Effects of diet quality and time lapse after meal termination on rumen load, rate of passage and feeding behaviour

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Dedication

This *Thesis* is dedicated to the entire Majola-Moyo clan, to my parents Julius and Thandiwe, to my aunt Ntombikayise, to my brother Sikhumbuzo and sister Bokani, to my late grandparents, and lastly to my future wife and kids.

Acknowledgements

List of Abbreviations

a	rapidly degradable water soluble fraction
AD	apparent degradability
ADF	acid detergent fibre
ADW	Animal Diversity Web
AFRC	Agricultural and Food Research Council (United Kingdom)
ANN	artificial neural networks
APL	animal production level
AWF	African Wildlife Foundation
b	slowly degradable portion of the insoluble fraction
BM	body mass
BMC	body mass change
C	caecum
c or k_d	rate of degradation of the "b" fraction
CF	crude fat
CL	compartment length
Co-EDTA	cobalt ethylenediaminetetraacetic acid
Comp.	compartment
CP	crude protein
CPD	crude protein digestibility
DA	dry abomasum
DC	dry colon
DEB	duration of eating bouts
DL or DayL	days in lactation
DLI	dry large intestine
DM	dry matter
DMD	dry matter digestibility
DMI	dry matter intake
DO	dry omasum
DP or DayP	days pregnant
DR	dry rumen
DRB	duration of ruminating bouts
DSI	dry small intestine
FAO	Food and Agriculture Organisation of the United Nations
FB	feeding behaviour
FM	fish meal
FPR	fractional passage rate
F-Typ	feeding type
GH	grass hay

GIT	gastrointestinal tract
Graz	grazing
Gr-In	grazing or indoors
HEM	hemicellulose
HG	hindgut
IRgbout	intake rate in grams per feeding bout
IRgmin	intake rate in grams per minute
IRQ	improved roughage quality
k_l	rate of passage of liquid
k_p	rate of passage of solid
L	time lag
LH	lucerne hay
LI	large intestines
LP	lespedeza
MBM	mature body mass
MRT	mean retention time
MRT_R	mean retention time in the reticulo-rumen
MSD	maize stover at dry stage
MSM	maize stover at milk stage
NDF	neutral detergent fibre
NDFI	neutral detergent fibre intake
NE	net energies
NEB	number of eating bouts
NE_c	net energies for conception
NE_f	net energies for fattening
NE_l	net energies for lactation
NE_m	net energies for maintenance
NE_p	net energies for production
NRB	number of ruminating bouts
Obs_L	observed liquid passage rate
OMD	organic matter digestibility
PA or PhyA	physiological age
PD	potential degradability
$PD\frac{1}{2}life$	potential degradability at half-life
Pre_L	predicted liquid passage rate
PRQ	poor roughage quality
PS	particle size
REDIM	Repository of Experimental Data and Intelligent Models
Restr.	restricted
RF	rumen fill

RR or R	reticulorumen
SF	selectivity factor
SFM	sunflower meal
SI	small intestines
SIRQ	semi improved roughage quality
$t\frac{1}{2}$ life	time at half-life
TNE_R	total net energy requirement
TSC	time spent chewing
TSE	time spent eating
TSIL	time spent idling whilst lying
TSIS	time spent idling whilst standing
TSR	time spent ruminating
TTH	*Themeda triandra* hay
WA	wet abomasum
WC	wet colon
WLI	wet large intestine
WO	wet omasum
WR	wet rumen
WSI	wet small intestines

Thesis output

Papers under-review

1. M. Moyo, R. A. Adebayo and I. V. Nsahlai. Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of Merino and Damara sheep, and Nguni goats under subtropical conditions. Animal Production Science (Manuscript ID: AN 16615).

2. M. Moyo, E. B. Gueguim Kana and I. V. Nsahlai. Modelling of digesta passage rates in grazing and browsing domestic and wild ruminant herbivores. South African Journal of Animal Science.

Symposium abstracts and poster presentations

1. M. Moyo, E. B. Gueguim Kana and I. V. Nsahlai. Modelling of digesta passage rates in grazing and browsing domestic and wild ruminant herbivores. College of Agriculture, Engineering and Science Postgraduate Research Symposium. 29th of November 2016. University of KwaZulu-Natal, Howard College campus. pp 89.

2. M. Moyo, R. A. Adebayo and I. V. Nsahlai. Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of Merino and Damara sheep, and Nguni goats under subtropical conditions. College of Agriculture, Engineering and Science Postgraduate Research Symposium. 29th of November 2016. University of KwaZulu-Natal, Howard College campus. pp 88.

To be submitted

1. M. Moyo and I. V. Nsahlai. Factors affecting rumen digesta load and rates of passage of liquid and solid through the rumen of grazing and browsing ruminant herbivores: a review.

2. M. Moyo and I. V. Nsahlai. Digesta passage rates and rumen digesta load at various times post-feeding termination in sheep fed on two different roughage qualities.

General Abstract

Ruminant utilisation of poor quality feeds is governed by rates of degradation and passage through the rumen. Firstly, the passage rate of feed material determines the degree of bypass nutrients and the efficiency of synthesis of microbial protein in the rumen, making modelling of passage rate important. Secondly, diurnal feeding behaviours are not normally used in predicting feed intake although their influences are vital in understanding the dynamics of intake. Lastly, critical to rumen kinetics studies lies in understanding the dynamics of rumen fill levels post meal termination. The objectives of the study were to: (1) develop digesta passage rate prediction models for climatically, nutritionally and genetically diverse classes of ruminant herbivores; (2) ascertain the effects of diet quality on diurnal feeding behaviour in sheep and goats; and (3) determine the influence of diet quality on passage rates and, the extent and trend of solid digesta disappearance after meal termination. Artificial neural networks were used to develop prediction models for liquid and solid passage rates. Studies that reported fractional passage rates, class and body mass of ruminants were included in the dataset. Factors that affect rates of passage included animal and feed factors. The database was composed of observations of domestic and wild ruminants of variable body mass (1.5 to 1238 kg) from 74 studies and 17 ruminant species from different climatic regions. Observations were randomly divided into 2 data subsets: 75% for training and 25% for validation. Developed models accounted for 66 and 82% of the variation in prediction of passage rates for solid and liquid, respectively. On validation using an independent dataset, these models attained 42 and 64% of precision in predicting passage rates for solid and liquid, respectively. The effects of tropical roughage and diet quality on dry matter intake, duration and number of daytime and night time eating bouts, idling sessions and ruminating activities in small ruminants were investigated. Roughage quality was improved by urea treatment of veld hay, while diet quality was improved by supplementing with lucerne hay, sunflower meal, lespedeza, fish meal and sunflower meal. Day-time (0600-1800 h) and night time (1800-0600 h) feeding behaviour activities of sheep and goats were recorded. Generally, roughage and diet quality, and time of the day had significant effects on time spent ruminating and eating. Intake rates (g/bout and g/min) were not affected by diet and roughage qualities. Generally, goats and sheep fed on roughage alone ruminate at night and eat more during the day but those fed roughage and supplemented with lucerne hay spent more time ruminating than eating. Time spent eating and ruminating had positive correlations to feed intake. Intake rates (g/min and g/bout) had strong positive correlations to intake, which were significant. Improvement of roughage quality increased solid

passage rate but did not affect liquid digesta passage rates from the rumen. Roughage quality had no effects on wet and dry digesta load in the foregut and hindgut compartments, except on abomasum dry matter load. Time lapse post feeding had no effects on rumen digesta load in the foregut and hindgut compartments, except on the dry and wet digesta load in the omasum. Proportions of digesta load in the rumen decreased linearly up to 24 h post feeding termination regardless of roughage quality. There is a possibility that this trend shapes into an exponential "decay" curve after 24 h post feeding termination. In conclusion, this study developed more précised prediction models for solid and liquid passage rates for ruminants fed on a variety of diets and/or feeds from different climatic regions. Roughage intake was limited as a result of increased rumination time of low quality roughages. There is a potential of using feeding behaviour to predict passage rates and predict intake. Digesta passage rate prediction models should include all animals, including those in a negative energy balance. The rate of clearance of digesta after meal termination was significantly greater for sheep fed on the improved roughage quality (IRQ) compared to the poor roughage quality (PRQ).

