Dolev, A., Shabtay, A., Orlov, A., Yehuda, Y. and Brosh, A., 2009. Grazing behavior and energy costs of activity: A comparison between two types of cattle. *Journal of animal science*, *87*(8), pp.2719-2731.

Aitchison, E.M., Gill, M., Dhanoa, M.S. and Osbourn, D.F., 1986. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. *British Journal of Nutrition*, *56*(2), pp.463-476.

Albright, J.L. and Arave, C.W., 1997. *The behaviour of cattle*. CAB international.

Albright, J.L., 1978. Social considerations in grouping cows. In *Large dairy herd management* (pp. 757-779). University Press of Florida, Gainesville.

Alcaide, E.M., Garcıa, A.M. and Aguilera, J.F., 2000. A comparative study of nutrient digestibility, kinetics of degradation and passage and rumen fermentation pattern in goats and sheep offered good quality diets. *Livestock Production Science*, *64*(2), pp.215-223.

Allen, M.S. and Mertens, D.R., 1988. Evaluating constraints on fibre digestion by rumen microbes. *The Journal of nutrition*, *118*(2), pp.261-270.

Allen, M.S., 1993. Troubleshooting silage-based ration problems: Ruminal fermentation of fibre and starch. In *silage production: from seed to animal national silage production conference* (pp. 186-195). Ithaca^ eNew York New York: NRAES.

Allen, M.S., 1996. Relationship between forage quality and dairy cattle production. *Animal Feed Science and Technology*, *59*(1), pp.51-60.

Allen, M.S., 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cattle. *Journal of Dairy Science*, *83*(7), pp.1598-1624.

Allen, M.S., 2014. Drives and limits to feed intake in ruminants. *Animal Production Science*, *54*(10), pp.1513-1524.

Allen, M.S., Bradford, B.J. and Harvatine, K.J., 2005. The cow as a model to study food intake regulation. *Annu. Rev. Nutr.*, *25*, pp.523-547.

Allison, C.D., 1985. Factors affecting forage intake by range ruminants: a review. *Journal of Range Management*, pp.305-311.

Andersson, M., 1987. Effects of number and location of water bowls and social rank on drinking behaviour and performance of loose-housed dairy cows. *Applied Animal Behaviour Science*, *17*(1-2), pp.19-31.

AOAC (1999) Official Methods of Analysis, 16th ed. Association of Official Analytical Chemists, Washington, DC, USA

Arachchige, A.D.H., Fisher, A.D., Auldist, M.J., Wales, W.J. and Jongman, E.C., 2013. Effects of different systems of feeding supplements on time budgets of cows grazing restricted pasture allowances. *Applied animal behaviour science*, *148*(1), pp.13-20.

Archibeque, S.L., Burns, J.C. and Huntington, G.B., 2001. Urea flux in beef steers: Effects of forage species and nitrogen fertilization. *Journal of animal science*, *79*(7), pp.1937-1943.

Ariyasu, H., Takaya, K., Tagami, T., Ogawa, Y., Hosoda, K., Akamizu, T., Suda, M., Koh, T., Natsui, K., Toyooka, S. and Shirakami, G., 2001. Stomach is a major source of circulating ghrelin, and feeding state determines plasma ghrelin-like immunoreactivity levels in humans. *The Journal of Clinical Endocrinology & Metabolism*, *86*(10), pp.4753-4758.

Armstrong, R.H., Common, T.G. and Smith, H.K., 1986. The voluntary intake and in vivo digestibility of herbage harvested from indigenous hill plant communities. *Grass and Forage Science*, *41*(1), pp.53-60.

Association of Official Analytical Chemists. 1990. Official methods of analysis of the AOAC, 15th ed. Methods 932.06, 925.09, 985.29, 923.03. Association of official analytical chemists. Arlington, VA, USA.

Association of Official Analytical Chemists. 2005. Official methods of analysis. 18th ed. AOAC, Arlington, VA.

Azizi, O., 2008. Relationships between feeding behaviour and feed intake in dairy cows during early lactation.

Balch, C.C. and Campling, R.C., 1962. Regulation of voluntary food intake in ruminants. In *Nutrition Abstracts and Reviews* (Vol. 32, pp. 669-686).

Bartocci, S., Amici, A., Verna, M., Terramoccia, S. and Martillotti, F., 1997. Solid and fluid passage rate in buffalo, cattle and sheep fed diets with different forage to concentrate ratios. *Livestock Production Science*, *52*(3), pp.201-208.

Baumont, R., 1996. Palatability and feeding behavior in ruminants. A review. In *Annales de zootechnie* (Vol 45, No. 5, pp. 385-400).

Baumont, R., Cohen-Salmon, D., Prache, S. and Sauvant, D., 2004. A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. *Animal Feed Science and Technology*, *112*(1), pp.5-28.

Baumont, R., Cohen-Salmon, D., Prache, S. and Sauvant, D., 2004. A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. *Animal Feed Science and Technology*, *112*(1), pp.5-28.

Baumont, R., Dulphy, J.P. and Andrieu, J.P., 1988. Feeding behavior and reticulo-ruminal fill in sheep fed ad libitum grass hay or lucerne hay with continuous or restricted access: effects on physical control of feed intake. *Reproduction Nutrition Developpement (France)*.

Baumont, R., Jailler, M. and Dulphy, J.P., 1997. Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay. In *Annales de zootechnie* (Vol. 46, No. 3, pp. 231-244).

Baumont, R., Prache, S., Meuret, M. and Morand-Fehr, P., 2000. How forage characteristics influence behaviour and intake in small ruminants: a review. *Livestock Production Science*, *64*(1), pp.15-28.

Bayne, K., Mainzer, H., Dexter, S., Campbell, G., Yamada, F. and Suomi, S., 1991. The reduction of abnormal behaviors in individually housed rhesus monkeys (Macaca mulatta) with a foraging/grooming board. *American Journal of Primatology*, *23*(1), pp.23-35.

Benvenutti, M.A., Gordon, I.J., Poppi, D.P., Crowther, R., Spinks, W. and Moreno, F.C., 2009. The horizontal barrier effect of stems on the foraging behaviour of cattle grazing five tropical grasses. *Livestock Science*, *126*(1), pp.229-238.

Bernard, L., Chaise, J.P., Baumont, R. and Poncet, C., 2000. The effect of physical form of orchardgrass hay on the passage of particulate matter through the rumen of sheep. *Journal of animal science*, *78*(5), pp.1338-1354.

Bildsoe, M., Heller, K.E. and Jeppesen, L.L., 1991. Effects of immobility stress and food restriction on stereotypies in low and high stereotyping female ranch mink. *Behavioural Processes*, *25*(2-3), pp.179-189.

Bohnert, D.W., DelCurto, T., Clark, A.A., Merrill, M.L., Falck, S.J. and Harmon, D.L., 2011. Protein supplementation of ruminants consuming low-quality cool-or warm-season forage: Differences in intake and digestibility. *Journal of animal science*, *89*(11), pp.3707-3717.

Bonsi, M.L.K., Tuah, A.K., Osuji, P.O., Nsahlai, V.I. and Umunna, N.N., 1996. The effect of protein supplement source or supply pattern on the intake, digestibility, rumen kinetics, nitrogen utilisation and growth of Ethiopian Menz sheep fed teff straw. *Animal Feed Science and Technology*, *64*(1), pp.11-25.

Boudon, A., Peyraud, J.L., Faverdin, P., Delagarde, R., Delaby, L. and Chaves, A.V., 2009. Effect of rumen fill on intake of fresh perennial ryegrass in young and mature dairy cows grazing or zero-grazing fresh perennial ryegrass. *animal*, *3*(12), pp.1706-1720.

Brito, A.F., Tremblay, G.F., Lapierre, H., Bertrand, A., Castonguay, Y., Bélanger, G., Michaud, R., Benchaar, C., Ouellet, D.R. and Berthiaume, R., 2009. Alfalfa cut at sundown and harvested as baleage increases bacterial protein synthesis in late-lactation dairy cows. *Journal of dairy science*, *92*(3), pp.1092-1107.

Butt, M.S. and Batool, R., 2010. Nutritional and functional properties of some promising legumes protein isolates. *Pakistan Journal of Nutrition*, *9*(4), pp.373-379.

Campling, R.C. and Freer, M., 1966. Factors affecting the voluntary intake of food by cows. 8. Experiments with ground, pelleted roughages. *Brit. J. Nutrition*, *20*, pp.229-244.

Campling, R.C. and Morgan, C.A., 1981. Eating behaviour of housed dairy cows-a review. In *Dairy Science Abstracts*.

Campling, R.C., 1964. Factors affecting the voluntary intake of grass. *Proceedings of the Nutrition Society*, *23*(1), pp.80-88.

Cappellozza, B.I., Bohnert, D.W., Schauer, C.S., Falck, S.J., Vanzant, E.S., Harmon, D.L. and Cooke, R.F., 2013. Daily and alternate day supplementation of urea or soybean meal to ruminants consuming low-quality cool-season forage: II. Effects on ruminal fermentation. *Livestock Science*, *155*(2), pp.214-222.

Cardot, V., Le Roux, Y. and Jurjanz, S., 2008. Drinking behavior of lactating dairy cows and prediction of their water intake. *Journal of dairy science*, *91*(6), pp.2257-2264.

Cardoza, R.S. and Mertens, D.R., 1986. Effect of fibre source and content on threshold size for passage and fecal particle distribution. *J. Dairy Sci*, *69*(Suppl 1), p.134.

Cavalcanti, C.V.D.A., Ferreira, M.D.A., Carvalho, M.C., Véras, A.S.C., Silva, F.M.D. and Lima, L.E.D., 2008. Spineless cactus plus urea in replacement of tifton 85 hay in Holstein lactating dairy cows diet. *Revista Brasileira de Zootecnia*, *37*(4), pp.689-693.