Additional keywords: Diurnal feeding behaviour, passage rate, prediction model, rumen load, ruminant.

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General Introduction

1.1 Background

Sub-Saharan Africa is covered by vast areas of grassland that lie between the tropics. Approximately 70% of resource-limited farmers in sub-Saharan Africa are situated in marginal agro-ecological zones that do not favour crop production (Lebbie and Ramsay 1999; Frydman and Kurauchi 2009). Hence, they rely on livestock production for their living. The major ruminant livestock kept by these farmers are cattle, sheep and goats (Olivier *et al*. 2002). Smaller ruminant species are becoming increasingly important because they can survive harsh semi-arid and arid environments (Degen 2007). Livestock are important as a source of protein, wealth, draught power, animal hides, ceremonial rituals, bride price and monetary security (FAO 2005). Natural grasslands are a major and most economical feed source for these ruminants. During the dry season most tropical veld grasses are of low nutritional quality (Coleman *et al*. 2004). Irregular rainfall patterns in the wet season compromise nutrient values of most grassland. Tropical grasses tend to be bulky, high in fibre, low in nitrogen and are poorly degraded in the rumen (Osuji *et al*. 1995). Rumen "fill" as a result of bulkiness and, slow rates of movement and digestion of forage grasses in the gut limits the amounts of feed ruminants need to meet their nutritional needs (Allen 1996). Roughage intake refers to the amount of fibrous plant material that a ruminant is able to naturally consume. Under-nutrition due to low intake of the already poor quality roughage causes low meat and milk yields, high mortality, and high body weight losses of ruminants in most tropical and sub-tropical regions in Africa.

Enhanced productivity is dependent on improving the nutritional status of ruminants through supplementation of poor quality roughages with feeds of high nutritional value (e.g. protein and energy concentrates). Concentrates are generally expensive for resource limited farmers in tropical and sub-tropical Africa. Hence, cost effective usage of these feeds is vital. Improvement of feed digestibility and quality by treating forages with urea may be another cost effective way of supplying crude protein and energy for animal maintenance and growth. Fundamental to cost effective concentrate supplementation for improved productivity of ruminant livestock in the tropics is accurate and precise prediction of roughage intake.

Roughage intake has a significant influence on ruminant livestock productivity. Roughage intake is affected by a number of variables; of particular importance are processes that occur in the rumen. These are rumen fill, degradation and passage rates of digesta. Amounts of digesta

in the rumen (rumen fill levels) at any given time depends on feeding behaviour, how fast digesta passes out of the rumen (passage rate of liquid and solid) and how fast digesta is degraded within the rumen (rate of degradation). Accurate prediction of these variables enables accurate prediction of intake. Accurate prediction of roughage intake would enable farmers to calculate precise quantities of energy and/or protein concentrates to be fed so as to achieve a cost effective desired level of production.

The appropriateness of the Illius and Gordon's (1991) model in prediction of roughage intake in ruminant livestock grazing on poor quality roughages in tropical regions was evaluated (Nsahlai and Apaloo 2007). Nsahlai and Apaloo (2007) showed that the Illius and Gordon's (1991) mathematical model, though structurally adequate, underestimated roughage intake and gut fill levels for grazing ruminants fed on poor quality roughages in the tropics. They concluded that the unsuitability of the model to accurately predict intake was due to calibrations used in estimating passage rates and rumen fill parameters which were largely inaccurate. Similarly, Clauss *et al.* (1998), Clauss and Lechner-Doll (2001) and Behrend *et al.* (2004) showed that the Illius and Gordon's (1991) model overestimated retention time in browsing ruminants for particle sizes less than 2 mm. Firstly, the model of Illius and Gordon (1991), as with other models, estimates rumen fill levels and passage rates as a function of body weight alone, which is erroneously insufficient. Another reason for underestimation of roughage intake of tropical grass in grazing ruminants lies in longer mean retention times of roughages of poor quality in the rumen (Nsahlai and Apaloo 2007). Secondly, most of the data used to develop current passage rate prediction models (Seo *et al.* 2006, 2007, 2009; Krizsan *et al.* 2010) have been collected from ruminant species reared in cold temperate regions. These breeds are usually fed on good quality temperate roughages with access to protein and energy supplements. Such prediction models may be unsuitable for usage in prediction of roughage intake for ruminants reared in tropical and subtropical areas. This is because ruminants in tropical regions graze on rather low quality tropical roughages, with no energy or protein supplementation and are exposed to high temperatures that greatly affect passage rates and intake.

Implicitly, it is important to determine rates of passage, rumen fill levels and rates of degradation in ruminants fed on non-supplemented poor quality tropical grass species. This will enable researchers to incorporate data into development of mathematical models that can be used to predict roughage intake for ruminants that graze on tropical grasslands. A holistic approach that seeks to enable accurate prediction of intake in ruminants irrespective of dietary differences, class of ruminant and climatic regions involves step by step determination and

prediction of all the important factors that affect intake. The first step that paves way to prediction of intake for all classes of ruminants feeding on different diets under variable climatic conditions involves accurate prediction of the rates of solid and liquid passage through the rumen; and feeding behaviour.

1.2 Problem Statement

Firstly, there is no single solid or liquid passage rate prediction model that can be used to predict passage rates for climatically, nutritionally and genetically diverse ruminant herbivores (both wild and domesticated). Secondly, there is limited passage rate, feeding behaviour and rumen fill information from ruminant livestock that graze on low quality tropical grass species in sub-Saharan Africa for use in development of passage rate and intake prediction models. Little is known on the effects of feeding sheep and goats on tropical veld hay of improved quality on diurnal feeding behaviour and rates of digesta passage through the rumen. Few studies have ascertained the effects of diet quality on rumen fill at various times after meal termination. To pave the way for the achievement of a broader objective to predict intake, this study seeks to answer the following research questions:

1. Is it possible to develop a single solid and liquid passage rate prediction model for all classes of ruminants that feed on a wide range of diet qualities in different climatic regions of the world?
2. Does roughage quality affect intake, feeding behaviour, digestibility and passage rates through the rumen of sheep?
3. Does the proportion of rumen digesta load (fractional clearance rate) decrease linearly or in an exponential decay trend with time after meal termination?

1.3 Justification

Prediction of fractional rate of passage is fundamental in the prediction of roughage intake, bypass protein and microbial protein yields. Accurate prediction of roughage intake is useful in determining how much nutrients ruminants get from grazing. This allows determination of the amount of protein and energy concentrate needed for supplementation to achieve desired lean growth and milk production. Technically, enables improvement of ruminant livestock production for resource limited smallholder farming systems throughout tropical Africa, thus improving food security. Knowing approximately how much a ruminant can eat may be used to predict how long a pasture can sustain grazing before it is depleted. Such information may be used to manage pastures in nomadic pastoral systems to avoid over grazing. Rumen kinetics

parameters from the study may also be useful in evaluation of existing passage rate prediction models. Improvement of roughage quality with treatment using urea may be useful in reducing body weight losses during the dry season. This would translate to increased survival of livestock during periods of feed scarcity in communal farming areas, thus improving food security.

1.4 Objectives

The broad objective of this study was to determine how feeding behaviour, rumen fill levels, degradation and digesta passage rates are influenced by improving tropical roughage and diet quality.