Champion, R.A., Rutter, S.M., Penning, P.D. and Rook, A.J., 1994. Temporal variation in grazing behaviour of sheep and the reliability of sampling periods. *Applied Animal Behaviour Science*, *42*(2), pp.99-108.

Chanjula, P. and Ngampongsai, W., 2008. Effect of supplemental nitrogen from urea on digestibility, rumen fermentation pattern, microbial populations and nitrogen balance in growing goats. *Songklanakarin Journal of Science & Technology*, *30*(5).

Charlton, G.L., Rutter, S.M., East, M. and Sinclair, L.A., 2011. Effects of providing total mixed rations indoors and on pasture on the behavior of lactating dairy cattle and their preference to be indoors or on pasture. *Journal of dairy science*, *94*(8), pp.3875-3884.

Chen, X.L., Wang, J.K., Wu, Y.M. and Liu, J.X., 2008. Effects of chemical treatments of rice straw on rumen fermentation characteristics, fibrolytic enzyme activities and populations of liquid-and solid-associated ruminal microbes in vitro. *Animal Feed Science and Technology*, *141*(1-2), pp.1-14.

Chenost, M. and Kayouli, C., 1997. Roughage utilization in warm climates. *FAO animal production and health paper*, (135).

Chenost, M., Aufrère, J. and Macheoeuf, D., 2001. The gas-test technique as a tool for predicting the energetic value of forage plants. *Animal Research*, *50*(5), pp.349-364.

Chermiti, A., Teller, E., Vanbelle, M., Collignon, G. and Matatu, B., 1994. Effect of ammonia or urea treatment of straw on chewing behaviour and ruminal digestion processes in non-lactating dairy cows. *Animal Feed Science and Technology*, *47*(1-2), pp.41-51.

Chilibroste, P., Gibb, M. and Tamminga, S., 2005. Pasture Characteristics and Animal Performance.

Christopherson, R.J. and Kennedy, P.M., 1983. Effect of the thermal environment on digestion in ruminants. *Canadian Journal of Animal Science*, *63*(3), pp.477-496.

Christopherson, R.J., 1976. Effects of prolonged cold and the outdoor winter environment on apparent digestibility in sheep and cattle. *Canadian Journal of Animal Science*, *56*(2), pp.201-212.

Church, D.C., 1988. *The Ruminant animal: digestive physiology and nutrition*.

Clauss, M. and Lechner-Doll, M., 2001. Differences in selective reticulo-ruminal particle retention as a key factor in ruminant diversification. *Oecologia*, *129*(3), pp.321-327.

Clauss, M., Fritz, J., Bayer, D., Hummel, J., Streich, W.J., Südekum, K.H. and Hatt, J.M., 2009. Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (Ovis ammon musimon) and the roe deer (Capreolus capreolus). *Zoology*, *112*(3), pp.195-205.

Clauss, M., Hume, I.D. and Hummel, J., 2010. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal*, *4*(7), pp.979-992.

Clauss, M., Hummel, J. and Streich, W.J., 2006. The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: an evaluation of available, comparable ruminant passage data. *European Journal of Wildlife Research*, *52*(2), pp.88-98.

Coffey, M.T., Hagler Jr, W.M. and Cullen, J.M., 1989. Influence of dietary protein, fat or amino acids on the response of weanling swine to aflatoxin B1. *Journal of Animal Science*, *67*(2), pp.465-472.

Coleman, S.W. and Moore, J.E., 2003. Feed quality and animal performance. *Field Crops Research*, *84*(1-2), pp.17-29.

Coleman, S.W., Hart, S.P. and Sahlu, T., 2003. Relationships among forage chemistry, rumination and retention time with intake and digestibility of hay by goats. *Small Ruminant Research*, *50*(1), pp.129-140.

Colucci, P.E., Macleod, G.K., Grovum, W.L., McMillan, I. and Barney, D.J., 1990. Digesta kinetics in sheep and cattle fed diets with different forage to concentrate ratios at high and low intakes. *Journal of dairy science*, *73*(8), pp.2143-2156.

Colucci, P.E., MacLeod, G.K., McMillan, I. and Grovum, W.L., 1984. Comparative digestion and digesta kinetics in sheep and cattle. *Canadian Journal of Animal Science*, *64*(5), pp.173-174.

Costa, LT, Silva, F.F., Veloso, C.M., Pires, A.J.V., Rocha Neto, A.L., Bonomo, P., Mendes, F.B.L., Oliveira, J.S., Azevêdo, S.T., and Silva, V.L., 2011. Ingestive behaviour of cows fed on the diet of cows fed on the diet of cows fed on the diet of cows fed a diet of cane and different levels of concentrate. *Animal husbandry* records, *60*(230), pp. 265-273.

Coulon, J.B., 1984. Feeding behaviour of crossbred Charolais cattle in a humid tropical environment. *Revue d'Elevage et de Med. Veterinaire des Pays Tropicaux*, *37*, pp.185-190.

Crichlow, E.C. and Leek, B.F., 1986. Forestomach epithelial receptor activation by rumen fluids from sheep given intraruminal infusions of volatile fatty acids. *American journal of veterinary research*, *47*(5), pp.1015-1018.

Dado, R.G. and Allen, M.S., 1994. Variation in and relationships among feeding, chewing, and drinking variables for lactating dairy cows. *Journal of Dairy Science*, *77*(1), pp.132-144.

Dado, R.G. and Allen, M.S., 1995. Intake limitations, feeding behaviour, and rumen function of cows challenged with rumen fill from dietary fibre or inert bulk. *Journal of dairy science*, *78*(1), pp.118-133.

Dann, H.M., Varga, G.A. and Putnam, D.E., 1999. Improving energy supply to late gestation and early postpartum dairy cows. *Journal of Dairy Science*, *82*(8), pp.1765-1778.

Dannenmann, K., Buchenauer, D. and Fliegner, H., 1985. The behaviour of calves under four levels of lighting. *Applied Animal Behaviour Science*, *13*(3), pp.243-258.

Degen, A.A. and Young, B.A., 1980. Effect of cold exposure on liveweight and body fluid compartments in sheep. *Canadian Journal of Animal Science*, *60*(1), pp.33-41.

Delagarde, R., Peyraud, J.L., Delaby, L. and Faverdin, P., 2000. Vertical distribution of biomass, chemical composition and pepsin—cellulase digestibility in a perennial ryegrass sward: interaction with month of year, regrowth age and time of day. *Animal Feed Science and Technology*, *84*(1-2), pp.49-68.

DelCurto, T., Cochran, R.C., Harmon, D.L., Beharka, A.A., Jacques, K.A., Towne, G. and Vanzant, E.S., 1990. Supplementation of dormant tallgrass-prairie forage: I. Influence of varying supplemental protein and (or) energy levels on forage utilization characteristics of beef steers in confinement. *Journal of Animal Science*, *68*(2), pp.515-531.

Detmann, E., Paulino, M.F., Mantovani, H.C., Valadares Filho, S.D.C., Sampaio, C.B., de Souza, M.A., Lazzarini, Í. and Detmann, K.S., 2009. Parameterization of ruminal fibre degradation in low-quality tropical forage using Michaelis–Menten kinetics. *Livestock Science*, *126*(1), pp.136-146.

DeVries, T.J., Von Keyserlingk, M.A.G., Weary, D.M. and Beauchemin, K.A., 2003. Measuring the feeding behavior of lactating dairy cows in early to peak lactation. *Journal of Dairy Science*, *86*(10), pp.3354-3361.

Dewhurst, R.J., Evans, R.T., Scollan, N.D., Moorby, J.M., Merry, R.J. and Wilkins, R.J., 2003. Comparison of grass and legume silages for milk production. 2. In vivo and in sacco evaluations of rumen function. *Journal of Dairy Science*, *86*(8), pp.2612-2621.

Dijkstra, J., Kebreab, E., Bannink, A., France, J. and Lopez, S., 2005. Application of the gas production technique to feed evaluation systems for ruminants. *Animal Feed Science and Technology*, *123*, pp.561-578.

Dohme, F., DeVries, T.J. and Beauchemin, K.A., 2008. Repeated ruminal acidosis challenges in lactating dairy cows at high and low risk for developing acidosis: Ruminal pH. *Journal of dairy science*, *91*(9), pp.3554-3567.

Dove, H., 1996. Constraints to the modelling of diet selection and intake in the grazing ruminant. *Australian Journal of Agricultural Research*, *47*(2), pp.257-275.

Dovie, D.B., Shackleton, C.M. and Witkowski, E.T.F., 2006. Valuation of communal area livestock benefits, rural livelihoods and related policy issues. *Land use policy*, *23*(3), pp.260-271.

Dulphy, J.P. and Demarquilly, C., 1994. The regulation and prediction of feed intake in ruminants in relation to feed characteristics. *Livestock Production Science*, *39*(1), pp.1-12.

Dumont, B., Petit, M. and D'hour, P., 1995. Choice of sheep and cattle between vegetative and reproductive cocksfoot patches. *Applied Animal Behaviour Science*, *43*(1), pp.1-15.

Ehle, F.R. and Stern, M.D., 1986. Influence of particle size and density on particulate passage through alimentary tract of Holstein heifers. *Journal of Dairy Science*, *69*(2), pp.564-568.

Ehrlein, HJ and Hill, H., 1969. Motility and nutritional transport in the omasum of the goat. *Central Journal of Veterinary Medicine. Row A*, *16* (7), p.573.

Ellis, W.C., 1978. Determinants of grazed forage intake and digestibility. *Journal of Dairy Science*, *61*(12), pp.1828-1840.