The specific objectives of the study were to:

1. Develop prediction models for solid and liquid passage rates through the rumen using Artificial Neural Network (ANN).
2. Ascertain the influence of different diet qualities on dry matter intake, live weight change and feeding behaviour of goats and sheep.
3. Determine how roughage quality influences in-sacco degradability and, solid and liquid passage rates in sheep, and use these empirical measures of passage rate to evaluate the passage rate prediction models developed in this study.
4. Determine the effects of improving roughage quality on in-vivo digestibility and of time lapse after meal termination on rumen fill.

1.5 Hypothesis

The study tested the hypothesis that:

1. It is possible to develop a single passage rate prediction model for diverse ruminant herbivores.
2. Roughage quality has an effect on feed intake, body weight change and diurnal feeding behaviour in goats and sheep.
3. Roughage quality has no effect on particulate and fluid passage rates through the rumen.
4. Rumen fill decreased exponentially with time up to 24 h after meal termination governed by rates of digestion and passage of particles through the rumen [RF=f(k_d; k_p)].

Chapter 2
Review of literature

Abstract

Roughage intake is affected by rumen fill levels and rates of digesta passage through the rumen. Current research work involving modelling of rumen digesta kinetics seek to incorporate various factors that affect rumen fill, and solid and liquid passage rates to develop intake and passage rate prediction models. The aim of this review paper was to discuss factors that affect rates of passage of digesta and rumen digesta load. The paper also sought to identify the major factors that affect digesta passage rates through the rumen. This would necessitate identification of factors critical to inclusion in passage rate prediction models for ruminants. Work done has identified environmental temperature, level of feed intake, body mass, ruminant species, digesta particle size and specific gravity, roughage quality, water intake, animal physiological status and reproductive state as the main factors affecting digesta passage and rumen fill. However, discrepancies on how ambient temperature and particle density (buoyancy) affect the passage rate of digesta in the rumen may cause uncertainty in calibration of temperature and buoyancy in prediction models. The roles of feeding behaviours; times spent eating, ruminating and idling in influencing digesta passage through rumen contractions is still not well understood. The role of animal physiology in influencing digesta passage rate is also critical. Computation of animal production level to account for all the physiological processes that affect passage rate is vital. Failure of mathematical procedures to achieve justifiable outcomes in prediction of rumen load suggests the occurrence of peculiar processes during the period after meal termination. Factors that are eligible for inclusion into passage rate prediction models include; ruminant feeding type, animal characteristics (body weight and mature body weight), feed compositional attributes (DM, NDF, ADF, CP, ash, presence of urea and tannins, and silage/non-silage), degradability parameters (PD, a, b and c), feeding regime (ad-libitum/restricted) and management (grazing/indoors), animal production level (animal physiological status), particle size, potential degradability at half-life (buoyancy), days in pregnancy and/or lactation, and the degree of maturity (physiological age).

Keywords: feeding behaviour, ruminant, rumen fill, rumen contractions, prediction model

2.1 Introduction

Rates of passage of solid digesta and fluid in the rumen play important roles in ruminant nutrition. Fluid passage rates through the rumen are known to influence digestion of soluble food nutrients (Illius and Gordon 1991), amount of short chain fatty acids absorbed in the rumen and that pass out of the rumen (Lopez *et al*. 2003), the amount of by-pass protein of dietary origin (Fox *et al*. 2004) and the amount of microbial protein available to the host as a protein source (Dijkstra *et al*. 2007). Extents to which dietary feed is degraded in the rumen depends on the rates of degradation and passage in the rumen and out of the rumen, respectively (Dhanoa *et al*. 1985). This makes the study and modelling of digesta passage rate relatively very important.

A lot of work has been carried out on rumen digesta passage kinetics, in each of which there are fixed treatment variables that have very little influence on the digesta passage rates being evaluated (Sauvant *et al*. 2008). A collation of controlled and uncontrolled variables such as animal genetic makeup, age, reproductive status, feed quality, feeding behaviour, desire to eat, plane of nutrition and environmental temperatures affect digesta passage rates. These variables vary amongst studies. This leads to differences in passage rate data collected on similar research topics. Results obtained from single passage rate trials are obtained under marginally narrow experimental conditions (St-Pierre 2007). Exploration of the dynamics of how various treatment effects influence digesta passage rates in ruminants across studies is critical in explaining observed passage rates. An understanding of the dynamics of factors that affect passage rates would allow collation and selection of input variables for inclusion into development of passage rate prediction models.

Prediction of passage rates in ruminants is done using mathematical models (Illius and Gordon 1991). Most passage rate prediction models are developed for specific classes of ruminants and climatic regions. Typical examples are models for dairy cattle (Seo *et al*. 2005; 2009), for cattle, sheep and goats (Nsahlai and Apaloo 2007) and for dairy cattle from Europe and the United States of America (Krizsan *et al*. 2010). Usage and application of these mathematical models should be carried out with caution because these models are empirical in nature rendering them as situation specific. Such models may be used to predict passage rates in similar animals, under the same environmental and feed factors in which they were developed. It becomes difficult to use these models to accurately predict passage rates for any ruminant. For example, wild and domesticated ruminant herbivores from various climatic regions of the world. There is need to explore the development of models that can be used to

predict passage rates for a wide range of ruminants in diverse climatic regions. Accurate prediction of passage rates would ultimately lead to prediction of roughage intake with a much greater degree of accuracy and precision.

Ruminants are labelled as major emitters of greenhouse gases through fermentation processes by fibrolytic bacteria in the rumen. Amounts of methane and carbon dioxide produced depend on dietary roughage quality, extent and rate of fibre degradation in the rumen, and passage rate of solid and liquid through the rumen. With the devastating effects of global warming on agriculture as a result of methane emissions, knowledge on the factors affecting rates of passage and extent of fibre degradation is critical. Understanding how various factors affect passage rate would be vital in development of strategies to mitigate effects posed by global warming as a result of methane emissions. Given that low intake of poor roughages and faster passage rates of digesta through the rumen reduces methane emissions, the long-term goal would be to select for ruminant animals that have low intake and faster passage rates. This can be made possible based on suggestions that intake and passage rates are partially under genetic control (Pinares-Patiño *et al*. 2007).

Before any passage rate modelling exercise can be effectively carried out, factors that affect passage rates need to be identified. After identification and collation of these factors, input factors for passage rate model development need to be carefully selected. Preceding these steps is an understanding of how and to what extent each identified factor influences digesta passage rates. The broad aim of this review was to identify factors that affect rumen fill levels and, solid and liquid digesta passage rates. This paper also sought to explain the fundamental mechanisms by which each identified factor possibly affected rates of digesta passage from the rumen. Based on collated findings from different studies, this paper also gives suggestions of the major factors that can be considered as critical input factors for development of passage rate prediction models.

2.2 Dynamics of intake, digesta load and passage kinetics in ruminant herbivores

Ruminants have evolved a digestive system that enables them to feed on roughage based diets (Forbes 1995). Evolutionary adaptation has allowed ruminants to develop strategies to utilise these poor quality roughages by developing a rumen where microbial fermentation of feed occurs. However, ruminants are not efficient in utilising poor quality high roughage diets (Faichney 1993) because high fibre diets reduce rates of passage of digesta through the rumen. Inefficiencies are based on the need for extended retention times in the rumen for effective microbial fermentation to take place. Although ruminants possess a fairly large gut to

accommodate high intakes of forage based diets to meet nutritional demands for maintenance and growth, in most cases they fail to consume enough feed to meet these requirements (Forbes 1995). One major reason for this is encapsulated in the concept of "rumen fill" which limits roughage intake in ruminants (Baumont *et al*. 2000). Rumen fill and capacity control roughage intake through coordination with stretch and mechanoreceptors on the rumen wall (Leek 1977; Izumi *et al*. 2004). This has led to assumptions that ruminants stop eating when maximal gut capacity is reached (Johnson and Combs 1991; Allen 1996). Ruminants eat to meet their requirements for energy, unless constrained not to consume more feed as a result of bulkiness of feed or rumen fill (Emmans and Kyriazakis 2001), suggesting that in the absence of constrains, ruminants achieve just a set level of fatness. This theory is not supported by other authors. Lirette and Milligan (1989) were convinced that the major factor that regulates roughage intake is clearance of rumen digesta, which occurs as a result of roughage degradation and passage out of the rumen. Illius and Gordon (1991) and Sauvant *et al*. (1996) concluded that the most important factor that affects roughage intake is rumen fill, after which rumen digesta load empties at rates determined by passage and degradation.

The rumen is the largest foregut compartment in adult ruminants where digestion of almost the entire feed occurs (McDonald *et al*. 2010). By virtue that ruminants mainly feed on low quality roughage and degrade it in the rumen, processes that occur in this compartment affect the nutrient supply for the host animal. The extent and site of feed digestion determines the amount and balance of nutrient supply to the ruminant. Digesta in the rumen is in liquid or solid phase (Faichney 1993), with both phases occurring together. This makes the rates of passage of these two phases important. Ruminal fluid content accounts for approximately 80-90% of the total content in the rumen with the other remainder being solid material (Fuller *et al*. 2004). Fluid in the rumen is derived from moisture in the feed, saliva and water intake (Froetschel *et al*. 1987), with saliva and water intake being major contributing sources (Fuller *et al*. 2004). Bacteria and insoluble solid feed particles form a fluid suspension in the rumen together with soluble nutrients such as short chain fatty acids, organic and inorganic solutes originating from dietary and/or endogenous sources (Fuller *et al*. 2004). Hence, the quantity of fluid flowing per unit time through the rumen is important in determining the quantity and quality of nutrients available for assimilation in the lower gut of the host animal (Robinson *et al*. 1987). This makes the study of the rate of fluid flow through the rumen important in ruminant nutrition.

Rumen fluid acts as the main transport medium for solid particles out of the rumen (Poncet 1991). Most studies neglect the role of rates of passage of rumen liquid in influencing

particulate passage rates. In other words, rapid clearance of fluid from the rumen is accompanied by rapid clearance of particulate matter, and vice versa. Passage rate of particulate matter through the rumen is dependent on how much material is passed out using liquid digesta at each rumen contraction (Ulyatt *et al*. 1986). Research focussing on how fluid passage rates influences and/or interacts with particulate passage rates would have a positive impact in improving prediction of solid passage and roughage intake.

Typically, rates of liquid passage through the rumen range from 0.05-0.2 per hour and 0.012-0.030 per hour for solids (McDonald *et al*. 2010). Fluid passage rate is greater than that of solids due to selective retention of solid particles in fibre mat (Barboza *et al*. 2006). High mean retention times observed for solid matter compared to liquids is an advantageous adaptation in compensation for slower degradation rates of fibrous cell wall material. This allows maximal retention of nutrients and energy from these slowly degradable fractions of fibre (Poncet 1991).

2.3 Rumen fill, gut capacity and its estimation

Gut fill is referred to as rumen fill with respect to ruminants based on the facts that the rumen is the only site in the gastrointestinal tract where distension has an effect of restricting digesta flow to a great extent (Allen 1996). Maximal rumen volume/capacity also termed rumen fill refers to the maximum amount of digesta in the reticulorumen (Fuller *et al*. 2004). Maximal rumen load for dry matter is determined by allometric procedures as a function of body weight (Illius and Gordon 1991; Nsahlai and Apaloo 2007). However, a ruminant's fill capacity also depends on the volume of digesta that causes rumen distension, and on rate of flow of digesta from and rates of degradation of digesta in the rumen (Forbes 1995; Allen 1996). As a result, criticism on determination of rumen fill based on body weight alone have been raised giving better models for rumen load based on body weight, mature body weight and dietary crude protein (Nsahlai and Apaloo 2007). This fill capacity may also be determined practically by manually emptying the rumen at a time when full gut capacity is reached, and weighing out digesta at that time (Fuller *et al*. 2004). Rumen fill varies greatly with body weight and feeding habit. Rumen fill is approximated to be about 9% and 13% of body weight for browsers and grazers, respectively (Fuller *et al*. 2004). This variation may be attributed to differences in digesta passage rates between browsing and grazing ruminants. A relationship that develops between rumen capacity, degradation and digesta passage rate may be visualised. When rumen capacity is large, an animal is permitted to have high feed intakes because presence of ample

space allows increased intake of bulky feed, and/or prolonged retention time in the rumen that allows effective fibre degradation in the rumen.

Based on rates of passage and digestion, estimation of rumen capacity using mathematical procedures gives variable but useable results. Based on the rate of digestion and passage, estimated rumen pool size at the point of meal termination gave values which were even twice as large when compared to average observed values obtained from literature (Nsahlai unpublished data). This makes validation of calculated and/or estimated values for rumen capacity using more direct measures such as rumen evacuations critical (Bruining *et al*. 1998). Besides estimation of rumen capacity, rumen evacuations may be utilised for estimation of mean retention time of digesta, especially for indigestible neutral detergent fibre. An advantage of using such a procedure to obtain data on digesta kinetics is that a probable distribution in retention times between escapable and non-escapable rumen digesta is accounted for (Bayat *et al*. 2010). Several assumptions are considered when deriving data from rumen evacuations. For example, assumptions that steady-state conditions prevail at the time of evacuation (Bayat *et al*. 2010) and that during evacuations rumen function is not affected, are accepted. The former assumption does not hold for meal fed ruminants (Bayat *et al*. 2010). To accommodate data from meal fed animals, evacuation times should be chosen and staggered for estimation of average rumen pool size (Bayat *et al*. 2010). Besides these advantages, rumen evacuation techniques have a number of setbacks associated with its application. These include inability of evacuations to account for selective retention of particulate matter when used to determine rates of passage for solid material (Stensig *et al*. 1998). Estimated parameters on passage rates represent passage of entire dietary fractions. It is impossible to relate individual feeds to each fraction where diets with more than one fibre source are fed (Stensig *et al*. 1998). This makes the technique not suitable for mixed diets. Failure of mathematical procedures to achieve tenable outcomes suggests that something uncertain takes place during the period after meal termination before evacuation.

Carrying out rumen evacuations to determine maximal rumen digesta load is not an easy task. It is assumed that the only or best way to know when an animal has reached its maximal gut capacity is when it stops or terminates feeding (Balch and Campling 1962). This theory is supported by Boudon *et al*. (2009) where termination of short-term feed intake was attributed to signalling from the rumen wall as a result of rumen fill. Taweel *et al*. (2004) and Williams *et al*. (2014) reported scenarios whereby maximal rumen fill was greater after termination of late afternoon feeding bouts just around sunset than bouts from other parts of the day. According to these results, measuring maximal rumen fill after termination of morning

feeding maybe misleading. However, Baumont *et al*. (1989) reported rumen fill to reach its first maximum after the main morning meals, with a daily maximal rumen fill being reached after the evening meal. Similar results were obtained by Thomson *et al*. (1985) where maximal rumen fill was observed after termination of first morning meal and late evening meal at 0900 h and 2000 h, respectively, in grazing sheep. Assuming that at meal termination ruminants would have reached maximal rumen capacity is misleading as well. This assumption is supported by Chilibroste *et al*. (1998) and Taweel *et al*. (2004) who reported findings where maximal rumen capacity had not been reached when grazing dairy cows terminated feeding bouts. Greenhalgh and Reid (1971) reported similar results where sheep fed on hay and straw terminated feed intake way before maximal gut capacity was reached. These and other experimental results therefore suggest the existence of different sets of rumen fill levels which are time dependent, either before or after feeding bouts. These fill levels may be a function of the rate of emptying of rumen digesta after eating has stopped. At any given time, rumen fill levels are a function of rates of feed intake, rates of digestion and particle breakdown, and rates of outflow (Williams *et al*. 2014). As such, rumen fill levels or values are dynamic and thus should not be regarded as constants and times in which rumen capacity is measured should be taken into account as well.