Ernst, P., Le Du, Y.L.P. and Carlier, L., 1980. Animal and sward production under rotational and continuous grazing management-a critical appraisal. *Animal and sward production under rotational and continuous grazing management-a critical appraisal.*, pp.119-126.

Estrada, J.C., Delagarde, R., Faverdin, P. and Peyraud, J.L., 2004. Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. *Animal Feed Science and Technology*, *114*(1-4), pp.59-74.

Evans, E., 1981. An evaluation of the relationships between dietary parameters and rumen solid turnover rate. *Canadian Journal of Animal Science*, *61*(1), pp.97-103.

Faichney, G.J. and White, G.A., 1988. Rates of passage of solutes, microbes and particulate matter through the gastro-intestinal tract of ewes fed at a constant rate throughout gestation. *Australian Journal of Agricultural Research*, *39*(3), pp.481-492.

Faichney, G.J., 1986. Kinetics of particulate matter in the rumen.

Faichney, G.J., 1993. Digesta flow. *Quantitative aspects of ruminant digestion and metabolism*, *2*, pp.49-86.

Faverdin, P., 1999. The effect of nutrients on feed intake in ruminants. *Proceedings of the Nutrition Society*, *58*(3), pp.523-531.

Faverdin, P., Baumont, R. and Ingvartsen, K.L., 1995. Control and prediction of feed intake in ruminants. In: *International Symposium on the Nutrition of Herbivores. 4. Symposium International sur la Nutrition des Herbivores, Clermont Ferrand (France), 11-15 Sep 1995*. INRA.

Faverdin, P., Delagarde, R. and Delaby, L., 2006. Prediction of ingestion of dairy cows during lactation. *Proceedings of the 13th Days on Ruminant Research, Ruminant Research Meetings*, pp.6-7.

Firkins, J.L., 1997. Effects of Feeding Non-forage Fiber Sources on Site of Fiber Digestion1. *Journal of Dairy Science*, *80*(7), pp.1426-1437.

Fisher, A.D., Crowe, M.A., O'kiely, P. and Enright, W.J., 1997. Growth, behaviour, adrenal and immune responses of finishing beef heifers housed on slatted floors at 1.5, 2.0, 2.5 or 3.0 m2 space allowance. *Livestock Production Science*, *51*(1), pp.245-254.

Fisher, D.S., 2002. A Review of a Few Key Factors Regulating Voluntary Feed Intake in Ruminants 1. *Crop Science*, *42*(5), pp.1651-1655.

Forbes, J. 1995. Specific Nutrients Affecting Intake In:"Voluntary Food Intake and Diet Selection in Farm Animals". CAB International. *Wallingford, United Kingdom***,** 226-246.

Forbes, J. M. and France, J. 1993. Quantitative aspects of ruminant digestion and metabolism, Cab International.

Forbes, J.M., 1995. Voluntary food intake and diet selection in farm animals. CAB International, Wallingford.

Forbes, J.M., 2000. Physiological and metabolic aspects of feed intake control. *Farm animal metabolism and nutrition. Wallingford: CAB International*, pp.319-334.

Fox, D.G., Tedeschi, L.O., Tylutki, T.P., Russell, J.B., Van Amburgh, M.E., Chase, L.E., Pell, A.N. and Overton, T.R., 2004. The Cornell Net Carbohydrate and Protein System model for evaluating herd nutrition and nutrient excretion. *Animal Feed Science and Technology*, *112*(1-4), pp.29-78.

Fraser, A.F. and Broom, D.M., 1997. *Farm animal behaviour and welfare* (No. Ed. 3). CAB international.

Fraser, D., 2004. Factors influencing livestock behaviour and performance.

Freer, M., 1981. The control of food intake by grazing animals. In *Grazing animals* (Vol. 1, pp. 105-124). Elsevier Amsterdam.

Freer, M., Campling, R.C. and Balch, C.C., 1962. Factors affecting the voluntary intake of food by cows. *British journal of nutrition*, *16*(01), pp.279-295.

Fregonesi, J.A. and Leaver, J.D., 2001. Behaviour, performance and health indicators of welfare for dairy cows housed in strawyard or cubicle systems. *Livestock production science*, *68*(2), pp.205-216.

Fritz, J., Hummel, J., Kienzle, E., Arnold, C., Nunn, C. and Clauss, M., 2009. Comparative chewing efficiency in mammalian herbivores. *Oikos*, *118*(11), pp.1623-1632.

Fuller, M.F., Benavenga, N.J., Lall, S.P., McCracken, K.J., Omed, H,M., Axford, R.F.E., Phillips, C.J.C., 2004. 'The Encyclopaedia of Farm Animal Nutrition'. (CAB International: Wallingford UK).

Furstenburg, D., 1992. The use of purified condensed tannin as a reference in determining its influence on rumen fermentation. *Comparative biochemistry and physiology. Comparative physiology*, *101*(2), pp.381-385.

Garcia, F., Carrere, P., Soussana, J.F. and Baumont, R., 2003. How do severity and frequency of grazing affect sward characteristics and the choices of sheep during the grazing season? *Grass and Forage Science*, *58*(2), pp.138-150.

Garcia, J., De Blas, J.C., Carabaño, R. and Garcia, P., 1995. Effect of type of lucerne hay on caecal fermentation and nitrogen contribution through caecotrophy in rabbits. *Reproduction Nutrition Development*, *35*(3), pp.267-275.

Ghana, D. M., Kimambo, A. E., Sandston, F., and Madsen, J., 1993. Influence of urea treatment or supplementation on degradation, intake and growth performance of goats fed rice straw diets. *Global Journal of Science*, 209-220.

Gibb, M.J., Huckle, C.A. and Nuthall, R., 1998. Effect of time of day on grazing behaviour by lactating dairy cows. *Grass and Forage Science*, *53*(1), pp.41-46.

Gibb, M.J., Huckle, C.A., Nuthall, R. and Rook, A.J., 1997. Effect of sward surface height on intake and grazing behaviour by lactating Holstein Friesian cows. *Grass and Forage Science*, *52*(3), pp.309-321.

Gibb, M.J., Huckle, C.A., Nuthall, R. and Rook, A.J., 1999. The effect of physiological state (lactating or dry) and sward surface height on grazing behaviour and intake by dairy cows. *Applied Animal Behaviour Science*, *63*(4), pp.269-287.

Gill, M. and Romney, D., 1994. The relationship between the control of meal size and the control of daily intake in ruminants. *Livestock Production Science*, *39*(1), pp.13-18.

Ginnett, T.F., Dankosky, J.A., Deo, G. and Demment, M.W., 1999. Patch depression in grazers: the roles of biomass distribution and residual stems. *Functional Ecology*, *13*(1), pp.37-44.

Gonyou, H.W., Christopherson, R.J. and Young, B.A., 1979. Effects of cold temperature and winter conditions on some aspects of behaviour of feedlot cattle. *Applied Animal Ethology*, *5*(2), pp.113-124.

Goto, M., Yokoe, Y., Takabe, K., Nisikawa, S. and Morita, O., 1993. Effects of gaseous ammonia on chemical and structural features of cell walls in spring barley straw. *Animal Feed Science and Technology*, *40*(2-3), pp.207-221.

Grandin, T. and Deesing, M.J., 1998. Genetics and behavior during handling, restraint, and herding. *Genetics and the behavior of domestic animals*, pp.113-144.

Grant, R.J. and Albright, J.L., 1995. Feeding behavior and management factors during the transition period in dairy cattle. *Journal of Animal Science*, *73*(9), pp.2791-2803.

Grant, R.J. and Albright, J.L., 2000. Feeding behaviour. *Farm animal metabolism and nutrition*, pp.365-382.

Grant, R.J. and Albright, J.L., 2001. Effect of animal grouping on feeding behavior and intake of dairy cattle. *Journal of dairy science*, *84*, pp.156-163.

Grant, R.J., 2006. Motivating Cows: creating the right environment. In *Penn State Dairy Cattle Nutrition Workshop* (pp. 43-47).

Gregorini, P., 2011. Internal state. stimuli that motivate consumption and certain ingestive behaviors of grazing ruminants. *Animal production in grazing. '(Eds CA Cangiano, MA Brizuela) pp* , pp.291-313.

Gregorini, P., 2012. Diurnal grazing pattern: its physiological basis and strategic management. *Animal Production Science*, *52*(7), pp.416-430.

Gregorini, P., Clark, C.E.F., Jago, J.G., Glassey, C.B., McLeod, K.L.M. and Romera, A.J., 2009. Restricting time at pasture: effects on dairy cow herbage intake, foraging behavior, hunger-related hormones, and metabolite concentration during the first grazing session. *Journal of Dairy Science*, *92*(9), pp.4572-4580.

Gregorini, P., Eirin, M., Agnelli, L., Refi, R., Ursino, M., Ansin, O.E., Masino, C., Wade, M.H., Soder, K.J. and Gunter, S.A., 2007. Diurnal eating pattern and performance of cattle strip grazed with afternoon herbage allocation or continuously variable stocked. *26 in Proc. Am. Forage Grassl. Counc. Annu. Meet. State College, PA*, p.23.

Gregorini, P., Gunter, S.A., Beck, P.A., Soder, K.J. and Tamminga, S., 2008. The interaction of diurnal grazing pattern, ruminal metabolism, nutrient supply, and management in cattle. *The Professional Animal Scientist*, *24*(4), pp.308-318.

Gregorini, P., Gunter, S.A., Masino, C.A. and Beck, P.A., 2007. Effects of ruminal fill on short-term herbage intake rate and grazing dynamics of beef heifers. *Grass and Forage Science*, *62*(3), pp.346-354.