2.4 Factors that affect rumen fill levels and rates of passage through the rumen

2.4.1 Animal species and feeding types

Ruminant livestock have different feeding habits (Clauss and Lechner-Doll 2001) with cattle, buffalo, and sheep classified as grazers, and goats as browsers or intermediate feeders (Hofmann 1989). Differences in type of diets and processes associated with feeding behaviour between these classes of animals may have an effect on rates of passage of liquid and solid phases in the rumen (Lechner *et al*. 2009) and their rumen fill.

Abdullah *et al*. (1991) showed that cattle had a higher liquid passage rate than buffaloes, although both species are predominantly grazers. However, Bartocci *et al*. (1997) got contradictory results to those of Abdullah *et al*. (1991) because buffalo had higher fluid passage rates than cattle. Rumen outflow rate may be calculated as a product of the dilution rate (k_1) and the rumen volume (Froetschel *et al*. 1987). According to Bartocci *et al*. (1997) rumen volume had an effect on the outflow rate of liquid through the rumen. Grazers with a large rumen volume have higher fractional rates of passage. Hence, Bartocci *et al*. (1997) attributed differences in passage rates between buffalo and cattle to rumen volume, and in this case the

volume of the rumen was greater in buffalo than in cattle. This sharply contrasted Abdullah *et al*. (1991) showing a much greater rumen fluid volume in cattle than buffaloes, hence, ruminal fluid volume may have a profound effect on fractional rate of liquid passage in the rumen.

Table 2.1 Effect of ruminant species and feeding type on rates of solid and fluid passage through the rumen

Phase	Parameter	Buffalo	Cattle	Sheep	Reference
liquid	Rumen outflow rate (l/h)	4.34	3.77	0.62	Bartocci *et al*. (1997)
liquid	Fluid outflow rate (l/h)	1.06	1.55	-	Abdullah *et al*. (1991)
liquid	Rumen fill (l)	65.80	59.10	9.20	Bartocci *et al*. (1997)
liquid	Rumen fluid volume (l)	25.80	27.00	-	Abdullah *et al*. (1991)
liquid	Dilution rate (%/h)	2.07	5.43	-	Abdullah *et al*. (1991)
liquid	MRT of fluid (h)	36.90	18.50	-	Abdullah *et al*. (1991)
solid	k_1 (%/h)	2.46	2.99	2.84	Bartocci *et al*. (1997)
solid	MRT (h)	57.73	64.55	58.42	Bartocci *et al*. (1997)

MRT: mean retention time; k_1: fractional passage rate

Sheep had higher fractional passage rate of solid in the rumen than cattle (Table 2.1). Lechner-Doll *et al*. (1991) added that selective retention of particles is more pronounced in cattle than in sheep, which may lead to an assumption that passage rate of large particles is greater in sheep than in cattle. Outflow rates of fine solid material is normally estimated by allometric procedures as an inverse function of body weight, which infers erroneously that the rate of passage in smaller ruminants is always greater than that in larger ruminants (Nsahlai and Apaloo 2007). Parra (1978) showed higher passage rates for smaller herbivores than larger herbivores with diet quality held constant. Differences between cattle and sheep with respect to solid retention times depend on chewing activities of these species. Average chewing rates are higher in sheep (80-100 chews per minute) than in cattle (40-60 chews per minute), suggesting that particle size reduction is twice as efficient in sheep as in cattle. Consequently, cattle have developed pronounced selective retention mechanisms for large particles in the floating fibre mat found in the dorsal rumen to improve particle size reduction and perhaps nutrient extraction, hence, retain particles for longer periods compared to sheep (Poppi *et al*. 1981; Ulyatt *et al*. 1986).

Oshita *et al*. (2008) reported differences in passage rates and rumen fill levels amongst cattle as a result of different grazing strategies. Rumen fluid dilution rates were higher for rotational grazed cattle (12.2%/h) compared to cattle fed pasture in confinement (9.9%/h). Similarly, rumen volume was lower for rotationally grazed cattle (79.9 litres) compared to

cattle fed in confinement (110 litres). Williams *et al*. (2014) showed no variations in rumen pool sizes with pasture allowance and time of day. Lack of differences in rumen fill levels with increasing pasture allowance is due to great variations in outflow rates.

Great variation in passage rates between animals of the same class of ruminants may occur, as a result of differences in feeding habits. Although very little or no evidence for this phenomena have been documented, it is highly likely to occur. Dorper sheep are less selective of feed, consumed more shrubs and bushes than Merino sheep during grazing in the Noorsveld Karoo, South Africa (Du Toit 1998). Dorpers would be expected to have slightly faster passage rates than Merinos because they consume more browse. Hence, it would be expected that Dorpers spend more time re-chewing twigs than Merinos resulting in more intense rumen contractions that forced digesta out of the rumen quickly. It can be concluded that passage rate in ruminants is affected by interactions between diet, ruminant species and their climatic environment.

Molina-Alcaide *et al*. (2000) observed no differences in particle passage rates in goats (a browser/intermediate feeder) and sheep (a grazer) fed on various diets with average rates of 0.030 and 0.025 per hour, respectively. However, Clauss *et al*. (2005) suggested that smaller browsing species had much greater solid and fluid passage rates through the rumen than grazers of a much similar size. On the contrary, a much different trend exists in larger individuals of each feeding habit. Larger grazers tend to show higher solid and fluid passage rates through the rumen than browsers of similar size (Clauss *et al*. 2005; Lechner *et al*. 2010). Processes that occur in the rumen when different diets are fed coupled with the anatomy of the fore stomach associated with each ruminant feeding type are implicated in these differences. Fluid and solid passage out of the rumen occurs through an opening between the reticulorumen and the omasum called the reticulo-omasal orifice (Kennedy and Murphy 1988). Positioning and size of the reticulo-omasal orifice may shed insight on the flow of liquid and solid digesta from the rumen. Hofmann (1989) showed that the size of the reticulo-omasal orifice was greater in browsers than in grazers. It may be hypothesized that due to the larger reticulo-omasal orifice in browsers a much greater volume of solid and fluid passes through the rumen per unit time than in grazers. This may cause browsers to have higher fluid passage rates than grazers in smaller animals (Kennedy and Murphy 1988).

With respect to the larger groups of animals, grazers possess larger omasum than browsers (Hofmann 1989). One of the functions of the omasum is to absorb water (Clauss *et al*. 2006) thus it may be logical to assume that there is a much greater water pulling effect (cohesion and capillary movement) of the grazers larger omasum than that of browsers. This

could result in higher passage rates of fluids out of the rumen of grazers. Due to a greater receptive space of the omasum, the pressure difference between the rumen and omasum (Kennedy and Murphy 1988) is larger in grazers than in browsers. Hence, greater rates of passage of fluid observed in grazers may be due to a larger pressure difference. This may not apply to small grazing and browsing animals. Hence, a gap in knowledge on the relative sizes of the omasum in smaller grazers and browsers exists.