Gregorini, P., Soder, K. and Kensinger, R., 2008, July. Effect of ruminal fill on foraging behavior, intake rate, and plasma ghrelin, serum insulin and glucose levels of cattle grazing a vegetative micro-sward. In *Joint Abstracts of the American Dairy Science and Society of Animal Science* (Vol. 86, p. 371).

Gregorini, P., Soder, K.J., Sanderson, M.A. and Ziegler, G.R., 2009. Toughness, particle size and chemical composition of meadow fescue (Festuca pratensis Hud.) herbage as affected by time of day. *Animal feed science and technology*, *151*(3), pp.330-336.

Grimaud, P., Richard, D., Kanwé, A., Durier, C. and Doreau, M., 1998. Effect of undernutrition and refeeding on digestion in Bos taurus and Bos indicus in a tropical environment. *Animal Science*, *67*(1), pp.49-58.

Groot, J.C.J., 1999. *Modelling grass digestibility on the basis of morphological and physiological plant characteristics*. sn].

Grovum, W.L. and Williams, V.J., 1973. Rate of passage of digesta in sheep: 4. Passage of marker through the alimentary tract and the biological relevance of rate-constants derived from the changes in concentration of marker in faeces. *British journal of Nutrition*, *30*(2), pp.313-329.

Grovum, W.L., 1986. The control of motility of the ruminoreticulum. In *Proceedings of 6th International Symposium on Ruminant Physiology, Banff (Canada), 10-14 Sep 1984*. Prentice-Hall.

Hafez, E.S.E., 1969. The behaviour of domestic animals. *The behaviour of domestic animals.* (2nd edn).

Hafez, E.S.E., 1975. The behaviour of cattle. *The behaviour of domestic animals*, pp.203-245.

Hales, J.R.S., 1973. Effects of exposure to hot environments on the regional distribution of blood flow and on cardiorespiratory function in sheep. *Pflügers Archiv*, *344*(2), pp.133-148.

Hansson, K., 2006. Comparison of the rumen passage rate of different forages using rare-earth markers.

Harrison, D.G. and McAllan, A.B., 1980. Factors affecting microbial growth yields in the reticulo-rumen. In *Digestive physiology and metabolism in ruminants* (pp. 205-226). Springer, Dordrecht.

Hatfield, P.G., Clanton, D.C., Sanson, D.W., Eskridge, K.M., 1990. Methods of administering ytterbium for estimation of faecal output. *Journal of Range Management* 1(3), pp.16-20.

Hayashida, T., Murakami, K., Mogi, K., Nishihara, M., Nakazato, M., Mondal, M.S., Horii, Y., Kojima, M., Kangawa, K. and Murakami, N., 2001. Ghrelin in domestic animals: distribution in stomach and its possible role. *Domestic animal endocrinology*, *21*(1), pp.17-24.

Helander, C., Nørgaard, P., Arnesson, A. and Nadeau, E., 2014. Effects of chopping grass silage and of mixing silage with concentrate on feed intake and performance in pregnant and lactating ewes and in growing lambs. *Small Ruminant Research*, *116*(2), pp.78-87.

Herzog, E.D. and Schwartz, W.J., 2002. Invited review: a neural clockwork for encoding circadian time. *Journal of Applied Physiology*, *92*(1), pp.401-408.

Hidari, H., 1984. Effect of altering the rumen load on the feeding behavior in sheep. *Canadian Journal of Animal Science*, *64*(5), pp.320-321.

Hodgson, J., 1966. The frequency of defoliation of individual tillers in a set-stocked sward. *Grass and Forage Science*, *21*(4), pp.258-263.

Hodgson, J., 1990. *Grazing management. Science into practice*. Longman Group UK Ltd.

Hooper, A.P. and Welch, J.G., 1985. Effects of particle size and forage composition on functional specific gravity. *Journal of Dairy Science*, *68*(5), pp.1181-1188.

Huhtanen, P., Ahvenjärvi, S., Weisbjerg, M.R. and Nørgaard, P., 2006. Digestion and passage of fibre in ruminants. In *Ruminant physiology: digestion, metabolism and impact of nutrition on gene expression, immunology and stress* (pp. 87-135). Wageningen Press, Wageningen, the Netherlands.

Hume, I.D. and Sakaguchi, E., 1991. Patterns of digesta flow and digestion in foregut and hindgut fermenters. In *Physiological aspects of digestion and metabolism in ruminants* (pp. 427-451).

Hummel, J., Südekum, K.H., Bayer, D., Ortmann, S., Streich, W.J., Hatt, J.M. and Clauss, M., 2009. Physical characteristics of reticulo-ruminal contents of oxen in relation to forage type and time after feeding. *Journal of animal physiology and animal nutrition*, *93*(2), pp.209-220.

Hummel, J., Südekum, K.H., Streich, W.J. and Clauss, M., 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. *Functional Ecology*, *20*(6), pp.989-1002.

Huston, J.E., Rector, B.S., Ellis, W.C. and Allen, M.L., 1986. Dynamics of Digestion in Cattle, Sheep, Goats and Deer 1. *Journal of Animal Science*, *62*(1), pp.208-215.

Hutjens, M.F., 2005. Feed efficiency and its economic impact on large herds. In *Proc. Southwest Nutr. Conf* (pp. 186-191).

Illius, A.W. and Jessop, N.S., 1996. Metabolic constraints on voluntary intake in ruminants. *Journal of animal Science*, *74*(12), pp.3052-3062.

Jackson, N. and Forbes, T.J., 1970. The voluntary intake by cattle of four silages differing in dry matter content. *Animal Science*, *12*(4), pp.591-599.

Jalali, A.R., Nørgaard, P., Weisbjerg, M.R. and Nielsen, M.O., 2012. Effect of forage quality on intake, chewing activity, faecal particle size distribution, and digestibility of neutral detergent fibre in sheep, goats, and llamas. *Small Ruminant Research*, *103*(2), pp.143-151.

Jarrige, R., Dulphy, J.P., Faverdin, P., Baumont, R. and Demarquilly, C., 1995. Activités d'ingestion et de rumination. *Jarrige, R.; Ruckebusch, Y.; Demarquilly, C*, pp.123-181.

Johnson, T.R. and Combs, D.K., 1991. Effects of pre-partum diet, inert rumen bulk, and dietary polyethylene glycol on dry matter intake of lactating dairy cows. *Journal of Dairy Science*, *74*(3), pp.933-944.

Judkins, M.B., Wallace, J.D., Galyean, M.L., Krysl, L.J. and Parker, E.E., 1987. Passage rates, rumen fermentation, and weight change in protein supplemented grazing cattle. *Journal of Range Management*, pp.100-105.

Kaske, M. and Engelhardt, W.V., 1990. The effect of size and density on mean retention time of particles in the gastrointestinal tract of sheep. *British Journal of Nutrition*, *63*(3), pp.457-465.

Kaske, M. and Groth, A., 1997. Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay. *Reproduction Nutrition Development*, *37*(5), pp.573-588.

Kaske, M. and Midasch, A., 1997. Effects of experimentally impaired reticular contractions on digesta passage in sheep. *British Journal of Nutrition*, *78*(1), pp.97-110.

Kaske, M., 1987. The effect of the density on the selective retention of big particles in the rumen of sheep. German. *Journal of Animal Physiology and Animal Nutrition*.

Katoh, K., Sato, F., Yamazaki, A., Sasaki, Y. and Tsuda, T., 1988. Passage of indigestible particles of various specific gravities in sheep and goats. *British Journal of Nutrition*, *60*(3), pp.683-687.

Kennedy, P.M. and Milligan, L.P., 1978. Transfer of urea from the blood to the rumen of sheep. *British journal of nutrition*, *40*(1), pp.149-154.

Kennedy, P.M. and Murphy, M.R., 1988. The nutritional implications of differential passage of particles through the ruminant alimentary tract. *Nutrition Research Reviews*, *1*(1), pp.189-208.

Kennedy, P.M. and Poppi, D.P., 1984. Critical particle size in sheep and cattle. *Techniques in particle size analysis of feed and digesta in ruminants*, *170*.

Kennedy, P.M., 1985. Effect of rumination on reduction of particle size of rumen digesta by cattle. *Australian Journal of Agricultural Research*, *36*(6), pp.819-828.

Kennedy, P.M., 2005. Particle dynamics. *Quantitative aspects of ruminant digestion and metabolism*, pp.123-156.

Kennedy, P.M., Christopherson, R.J. and Milligan, L.P., 1976. The effect of cold exposure of sheep on digestion, rumen turnover time and efficiency of microbial synthesis. *British Journal of Nutrition*, *36*(2), pp.231-242.

Kennedy, P.M., Christopherson, R.J. and Milligan, L.P., 1982. Effects of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. *British Journal of Nutrition*, *47*(3), pp.521-535.

Kennedy, P.M., Young, B.A. and Christopherson, R.J., 1977. Studies on the Relationship between Thyroid Function, Cold Acclimation and Retention Time of Digesta in Sheep 1, 2. *Journal of animal science*, *45*(5), pp.1084-1090.

King, K.W. and Moore, W.E.C., 1957. Density and Size as Factors Affecting Passage Rate of Ingesta in the Bovine and Human Digestive Tracts1. *Journal of Dairy Science*, *40*(5), pp.528-536.

Kolver, E.S. and MacMillan, K.L., 1993. Short term changes in selected metabolites in pasture-fed dairy cows during peak lactation. In *proceedings-new zealand society of animal production* (Vol. 53, pp. 77-77). New Zealand Society of Animal Prod Publ.

Krysl, L.J. and Hess, B.W., 1993. Influence of supplementation on behavior of grazing cattle. *Journal of Animal Science*, *71*(9), pp.2546-2555.

Laca, E.A., Ungar, E.D., Seligman, N. and Demment, M.W., 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and forage science*, *47*(1), pp.91-102.

Langbein, J. and Nichelmann, M., 1993. Differences in behaviour of free-ranging cattle in the tropical climate. *Applied Animal Behaviour Science*, *37*(3), pp.197-209.

Larsen, M., Lund, P., Weisbjerg, M.R. and Hvelplund, T., 2009. Digestion site of starch from cereals and legumes in lactating dairy cows. *Animal Feed Science and Technology*, *153*(3-4), pp.236-248.

Lazzarini, I., Detmann, E., Sampaio, C.B., Paulino, M.F., Valadares Filho, S.D.C., Souza, M.A.D. and Oliveira, F.A., 2009. Intake and digestibility in cattle fed low-quality tropical forage and supplemented with nitrogenous compounds. *Revista Brasileira de Zootecnia*, *38*(10), pp.2021-2030.

Le Magnen, J., 1985. *Hunger* (Vol. 3). CUP Archive.

Lechner-Doll, M., Kaske, M. and Engelhardt, W.V., 1991. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. *Physiological aspects of digestion and metabolism in ruminants*, pp.455-482.

Lechner-Doll, M., Rutagwenda, T., Schwartz, H.J., Schultka, W. and Engelhardt, W.V., 1990. Seasonal changes of ingesta mean retention time and forestomach fluid volume in indigenous camels, cattle, sheep and goats grazing a thornbush savannah pasture in Kenya. *The Journal of Agricultural Science*, *115*(3), pp.409-420.

Leek, B.F. and Harding, R.H., 1975. Sensory nervous receptors in the ruminant stomach and the reflex control of reticulo-ruminal motility. *Digestion and Metabolism in the Ruminant*, pp.60-76.

Lengarite, M.I., Getachew, G., Akudabweni, L. and Hoag, D., 2014. Supplementary feeding of lactating goats with processed and unprocessed Acacia tortilis pods and local grass in the dry season in northern Kenya. *Agricultural Science Research Journal*, *4*(3), pp.63-71.

Levin, R.J., 1969. The effects of hormones on the absorptive, metabolic and digestive functions of the small intestine. *Journal of endocrinology*, *45*(2), pp.315-348.

Lindstrom, T. and Redbo, I., 2000. Effect of feeding duration and rumen fill on behaviour in dairy cows. *Applied Animal Behaviour Science*, *70*(2), pp.83-97.

Lindström, T., 2000. *Feeding behaviour in dairy cows* (Vol. 250).

Lopez, S., Hovell, F.D.D., Dijkstra, J. and France, J., 2003. Effects of volatile fatty acid supply on their absorption and on water kinetics in the rumen of sheep sustained by intragastric infusions 1. *Journal of animal science*, *81*(10), pp.2609-2616.

Lund, P., Weisbjerg, M.R. and Hvelplund, T., 2007. Digestible NDF is selectively retained in the rumen of dairy cows compared to indigestible NDF. *Animal feed science and technology*, *134*(1-2), pp.1-17.

Lunn, D.E., Mutsvangwa, T., Odongo, N.E., Duffield, T.F., Bagg, R., Dick, P., Vessie, G. and McBride, B.W., 2004, January. The effects of monensin on feed intake pattern during sub-acute ruminal acidosis in dairy cows. In *Journal of Dairy Science* (Vol. 87, pp. 341-342). 1111 N Dunlap Ave, Savoy, IL 61874 USA: Amer Dairy Science Assoc.

Manser, C.E., 1992. The assessment of stress in laboratory animals. *The assessment of stress in laboratory animals.*

Mason, G. and Rushen, J. 2008. *Stereotypic animal behaviour: fundamentals and applications to welfare*. Cabi.

Mathis, C.P., Cochran, R.C., Heldt, J.S., Woods, B.C., Abdelgadir, I.E., Olson, K.C., Titgemeyer, E.C. and Vanzant, E.S., 2000. Effects of supplemental degradable intake protein on utilization of medium-to low-quality forages. *Journal of Animal Science*, *78*(1), pp.224-232.

Mathison, G.W., Okine, E.K., Vaage, A.S., Kaske, M. and Milligan, L.P., 1994. Current understanding of the contribution of the propulsive activities in the forestomach in the flow of digesta. In *Proceedings of the Society of Nutrition Physiology (Germany)*. DLG.

Mayes, R.W. and Dove, H., 2000. Measurement of dietary nutrient intake in free-ranging mammalian herbivores. *Nutrition Research Reviews*, *13*(1), pp.107-138.

McCollum, F.T. and Galyean, M.L., 1985. Cattle grazing blue grama rangeland II. Seasonal forage intake and digesta kinetics. *Journal of Range Management*, pp.543-546.

McDonald, I., 1981. A revised model for the estimation of protein degradability in the rumen. *The Journal of Agricultural Science*, *96*(1), pp.251-252.

McDonald, P., 2002. *Animal nutrition*. Pearson education.

McLeod, M.N. and Minson, D.J., 1988. Breakdown of large particles in forage by simulated digestion and detrition. *Journal of animal science*, *66*(4), pp.1000-1004.

Meier, S., Kolver, E.S., Verkerk, G.A. and Roche, J.R., 2010. Effects of divergent Holstein-Friesian strain and diet on diurnal patterns of plasma metabolites and hormones. *Journal of dairy research*, *77*(04), pp.432-437.

Mench, J., 1998. Why it is important to understand animal behavior. *ILAR journal*, *39*(1), pp.20-26.

Mendonça, D., Webb, G., Butts, C. and Brooks, J., 2014. Cognitive correlates of improvised behaviour in disaster response: The cases of the Murrah building and the World Trade Center. *Journal of Contingencies and Crisis Management*, *22*(4), pp.185-195.

Meneses, M.D.A., Silva, F.F.D., Schio, A.R., Silva, R.R., Souza, D.D.D., Junior, P. and Ferraz, A., 2014. Feeding behavior of dairy cows in feedlot and fed on crude glycerin levels in the diet. *Acta Scientiarum. Animal Sciences*, *36*(2), pp.171-176.

Mertens, D.R., 1973. Application of Mathematical Models to Cell Wall Digestion and Forage Intake in Ruminants (Cornell University Ph. D. Thesis). *Ann Arbor, Michigan: University Microfilms*.

Mertens, D.R., 1987. Predicting Intake and Digestibility Using Mathematical Models of Ruminal Function. *Journal of animal science*, *64*(5), pp.1548-1558.

Mertens, D.R., 1993. Kinetics of cell wall digestion and passage in ruminants. *Forage cell wall structure and digestibility*, (foragecellwalls), pp.535-570.

Mertens, D.R., 1994. Regulation of forage intake. *Forage quality, evaluation, and utilization*, (foragequalityev), pp.450-493.

Mesfin, R. and Ledin, I., 2004. Comparison of feeding urea-treated teff and barley straw based diets with hay based diet to crossbred dairy cows on feed intake, milk yield, milk composition and economic benefits. *Livestock Research for Rural Development*, *16*, p.104.

Metz, J.H.M., 1975. *Time patterns of feeding and rumination in domestic cattle* (Doctoral dissertation, Veenman).

Metz, J.H.M., 1985. The reaction of cows to a short-term deprivation of lying. *Applied Animal Behaviour Science*, *13*(4), pp.301-307.

Minervino, A.H.H., Kaminishikawahara, C.M., Soares, F.B., Araújo, C.A.S.C., Reis, L.F., Rodrigues, F.A.M.L., Vechiato, T.A.F., Ferreira, R.N.F., Barrêto-Júnior, R.A., Mori, C.S. and Ortolani, E.L., 2014. Behaviour of confined sheep fed with different concentrate sources. *Arquivo Brasileiro de Medicina Veterinária e Zootecnia*, *66*(4), pp.1163-1170.

Miron, J., Solomon, R., Bruckental, I. and Ben-Ghedalia, D., 1996. Effect of changing the proportion, wheat: sorghum in dairy cow rations on carbohydrate digestibility and NAN flow to the intestine. *Animal feed science and technology*, *57*(1-2), pp.75-86.

Moghaddam, P.R. and Wilman, D., 1998. Cell wall thickness and cell dimensions in plant parts of eight forage species. *The journal of agricultural science*, *131*(1), pp.59-67.

Moore, J.A., Poore, M.H. and Swingle, R.S., 1990. Influence of roughage source on kinetics of digestion and passage, and on calculated extents of ruminal digestion in beef steers fed 65% concentrate diets. *Journal of animal science*, *68*(10), pp.3412-3420.

Moyo, M., 2016. Effects of diet quality and time lapse after meal termination on rumen load, rate of passage and feeding behaviour (Masters Dissertation, University of KwaZulu-Natal, Pietermaritzburg).

Moyo, M., Adebayo, R.A. and Nsahlai, I.V., 2018. Effects of roughage quality, period of day and time lapse after meal termination on rumen digesta load in goats and sheep. *Asian-Australasian journal of animal sciences*.

Moyo, M., Gueguim Kana, E.B. and Nsahlai, I.V., 2017. Modelling of digesta passage rates in grazing and browsing domestic and wild ruminant herbivores. *South African Journal of Animal Science*, *47*(3), pp.362-377.

Munro, J.M.M. & R.J.K. Walters, 1986. The feeding value of grass. In: Grazing (ed. J. Frame). Britsh Grassland Society, Occasional Symposium No. 19: 65–78.

National Research Council, 2001. *Nutrient requirements of dairy cattle: 2001*. National Academies Press.

Ndlovu, L.R. and Buchanan-Smith, J.G., 1985. Utilization of poor quality roughages by sheep: effects of alfalfa supplementation on ruminal parameters, fibre digestion and rate of passage from the rumen. *Canadian Journal of Animal Science*, *65*(3), pp.693-703.