Indirect evidence suggests that browsing ruminants have lower mean retention times for liquid and solid digesta in the rumen compare to grazers. These include post ruminal absence of glucose transport mechanisms (GLUT transporters) in grazers which are present in browsers (Rowel *et al*. 1996; 1999; Clauss and Lechner-Doll 2001), deposition of large quantities of polyunsaturated fatty acids in browser carcasses compared to grazers (Meyer *et al*. 1998; Clauss and Lechner-Doll 2001), lower efficiency of fermentation in browsers than grazers (Van Wieren 1996; Clauss and Lechner-Doll 2001), and presence of large amounts of particles that are greater than 1 mm in faecal samples from browsers compared to grazers (Hofmann 1989; Clauss *et al*. 1998; Nygren *et al*. 2001; Clauss *et al*. 2002).

Differences in viscosity of rumen fluid and saliva between grazers and browsers exist (Hofmann *et al*. 2008). Browsers have more viscous rumen fluid (Lechner *et al*. 2010) and saliva (Hofmann 1989) than grazers. The thicker and stickier the fluid digesta may have an effect of reduced movement of the fluid through the rumen due to increased attachment of water molecules to feed particles. Hence, fluid is less likely to escape from the rumen thus resulting in reduced fractional passage rate of fluid in the rumen of browsing animals. However, Silanikove *et al*. (2001) obtained conflicting results to Lechner *et al*. (2010) where polyphenolic compounds increased the rate of fluid passage through the rumen. Polyphenolic compounds cause fluid digesta to be thick and sticky as a result of more viscous saliva production, which is a case in browsers (Hofmann *et al*. 2008). Hence, viscosity of rumen fluid increases due to the presence of polyphenolic compounds. The expected outcome is decreased fluid outflow rate. Contrary to that, increased viscosity due to tannins may increase the rate of passage of fluid. Fluid from the interstitial spaces may be drawn into the rumen in an attempt to wash off these polyphenolic compounds (Silanikove *et al*. 2001) as a physiological response by the animal against polyphenolic compounds. This occurrence may then result to increased rates of fluid passage through the rumen.

Due to observed differences in passage rates amongst ruminant species, possible differences in rumen fill may be expected given that the passage rate is related to the amount of digesta in the rumen at any given time. Significant differences in rumen fill among buffalo,

cattle and sheep were observed by Bartocci *et al*. (1997) as shown in Table 2.1. However, Abdullah *et al*. (1991) observed no differences in rumen fill between buffalo and cattle of a similar size. Molina-Alcaide *et al*. (2000) showed that rumen fill and amount of rumen contents is larger for goats compared to sheep. It was concluded that goats possessed a unique characteristic of being able to maintain larger rumen fill levels without noticeable rumen distension than sheep when fed medium quality diets. These results were not expected taking into account observations by Clauss *et al*. (2005) showing that smaller browsing species had much greater fluid and solid passage rates through the rumen than grazers of a much similar size, suggesting that goats should have lower rumen fills than sheep. Demment and van Soest (1985) showed that gut capacity increased linearly with body weight. Cattle are expected to have a much larger gut capacity than sheep and goats when scaled to body weight. Parra (1978) showed that metabolic rate increased as a fractional power of mass suggesting that small ruminants have smaller rumen capacity per unit metabolic need. Hence, as a result, cattle would be expected to have a greater rumen capacity than sheep and goats. Due to the above mentioned theories, small bodied herbivorous ruminants with smaller gut capacity must compensate for this constraint by increasing passage rate to ensure they maintain adequate feed intakes to meet metabolic needs (Gross *et al*. 1996). This may help explain why sheep had higher passage rates compared to cattle, as shown in Table 2.1. Small species (small body weight) of browsers such as duikers achieve comparatively long mean retention times in the rumen that may match that of larger ruminants (Clauss *et al*. 2010).

There is a strong sense that body weight is correlated to digesta passage rates, but there is no allometric relationship between these parameters. As such body weight may not be convincingly classified as a factor that affects mean retention time (Clauss *et al*. 2010). At body masses less than 100 kg, Wenninger and Shipley (2000) showed that within a ruminant species there was no relationship between the body weight and mean retention time.

Differences in passage rates amongst ruminants exist as a result of differences in habitats in which they live and are adapted, which is dependent on the type of diet available. Silanikove *et al*. (1993) showed that average fractional flow rates tended to be lower for desert goats (0.084 per hour) than non-desert goats (0.099 per hour). This translates to +39% higher fluid passage rate in non-desert goats per unit body weight. Again, mean retention time of solid particles was 10 hours greater for desert goats with intake being predominantly limited by high levels of rumen fill (Silanikove *et al*. 1993). These findings indicate that desert ("tropical" or hot climate) goats may possess greater digestive capacity than other breeds of goats as a result of adaptation to feed and climatic conditions in the desert. Passage rate and rumen fill data for

goats adapted to subtropical and tropical climates in sub-Saharan African is limited, thus necessitating data on how climatic adaptation influences rumen fill.

Rumen capacity and fill levels at any given time vary according to breeds as well. Breeds better adapted to low quality forages tend to possess increased rumen capacity for both digesta phases. Weyreter and Engelhardt (1984) found that Heidschnucken sheep (well adapted to high fibre roughages) were better able to consume large amounts of fibrous diets compared to Merino sheep (less adapted to high fibre roughages). This suggest that Heidschnucken sheep have greater potentials in expanding their rumen capacity compared to Merino sheep. Black head sheep are also unable to make such an adaptation relative to Heidschnucken sheep.

Using anatomical features of the rumen in different ruminant feeding types, a new theory on passage rate begins to unfold. Clauss *et al.* (2009) suggested that digesta passage patterns are correlated to and influenced by intraruminal papillation patterns. Differentiation between grazers and browsers using papillation patterns characterises grazers as having long, thick papillae, and deep reticular crests and ridges. Browsers characteristically have short and much thinner papillae, and shallower reticular crests compared to grazers. Presence of deep reticuloruminal papillae and crests would cause entrapment of small particles in the ridges of grazing ruminants than in browsers, causing longer retention times in grazers (Clauss *et al.* 2010).

2.4.2 Level of nutrition and feed intake

Plane of nutrition may be referred to as the level of feeding and animal production level (APL) (Fuller *et al.* 2004). Level of feeding is the amount of feed the animal consumes relative to its level of feeding to meet maintenance requirements (Fuller *et al.* 2004). Cases of hyperphagia increase demands for expanded rumen capacity so as to accommodate much greater digesta load (Barboza *et al.* 2006). Quantities of feed ingested by ruminants depend on animal species and the variability in intake levels occur between breeds and/or individual within a breed (Scott and Provenza 1999; Pearson *et al.* 2006).

Haaland and Tyrrell (1982) observed that rates of passage of fluid through the rumen increased by 13% when animals were fed at two times maintenance (L=2) from feeding at maintenance level (L=1). Varga and Prigge (1982), Lindberg (1987), Kovács *et al.* (1998) and Seo *et al.* (2005) observed that an increase in dry matter intake was associated with linear increases in fluid passage rate. As an animal eats more dry matter, solid material entering the rumen accumulates and there is a possibility of the dry matter taking up space occupied by the fluid in the rumen thus exerting pressure on the rumen contents (Van Soest 1975). With dry