Newman, J.A., Penning, P.D., Parsons, A.J., Harvey, A. and Orr, R.J., 1994. Fasting affects intake behaviour and diet preference of grazing sheep. *Animal Behaviour*, *47*(1), pp.185-193.

Nocek, J.E. and Kohn, R.A., 1987. Initial particle form and size on change in functional specific gravity of alfalfa and timothy hay. *Journal of Dairy Science*, *70*(9), pp.1850-1863.

Nocek, J.E. and Tamminga, S., 1991. Site of digestion of starch in the gastrointestinal tract of dairy cows and its effect on milk yield and composition. *Journal of Dairy Science*, *74*(10), pp.3598-3629.

Nsahlai, I.V. and Apaloo, J., 2007. On the suitability of Illius and Gordon\'s model for simulating the intake and digestibility of roughage diets by ruminants. *South African Journal of Animal Science*, *37*(4), pp.275-289.

Nsahlai, I.V., 1991. *The effect of quantity and quality of dietary nitrogen straw utilization by steers* (Doctoral dissertation, University of Reading).

Nsahlai, I.V., Umunna, N.N. and Bonsi, M.L.K., 1998. The utilization of teff (Eragrotis tef) straw by sheep fed supplementary forage legumes with or without either crushed maize grain or wheat bran. *Small Ruminant Research*, *29*(3), pp.303-315.

Nsahlai, I.V., Umunna, N.N. and Osuji, P.O., 1996. An empirical mathematical model for predicting voluntary intake of forage-legume-supplemented roughages by cattle.

Okine, E.K. and Mathison, G.W., 1991. Effects of feed intake on particle distribution, passage of digesta, and extent of digestion in the gastrointestinal tract of cattle. *Journal of animal science*, *69*(8), pp.3435-3445.

Okine, E.K., Mathison, G.W., Kaske, M., Kennelly, J.J. and Christopherson, R.J., 1998. Current understanding of the role of the reticulum and reticulo-omasal orifice in the control of digesta passage from the ruminoreticulum of sheep and cattle. *Canadian journal of animal science*, *78*(1), pp.15-21.

Orr, R.J., Penning, P.D., Harvey, A. and Champion, R.A., 1997. Diurnal patterns of intake rate by sheep grazing monocultures of ryegrass or white clover. *Applied Animal Behaviour Science*, *52*(1-2), pp.65-77.

Orskov, E.R., Hovell, F.D.B. and Mould, F., 1980. The use of the nylon bag technique for the evaluation of feedstuffs. *Tropical Animal Production*, *5*(3), pp.195-213.

Ortiz-Rubio, M.A., Ørskov, E.R., Milne, J. and Galina, H.M.A., 2007. Effect of different sources of nitrogen on in situ degradability and feed intake of Zebu cattle fed sugarcane tops (Saccharum officinarum). *Animal Feed Science and Technology*, *139*(3-4), pp.143-158.

Osuji, P.O., Nsahlai, I.V. and Khalili, H., 1993. *Feed evaluation* (No. 5). ILRI (aka ILCA and ILRAD).

Owens, F.N. and Goetsch, A.L., 1988. Ruminal fermentation In: D. C. Church (Ed.) The Ruminant Animal. Digestive Physiology and Nutrition. p 145.

Palhano, AL, Carvalho, PCDF, Dittrich, JR, Moraes, AD, Silva, SCD and Monteiro, ALG, 2007. Characteristics of forage intake by Dutch heifers in pastures of Mombasa grass. *Brazilian journal of zootechnics = Brazilian journal of animal science. Viçosa, MG. Vol. 36, n. 4 Suppl. (Jul./August 2007), p. 1014-1021* .

Parra, R., 1978. Comparison of foregut and hindgut fermentation in herbivores. *The ecology of arboreal folivores*.

Pearce, G.R., 1965. Rumination in sheep. II. The circadian pattern of rumination. *Crop and Pasture Science*, *16*(4), pp.635-648.

Penning, P., Rook, A.J. and Orr, R.J., 1991. Patterns of ingestive behaviour of sheep continuously stocked on monocultures of ryegrass or white clover. *Applied animal behaviour science*, *31*(3), pp.237-250.

Phillips, C. and Leaver, J.D., 1985. Seasonal and Diurnal Variation in grazing behaviour of dairy cows.

Phillips, C., 2008. *Cattle behaviour and welfare*. John Wiley & Sons.

Phillips, C.J.C. (1993). *Cattle Behaviour*. Farming Press, Ipswich.

Phillips, C.J.C. and Denne, S.K.P.J., 1988. Variation in the grazing behaviour of dairy cows measured by a vibrarecorder and bite count monitor. *Applied Animal Behaviour Science*, *21*(4), pp.329-335.

Playne, M.J., 1978. Differences between cattle and sheep in their digestion and relative intake of a mature tropical grass hay. *Animal Feed Science and Technology*, *3*(1), pp.41-49.

Poncet, C., 1991. The outflow of particles from the reticulo-rumen. *Rumen Microbial Metabolism dan Ruminant Digestion. INRA Editions, Paris*, pp.297-322.

Poppi, D.P., Hendricksen, R.E. and Minson, D.J., 1985. The relative resistance to escape of leaf and stem particles from the rumen of cattle and sheep. *The Journal of Agricultural Science*, *105*(1), pp.9-14.

Poppi, D.P., Minson, D.J. and Ternouth, J.H., 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. 3. The retention time in the rumen of large feed particles. *Australian Journal of Agricultural Research*, *32*(1), pp.123-137.

Poppi, D.P., Norton, B.W., Minson, D.J. and Hendricksen, R.E., 1980. The validity of the critical size theory for particles leaving the rumen. *The Journal of Agricultural Science*, *94*(2), pp.275-280.

Preston, R.L., 1995. Feeding programs to minimize rumen acidosis. In *Proc. 16th Western Nutrition Conference, Saskatoon, Saskatchewan* (pp. 245-266).

Proudfoot, K.L., Weary, D.M. and von Keyserlingk, M.A., 2012. Linking the social environment to illness in farm animals. *Applied Animal Behaviour Science*, *138*(3), pp.203-215.

Provenza, F.D., 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *Journal of animal science*, *74*(8), pp.2010-2020.

Ramanzin, M., Bailoni, L. and Bittante, G., 1994. Solubility, Water-Holding Capacity, and Specific Gravity of Different Concentrates1. *Journal of dairy science*, *77*(3), pp.774-781.

Read, N.W., 1992. Role of gastrointestinal factors in hunger and satiety in man. *Proceedings of the Nutrition Society*, *51*(1), pp.7-11.

Redbo, I. and Nordblad, A., 1997. Stereotypies in heifers are affected by feeding regime. *Applied Animal Behaviour Science*, *53*(3), pp.193-202.

Redbo, I., 1990. Changes in duration and frequency of stereotypies and their adjoining behaviours in heifers, before, during and after the grazing period. *Applied animal behaviour science*, *26*(1-2), pp.57-67.

Redbo, I., 1992. The influence of restraint on the occurrence of oral stereotypies in dairy cows. *Applied Animal Behaviour Science*, *35*(2), pp.115-123.

Redbo, I., 1993. Stereotypies and cortisol secretion in heifers subjected to tethering. *Applied Animal Behaviour Science*, *38*(3-4), pp.213-225.

Redbo, I., Emanuelson, M., Lundberg, K. and Oredsson, N., 1996. Feeding level and oral stereotypies in dairy cows. *Animal Science*, *62*(02), pp.199-206.

Reid, G., Bruce, A.W., McGroarty, J.A., Cheng, K.J. and Costerton, J.W., 1990. Is there a role for lactobacilli in prevention of urogenital and intestinal infections? *Clinical microbiology reviews*, *3*(4), pp.335-344.

Rinne, M., Huhtanen, P. and Jaakkola, S., 2002. Digestive processes of dairy cows fed silages harvested at four stages of grass maturity 1. *Journal of Animal Science*, *80*(7), pp.1986-1998.

Robert, S., Matte, J.J., Farmer, C., Girard, C.L. and Martineau, G.P., 1993. High-fibre diets for sows: effects on stereotypies and adjunctive drinking. *Applied Animal Behaviour Science*, *37*(4), pp.297-309.

Roche, B., Lebarbenchon, C., Gauthier-Clerc, M., Chang, C.M., Thomas, F., Renaud, F., Van Der Werf, S. and Guégan, J.F., 2009. Water-borne transmission drives avian influenza dynamics in wild birds: the case of the 2005–2006 epidemics in the Camargue area. *Infection, Genetics and Evolution*, *9*(5), pp.800-805.

Roche, J.R., Blache, D., Kay, J.K., Miller, D.R., Sheahan, A.J. and Miller, D.W., 2008. Neuroendocrine and physiological regulation of intake with particular reference to domesticated ruminant animals. *Nutrition Research Reviews*, *21*(02), pp.207-234.

Roguet, C., Dumont, B. and Prache, S., 1998. Selection and utilization of forage resources by herbivores: theories and experiments at the site and food station scale. *Productions Animales 4 (11), 273-284 (1998)*.

Rook, A.J. and Huckle, C.A., 1997. Activity bout criteria for grazing dairy cows. *Applied Animal Behaviour Science*, *54*(2), pp.89-96.

Rook, A.J., 2000. Principles of foraging and grazing behaviour. *Grass: its production and utilization. A. Hopkins, ed. Blackwell Science*, p.229.

Ruckebusch, Y., 1970. The electrical activity of the digestive tract of the sheep as an indication of the mechanical events in various regions. *The Journal of physiology*, *210*(4), p.857.