matter being more bulky (Hummel *et al*. 2008) than liquid there is a possibility of the bulk forcing liquid out of the rumen at a much faster rate as the pressure builds up in the rumen compared to low intake levels. In muskoxen, Barboza *et al*. (2006) showed that elevation of feed intake by 74% increased gut fill by 31-34%. Hyperphagia increases gut fill, and gut fill is usually a result of reduced passage rate of solid material. On the other hand, this observation is inconsistent with studies where increased feed intake has been shown to increase passage rates. Although Lindberg (1987) showed a strong relationship between liquid passage rate and feed intake in dairy goats, no correlation was reported between dry matter intake and mean retention time in addax (Hummel *et al*. 2008). This suggests that high dry matter intakes may not necessarily influence passage rates through the rumen. Long mean retention times for particulate matter at high dry matter intakes in addax may have been due to a high reserve capacity of the reticulorumen. Accurate determination of the extent to which rumen capacity may expand to accommodate various types of forage diets in different ruminants would be important. This would elicit determination of maximal rumen fill levels in ruminants. Body weight had high positive correlation to rumen capacity (Adams *et al*. 1987). Distension of abdominal cavities during the projected increases in rumen capacity have not yet been quantified and documented in any species (Clauss *et al*. 2007). Estimates to which ruminant gastrointestinal tracts stretch to accommodate a given diet range roughly lies between 10-17% of the body mass in ruminants, with an upper limit of 20% for cattle. Goats and sheep reach this upper limit more frequently and easily than cattle (Varga and Harpster 1995). Body weight alone is not a good indicator of maximal rumen fill, with Purser and Moir (1966) reporting variation in gut capacity amongst animals of similar body weight. Tulloh and Hughes (1965) reported larger rumen volumes in lactating than dry cows. Hence, rumen fill volumes may be a function of various physiological states.

2.4.3 Forage to concentrate ratio in the diet

Supplementation of predominantly roughage based diets has become a major practice in ruminant nutrition. Protein concentrate supplementation of animals grazed on pasture increases the nutritional status of ruminants (Ben Salem and Smith 2008). Levels of concentrates added to predominantly roughage feed in ruminant affects the rate of passage of liquid and solid through the rumen (Varga and Prigge 1982). High roughage to concentrate ratios in the diet lead to greater fluid and particulate passage rates from the rumen (Table 2.2). Passage rate is affected by roughage quality and the rate at which rumen digesta disappeared from the rumen is positively related to diet quality (Nsahlai and Apaloo 2007).

Bartocci *et al*. (1997) reported an increase in passage rates of fluid and particulate matter from the rumen with an increase in the proportion of dietary fibre in diets fed to buffalo, cattle and sheep. Evans (1981), Okeke *et al*. (1983), Merchen *et al*. (1986), Owens and Goetsch (1986), and Poore *et al*. (1990) all reported that high proportions of concentrate in diets decreased the rates of fluid dilution and turnover in the rumen.

Table 2.2 Effect of forage to concentrate ratio in diet on rate of solid and fluid passage through the rumen (Bartocci *et al*. 1997)

Phase	Diet	F:C=87.5: 12.5	F:C=75: 25	F:C=62.5: 37.5	F:C=50: 50
	Parameter				
liquid	Outflow rate (l/h)	3.47	3.16	2.76	2.41
liquid	Rumen fill (l)	49.10	46.10	43.60	40.00
solid	k_1 (%/h)	3.15	2.71	2.71	2.48

F:C: forage to concentrate ratio; k_1: fractional passage rate in the rumen.

Although similar trends on the effects of forage to concentrate ratio on fluid dilution rate and fractional passage of solid were observed, a number of suggestions have been given towards explaining these observations. Forage to concentrate ratios can alter a number of processes in ruminants and these processes have been implicated to changes in fluid and solid outflow rates from the rumen. These processes include the amount of saliva produced and the degree of stratification of rumen contents.

Froetschel (1995) showed that cattle produced an average of 100-200 litres of saliva in a single day when fed high fibre diets. Saliva is mainly used as a buffering agent and lubricant as roughage digestion produces large amounts of short chain fatty acids that may lower rumen pH. Increased amounts of saliva forces ruminal wall contractions to escalate (Froetschel 1995). An increase in these contractions may be stimulated by increased distension and tactile stimulation of the rumen wall (Reid and Titchen 1984) due to filling by the saliva leading to contraction that result in emptying of the rumen fluid and solid digesta to prevent filling of the rumen. Hence, contractions squeeze solid and fluid digesta out of the rumen at an increased rate. Bartocci *et al*. (1997) observed decreased amounts of saliva production in animals fed high concentrate diets that constituted 50% of the diet. Hence, reduced salivation may be responsible for lower passage rates in high concentrate fed animals due to reduced rumen contractions. Another possibility is that occurrence of these increased contractions might be due to mineral ions present in saliva (Thomson *et al*. 1978).

Due to the bulky nature of forage, high roughage diets (Hummel *et al*. 2008) may occupy a large space in the rumen. Bulky forage may force liquid out of the rumen at a much faster rate as competition for space increases. Tactile stimulation of the rumen wall by the roughage is a likely facilitator. Because of a much greater degree of tactile stimulation, rumen wall contractions may occur, thus forcing rumen fluid to pass through the rumen at a much faster rate (Reid and Titchen 1984). Okine and Mathison (1991) showed that an increase in duration and amplitude of reticulorumen contractions resulted in an increase in passage rate of both solids and liquid matter out of the rumen. Due to the less bulk, concentrates would occupy far much less space in the rumen than forages. The resulting effect would be that high concentrate diets induce low amplitude rumen contractions due to reduced tactile stimulation of the rumen wall. Low power contractions would force less fluid out of the rumen per unit time compared to roughages leading to lower fluid and solid passage rates. These views are supported by rumen liquid fill values (Table 2.2; Bartocci *et al*. (1997)). Rumen fill was reported to be greater in diets that had higher proportion of roughage because roughages contribute to rumen fill more than concentrates in view of longer retention times in the rumen and selective retention in the fibre mat. Lui *et al*. (1999) observed reduced clearance rates of solid digesta in the rumen of animals fed bulky high fibre crop residues. Lui *et al*. (1999) gave clear evidence of enhanced rumen fill levels as a result of high fibre/roughage content in ruminant diets. Concentrate particles are small and the chance of being trapped in the floating mat is minimal and thus passes out of the rumen at a much faster rate than roughage particles.

In the rumen, stratification occurs (Figure 2.1). Stratification involves separation of liquid and solid components into distinct layers according to density (Tschuor and Clauss 2008). Stratification is evident when a mat-like layer forms, and floats on the liquid phase. Fibre promotes the formation of the floating mat (Moore *et al*. 1990) in roughage more than concentrate diets because concentrate particles are smaller forming more homogenous mixtures in the rumen. Formation and presence of a floating mat in the rumen stimulates ruminal wall contraction (Varga and Harpster 1995), possibly due to tactile stimulation of the rumen wall. These contractions may lead to a rapid outflow of liquid and/or solid digesta through the rumen. Faichney (1986) showed that entrapment of large solid particles in the filter-bed of the rumen restricted their outflow. Entrapment increases retention time of large particles, hence fibre-mat formation may be a factor labelled as affecting rate of passage of solid through the rumen.
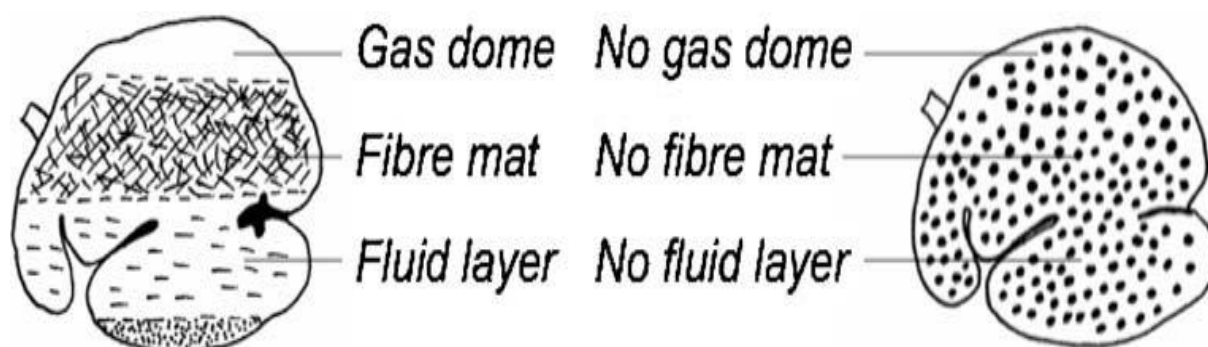
Figure 2.1 Proposed degree of stratification in rumen due to roughage (left) and concentrate (right) (picture adopted from Tschuor and Clauss 2008)