Rushen, J. and Mason, G., 2006. A decade-or-more's progress in understanding stereotypic behaviour. *Stereotypic Animal Behaviours—Fundamentals and Applications to Welfare*, pp.1-17.

Russell, J.B. and Rychlik, J.L., 2001. Factors that alter rumen microbial ecology. *Science*, *292*(5519), pp.1119-1122.

Rust, J.M. and Rust, T., 2013. Climate change and livestock production: A review with emphasis on Africa. *South African Journal of Animal Science*, *43*(3), pp.256-267.

Rutter, S.M., 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. *Applied Animal Behaviour Science*, *97*(1), pp.17-35.

Rutter, S.M., Tainton, V., Champion, R.A. and Le Grice, P., 2002. The effect of a total solar eclipse on the grazing behaviour of dairy cattle. *Applied Animal Behaviour Science*, *79*(4), pp.273-283.

SAS (2011) SAS® 9.3 Software (2nd ed.). SAS Institute Inc., Raleigh, North Carolina, USA.

Sato, S., Nagamine, R. and Kubo, T., 1994. Tongue-playing in tethered Japanese Black cattle: diurnal patterns, analysis of variance and behaviour sequences. *Applied Animal Behaviour Science*, *39*(1), pp.39-47.

Satter, L.D. and Slyter, L.L., 1974. Effect of ammonia concentration on rumen microbial protein production in vitro. *British journal of nutrition*, *32*(2), pp.199-208.

Sauvant, D., Baumont, R. and Faverdin, P., 1996. Development of a mechanistic model of intake and chewing activities of sheep. *Journal of animal science*, *74*(11), pp.2785-2802.

Sauvé, A.K., Huntington, G.B., Whisnant, C.S. and Burns, J.C., 2010. Intake, digestibility, and nitrogen balance of steers fed gamagrass baleage topdressed at two rates of nitrogen and harvested at sunset and sunrise. *Crop science*, *50*(1), pp.427-437.

Scaglia, G., Boland, H.T. and Wyatt, W.E., 2009. Effects of Time of Supplementation on Beef Stocker Calves Grazing Ryegrass. II. Grazing Behavior and Dry Matter Intake1. *The Professional Animal Scientist*, *25*(6), pp.749-756.

Schlecht, E., Fernández-Rivera, S. and Becker, K., 2002. Gastrointestinal passage of different Sahelian roughages fed to cattle, sheep and goats. In *Proceedings of the Society of Nutrition Physiology* (Vol. 11, p. 146).

Schlecht, E., Richter, H., Fernández-Rivera, S. and Becker, K., 2007. Gastrointestinal passage of Sahelian roughages in cattle, sheep and goats, and implications for livestock-mediated nutrient transfers. *Animal feed science and technology*, *137*(1-2), pp.93-114.

Sellers, A.F. and Stevens, C.E., 1966. Motor functions of the ruminant forestomach. *Physiological reviews*, *46*(4), pp.634-661.

Seo, S., Lanzas, C., Tedeschi, L.O., Pell, A.N. and Fox, D.G., 2009. Development of a mechanistic model to represent the dynamics of particle flow out of the rumen and to predict rate of passage of forage particles in dairy cattle. *Journal of dairy science*, *92*(8), pp.3981-4000.

Seo, T., Sato, S., Kosaka, K., Sakamoto, N., Tokumoto, K. and Katoh, K., 1998. Development of tongue-playing in artificially reared calves: effects of offering a dummy-teat, feeding of short cut hay and housing system. *Applied Animal Behaviour Science*, *56*(1), pp.1-12.

Shabi, Z., Murphy, M.R. and Moallem, U., 2005. Within-day feeding behavior of lactating dairy cows measured using a real-time control system. *Journal of dairy science*, *88*(5), pp.1848-1854.

Shahhosseini, Y., 2013. Cow behaviour in AMS.

Sheahan, A.J., Gibbs, S.J. and Roche, J.R., 2013. Timing of supplementation alters grazing behavior and milk production response in dairy cows. *Journal of dairy Science*, *96*(1), pp.477-483.

Sissons, J.W., Thurston, S.M. and Smith, R.H., 1984. Reticular myoelectric activity and turnover of rumen digesta in the growing steer. *Canadian Journal of Animal Science*, *64*(5), pp.70-71.

Sniffen, C.J. and Robinson, P.H., 1987. Microbial growth and flow as influenced by dietary manipulations. *Journal of Dairy Science, 70*(2), pp.425-441.

Sniffen, C.J., Beverly, R.W., Mooney, C.S., Roe, M.B., Skidmore, A.L. and Black, J.R., 1993. Nutrient requirements versus supply in the dairy cow: strategies to account for variability. *Journal of Dairy Science*, *76*(10), pp.3160-3178.

Solaiman, S.G., Shoemaker, C.E., Jones, W.R. and Kerth, C.R., 2006. The effects of high levels of supplemental copper on the serum lipid profile, carcass traits, and carcass composition of goat kids. *Journal of animal science*, *84*(1), pp.171-177.

Sowell, B.F., Branine, M.E., Bowman, J.G., Hubbert, M.E., Sherwood, H.E. and Quimby, W., 1999. Feeding and watering behavior of healthy and morbid steers in a commercial feedlot. *Journal of animal science*, *77*(5), pp.1105-1112.

Spalinger, D.E., Robbins, C.T. and Hanley, T.A., 1993. Adaptive rumen function in elk (Cervus elaphus nelsoni) and mule deer (Odocoileus hemionus hemionus). *Canadian journal of zoology*, *71*(3), pp.601-610.

Stakelum, G., O'Donnovan, M. and Maher, J., 1997. Simplified grazing management for high performances from the cows. In *Technology for profitable farming. National Dairy Conference, Fermoy 20th March, Teagasc* (pp. 33-53).

Stanley, T.A., Cochran, R.C., Vanzant, E.S., Harmon, D.L. and Corah, L.R., 1993. Periparturient changes in intake, ruminal capacity, and digestive characteristics in beef cows consuming alfalfa hay. *Journal of animal science*, *71*(3), pp.788-795.

Stern, M.D., Varga, G.A., Clark, J.H., Firkins, J.L., Huber, J.T. and Palmquist, D.L., 1994. Evaluation of chemical and physical properties of feeds that affect protein metabolism in the Rumen1. *Journal of Dairy Science*, *77*(9), pp.2762-2786.

Stobbs, T.H., 1973. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Australian Journal of Agricultural Research*, *24*(6), pp.809-819.

Sugino, T., Hasegawa, Y., Kurose, Y., Kojima, M., Kangawa, K. and Terashima, Y., 2004. Effects of ghrelin on food intake and neuroendocrine function in sheep. *Animal Reproduction Science*, *82*, pp.183-194.

Sutherland, T.M., 1988. Particle separation in the forestomachs of sheep. *Aspects of digestive physiology in ruminants*.

Tahir, M.N., 2008. *Voluntary feed intake by dairy cattle* (No. 2008: 3).

Taweel, H.Z., Tas, B.M., Dijkstra, J. and Tamminga, S., 2004. Intake regulation and grazing behavior of dairy cows under continuous stocking. *Journal of Dairy Science*, *87*(10), pp.3417-3427.

Tedeschi, L.O., Cannas, A., Solaiman, S.G., Vieira, R.A.M. and Gurung, N.K., 2012. Development and evaluation of empirical equations to predict ruminal fractional passage rate of forages in goats. *The Journal of Agricultural Science*, *150*(1), pp.95-107.

Terry, R.A. and Tilley, J.M.A., 1964. The digestibility of the leaves and stems of perennial ryegrass, cocksfoot, timothy, tall fescue, lucerne and sainfoin, as measured by an in vitro procedure. *Grass and Forage Science*, *19*(4), pp.363-372.

Tesfayohannes, S.T., Nsahlai, I.V. and Bengaly, K., 2013. Effect of urea treatment and concentrate proportions on dry matter degradation of different roughages in the rumen of Jersey cows. *Global J. Sci. Frontier Res.(D)*, *13*(8).

Tharmaraj, J., Wales, W.J., Chapman, D.F. and Egan, A.R., 2003. Defoliation pattern, foraging behaviour and diet selection by lactating dairy cows in response to sward height and herbage allowance of a ryegrass-dominated pasture. *Grass and Forage Science*, *58*(3), pp.225-238.

Thiago, L.D.S., 1988. *Voluntary intake of forages by ruminants: factors related to eating behaviour and rumen fill*.

Thomson, B.C., Cruickshank, G.J., Poppi, D.P. and Sykes, A.R., 1985. Diurnal patterns of rumen fill in grazing sheep. In *Proceedings of the New Zealand Society of Animal Production* (Vol. 45, pp. 117-120).

Thomson, D.J., Beever, D.E., Latham, M.J., Sharpe, M.E. and Terry, R.A., 1978. The effect of inclusion of mineral salts in the diet on dilution rate, the pattern of rumen fermentation and the composition of the rumen microflora. *The Journal of Agricultural Science*, *91*(1), pp.1-7.

Toates, F., 2002. Physiology, motivation and the organization of behaviour. *The ethology of domestic animals: an introductory text. (Ed. P Jensen) pp*, pp.31-50.

Toates, F.M. and Toates, F.M., 1980. *Animal behaviour: A systems approach*. New York: Wiley.

Todini, L., 2007. Thyroid hormones in small ruminants: effects of endogenous, environmental and nutritional factors. *Animal*, *1*(7), pp.997-1008.

Trach, N.X., Mo, M. and Dan, C.X., 2001. Effects of treatment of rice straw with lime and/or urea on responses of growing cattle. *Livestock research for rural development*, *13*(5).

Tripon, I., Stanciu, G., Acatincăi, S., Cziszter, L.T., Gavojdian, D., Bognar, A. and Erina, S., 2008. Study on feeding and rumination behavior in three months of age romanian black and white calves. *Scientific Papers Animal Science and Biotechnologies*, *41*(2), pp.496-499.

Tschuor, A. and Clauss, M., 2008. Investigations on the stratification of forestomach contents in ruminants: an ultrasonographic approach. *European Journal of Wildlife Research*, *54*(4), pp.627-633.

Tsiplakou, E., Hadjigeorgiou, I., Sotirakoglou, K. and Zervas, G., 2011. Differences in mean retention time of sheep and goats under controlled feeding practices. *Small ruminant research*, *95*(1), pp.48-53.

Uden, P. and Van Soest, P.J., 1982. Comparative digestion of timothy (Phleum pratense) fibre by ruminants, equines and rabbits. *British Journal of Nutrition*, *47*(2), pp.267-272.

Udén, P., Colucci, P.E. and Van Soest, P.J., 1980. Investigation of chromium, cerium and cobalt as markers in digesta. Rate of passage studies. *Journal of the Science of Food and Agriculture*, *31*(7), pp.625-632.

Uden, P., Rounsaville, T.R., Wiggans, G.R. and Van Soest, P.J., 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (Phleum pratense) hay. *British Journal of Nutrition*, *48*(2), pp.329-339.

Ulyatt, M. J., Dellow, D. W, John, A., Reid, C. S. W., and Waghron, G. C., 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. In: Proceedings of 6th International Symposium on Ruminant Physiology, Banff (Canada), 10-14 Sep. Prentice-Hall.

Ulyatt, M.J., 1983. Plant fibre and regulation of digestion in the ruminant. *Fibre in human and animal nutrition*, *20*, pp.103-107.

Ulyatt, M.J., Dellow, D.W., John, A., Reid, C.S.W. and Waghorn, G.C., 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. In *Proceedings of 6th International Symposium on Ruminant Physiology, Banff (Canada), 10-14 Sep 1984*. Prentice-Hall.

Uzal, S. and Ugurlu, N., 2010. The dairy cattle behaviors and time budget and barn area usage in freestall housing. *Journal of Animal and Veterinary Advances*, *9*(2), pp.248-254.

Van Soest, P.J., 1975. Physico-chemical aspects of fibre digestion. *Digestion and Metabolism in the Ruminant*, *1*, pp.351-365.

Van Soest, P.J., 1994. Nutritional ecology of the ruminant. Cornell University Press.

Van Weyenberg, S., Sales, J. and Janssens, G.P.J., 2006. Passage rate of digesta through the equine gastrointestinal tract: A review. *Livestock science*, *99*(1), pp.3-12.

Varga, G.A. and Harpster, H.W., 1995. Gut size and rate of passage. In *Intake by Feedlot Cattle Symposium* (Vol. 95, pp. 85-96).

Vibart, R.E., Pacheco, D., Lowe, K. and Barrett, B.A., 2011. Performance, nitrogen utilization, and grazing behaviour from late-lactation dairy cows offered a fresh allocation of a ryegrass-based pasture either in the morning or in the afternoon. In ‘Adding to the knowledge base for the nutrient manager’. In *Adding to the Knowledge Base for the Nutrient Manager* (p. 12). Fertilizer and Lime Research Centre, Massey University, Palmerston North, New Zealand.

Wade, MH, 1991. *Factors affecting the availability of vegetative Lolium perenne to grazing dairy products with special reference to sward characteristics, stocking rate and grazing method.* (Ph.D., Rennes 1).

Waldo, D.R., 1986. Effect of forage quality on intake and forage-concentrate interactions. *Journal of dairy science*, *69*(2), pp.617-631.

Wanapat, M. and Cherdthong, A., 2009. Use of real-time PCR technique in studying rumen cellulolytic bacteria population as affected by level of roughage in swamp buffalo. *Current microbiology*, *58*(4), pp.294-299.

Warren, W.P., Martz, F.A., Asay, K.H., Hilderbrand, E.S., Payne, C.G. and Vogt, J.R., 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchardgrass hay in 18 and 32 C ambient temperatures. *Journal of Animal Science*, *39*(1), pp.93-96.

Wattiaux, M.A., Mertens, D.R. and Satter, L.D., 1992. Kinetics of hydration and effect of liquid uptake on specific gravity of small hay and silage particles. *Journal of animal science*, *70*(11), pp.3597-3606.

Welch, J.G. and Smith, A.M., 1969. Influence of forage quality on rumination time in sheep. *Journal of animal science*, *28*(6), pp.813-818.

Welch, J.G., 1990. Inert plastics as indicators of physiological processes in the gastrointestinal tract of ruminants. *Journal of animal science*, *68*(9), pp.2930-2935.

Weston, R.H. and Hogan, J.P., 1967. The transfer of nitrogen from the blood to the rumen in sheep. *Australian journal of biological sciences*, *20*, pp.967-973.

Weston, R.H., 1982. Animal factors affecting feed intake. In *Nutritional Limits to Animal Production from Pastures: proceedings of an international symposium held at St. Lucia, Queensland, Australia, August 24-28, 1981/edited by JB Hacker*. Farnham Royal, UK: Commonwealth Agricultural Bureaux, 1982.

Weston, R.H., 1985. The regulation of feed intake in herbage-fed ruminants. In *Proceedings of the Nutrition Society of Australia* (Vol. 10, pp. 55-62).

Weston, R.H., 1988. Factors limiting the intake of feed by sheep. 11. The effect of pregnancy and early lactation on the digestion of a medium-quality roughage. *Australian Journal of Agricultural Research*, *39*(4), pp.659-669.

Weston, R.H., 1996. Some aspects of constraint to forage consumption by ruminants. *Australian Journal of Agricultural Research*, *47*(2), pp.175-197.

Westra, R. and Christopherson, R.J., 1976. Effects of cold on digestibility, retention time of digesta, reticulum motility and thyroid hormones in sheep. *Canadian Journal of Animal Science*, *56*(4), pp.699-708.

Wilkins, R.J., 2000. Forages and their role in animal systems. *Forage Evaluation in Ruminant Nutrition, CAB International*, pp.1-14.

Williams, Y.J., Doyle, P.T. and Egan, A.R., 2014. Diurnal variation in rumen fill of dairy cows grazing Persian clover at different pasture allowances. *Animal Production Science*, *54*(9), pp.1388-1393.

Wilson, J.R., 1993. Organization of forage plant tissues. *Forage cell wall structure and digestibility*, (foragecellwalls), pp.1-32.

Wood, J.T., 1977. Leading in purposive discussions: A study of adaptive behavior.

Woods, S.C. and Strubbe, J.H., 1994. The psychobiology of meals. *Psychonomic bulletin & review*, *1*(2), pp.141-155.

Yansari, A.T., Valizadeh, R., Naserian, A., Christensen, D.A., Yu, P. and Shahroodi, F.E., 2004. Effects of alfalfa particle size and specific gravity on chewing activity, digestibility, and performance of Holstein dairy cows. *Journal of dairy science*, *87*(11), pp.3912-3924.

Yansari, T., Hamidi, A., PirMohamadi, R. and Azary, M., 2007. Rumen contents and ruminal digesta particle size distribution in buffalo steers fed three different size of alfalfa. *Italian Journal of Animal Science*, *6*(sup2), pp.429-443.

Young, B.A., 1981. Cold Stress as it Affects Animal Production 1. *Journal of Animal Science*, *52*(1), pp.154-163.

Zinn, R.A., Corona, L. and Ware, R.A., 2004, December. Forage Quality: Impacts on cattle performance and economics. In *Proc. National Alfalfa Symposium* (pp. 13-15).

Ethical clearance

UNIVERSITY OF KWAZULU-NATAL
INYUVESI YAKWAZULU-NATALI

24 October 2016

Mr Siyabonga Thapelo Bhiya (216075544)
School of Agricultural, Earth & Environmental Sciences
Pietermaritzburg Campus

Dear Mr Bhiya,

Protocol reference number: AREC/066/016M
Project title: The effect of roughage quality on rumen fill and passage rate in cattle

Full Approval – Research Application

With regards to your revised application received on 12 October 2016. The documents submitted have been accepted by the Animal Research Ethics Committee and **FULL APPROVAL** for the protocol has been granted.

Any alteration/s to the approved research protocol, i.e Title of Project, Location of the Study, Research Approach and Methods must be reviewed and approved through the amendment/modification prior to its implementation. In case you have further queries, please quote the above reference number.

Please note: Research data should be securely stored in the discipline/department for a period of 5 years.

The ethical clearance certificate is only valid for a period of one year from the date of issue. Renewal for the study must be applied for before 24 October 2017.

I take this opportunity of wishing you everything of the best with your study.

Yours faithfully

....

Prof S Islam, PhD
Chair: Animal Research Ethics Committee

/ms

Cc Supervisor: Professor IV Nsahlai
Cc Academic Leader Research: Professor O Mutanga
Cc Registrar: Mr Simon Mokoena
Cc NSPCA: Ms Jessica Light
Cc Ukulinga Research Farm – Ms Alec Botha

Animal Research Ethics Committee (AREC)
Ms Mariette Snyman (Administrator)
Westville Campus, Govan Mbeki Building
Postal Address: Private Bag X54001, Durban 4000
Telephone: +27 (0) 31 260 8350 **Facsimile:** +27 (0) 31 260 4609 **Email:** animalethics@ukzn.ac.za
Website: http://research.ukzn.ac.za/Research-Ethics/Animal-Ethics.aspx

1910 - 2010
100 YEARS OF ACADEMIC EXCELLENCE

Founding Campuses: Edgewood, Howard College, Medical School, Pietermaritzburg, Westville