However, the theory of stratification may be challenged. Moore *et al*. (1990) showed that cottonseed hull diets, even though fibrous and elicit a faster rate of liquid flow through the rumen, do not promote stratification. Hulls are smaller and denser, and form a more homogenous-like mixture in the rumen (Varga and Harpster 1995). Moore *et al*. (1990) concluded that rates of fluid flow through the rumen increased because of increased intake of the hull diet. Contrary to that, Owens and Goetsch (1988) reported that cottonseed hulls resulted in decreased passage rates of fluid in the rumen thus supporting the theory of stratification. Further studies on the effect of cottonseed hulls on the rate of passage need to be done. The theory of stratification that supports increased flow rate of fluid through the rumen may be applied to higher passage rates in grazers than in browsers due to differences in diet. Grazers are mainly roughage eaters and browsers are concentrate feeders (Hofmann 1989). Hence, higher rates of passage of fluid are seen in grazers than browsers (Lechner *et al*. 2010).

Stage of development of forage may also have an effect on the fluid dilution rate and solid passage rate (Adams *et al*. 1987). When a plant is young, it contains a higher proportion of water than old plants, with older plants tending to have a larger proportion of lignin (Dove and Milne 1994). With older plants having large proportions of lignin than younger plants, it is expected that forages at a late stage of development may induce higher passage rate of liquid. However, animals that graze on grass that is at an earlier stage of development have high fluid passage rates through the rumen than animals that graze on mature pasture. Work by Estell and Galyean (1985), McCollum and Galyean (1985) and Adams *et al*. (1987) showed that animals grazed on young pastures have higher dilution rates (18.3%/h) than animals grazed on mature pastures (9%/h). Presence of high mineral and water content in young forage may have led to increased osmotic pressure in the rumen causing the relaxation of the reticulo-omasal orifice thus increasing fractional rates of passage of fluid through the rumen. Lignin and hemicellulose

contents of forages may have a substantial effect on passage rates of both solid and liquid mater in the rumen. Mature forage contains a higher proportion of hemicellulose than young forages (Rencoret *et al*. 2011). Hemicellulose has hydrophilic properties (van Weyenburg *et al*. 2006) and capabilities of absorbing and holding water in the rumen are high. Due to hydrophilic properties of hemicellulose, fractional rate of passage of fluid through the rumen decreases because hemicellulose absorbs a greater proportion of the fluid and reduces fluid outflow rate. This phenomenon is most likely to occur when high roughage diets are fed.

Use of different roughage sources in studies is likely to overcome discrepancies in fluid turnover rates due to high fibre proportions. This leads to the hypothesis that the type of forage in a diet may affect the rate of passage of liquid through the rumen. Van Weyenburg *et al*. (2006) observed higher fluid passage rates in lucerne hay than in grass hay. Analysis of the hemicellulose content in both feeds showed higher hemicellulose content in grass hay than in lucerne hay. The water holding capacity of the hemicellulose is approximately 260 g water/kg DM for grass hay and 59 g water/kg DM for lucerne hay (Van Weyenburg *et al*. 2006). This suggests that the greater the hemicellulose content of forages the greater the amount of water that forage can hold. The greater the quantity of water held by the forage then the lesser the proportion that leaves the rumen, resulting in a decrease in the fractional rate of fluid passing through the rumen. Seemingly, Froetschel and Amos (1991) found no correlation between water holding capacity of digesta and fluid outflow rate, but a positive correlation between water holding capacity and ruminal fluid volume. More evidence of this subject is needed.

Dietary roughage quality affects rates of passage of solid material through the rumen (Nsahlai and Apaloo 2007). Rinne *et al*. (2002) found out that clearance of digestible plant cell wall fractions of particulate matter was slower compared to indigestible fraction of matter. This is perhaps due to sorting of particles in the rumen by stratification (Kennedy 2005) and entrapment of digestible material in the floating fibre mat. Digestible portions of feed retain for longer periods in the rumen and degrade slowly to a high extent whilst indigestible portions clear from the rumen through passage quickly because of their size and density. As a result, fractional clearance rate of indigestible part of fibre such as lignin is more rapid than that of digestible fractions such as hemicellulose (Egan and Doyle 1985) and may reduce rumen fill (Allen 1996). Contrary to this view, Baumont *et al*. (2000) suggested that increases in lignin content of roughage would make it stay much longer in the rumen before being cleared through passage out of the rumen, increasing rumen fill as a result. Baumont *et al*. (2000) was of the view that retention time in the reticulorumen depended on rate of degradation of the degradable fraction and on the proportion of undegradable fraction. This suggests that increased

proportions of undegradable fractions slowed down the rate of degradation of the degradable fractions, with overall effects of slowing down passage rate but increasing rumen fill. For microbes to get access to the digestible fractions of fibre, microbes must etch into and remove lignin so as to access these digestible fractions. Hence, rate of degradation is greatly reduced thus increasing retention time in the reticulorumen, as a result of high lignin content. Grasses tend to contain high contents of neutral detergent fibre compared to browse leaves and legumes. Browse leaves are shown to contain much more lignin compared to grasses (Hummel *et al*. 2006). Panjaitan *et al*. (2010) reported mean retention times of lignin fraction that were three times greater than those of neutral detergent fibre fraction across four grass species.

Rumen fill is at times described based on fibre (neutral detergent fibre, NDF) fraction (Mertens 2005) on the basis that fermentation and passage rate of neutral detergent fibre through the rumen is slower than of any other dietary constituent. Fibre exerts a greater filling effect in the rumen (Allen 1996). Indirect evidence on the effects of NDF content on rumen fill exists. Using sheep fed on alfalfa hay and orchard grass hay, Baumont *et al*. (1990) observed higher dry matter intakes in sheep fed alfalfa hay relative to orchard grass hay, which was attributed to lower NDF content in alfalfa hay. Due to lower NDF content in alfalfa hay compared to orchard grass hay, alfalfa had a lower filling effect on the rumen due to rapid rates of fermentation and passage through the rumen (Jung and Allen 1995). In conclusion, low NDF content is associated with low rumen fill levels, suggesting a positive linear relationship between NDF content (x-axis) and rumen fill (y-axis), which reaches a plateau when rumen capacity cannot increase further with additional increase in NDF content.

Grazing herbivores have an ability to gradually modify rumen volume and increase passage rates in accordance with a reduction in roughage quality (Johnson and Combs 1991). Due to slower passage rates of the digestible fraction, ruminants fed on highly digestible feed may experience maximal rumen fill. Boudon *et al*. (2009) stated that attainment of maximal rumen fill would limit feed intake in dairy cows grazed on highly digestible rye grass. Also, rumen fill in grazing animals varies greatly from the beginning to the end of a feeding session (Boudon *et al*. 2009). On the contrary, Dove (1996) suggested a relationship whereby rumen fill played a major role in regulation of feed intake with decreasing digestibility of a feed. Digestibility is negatively related to lignin content. Conclusions by Rinne *et al*. (2002) that high lignin content caused slow passage rate in the rumen support the view of Dove (1996). This actually suggests that passage rate of solid material was slower for low digestible feeds. Slower passage rates increased rumen fill because feed stays for a much longer time in the rumen. Faverdin *et al*. (1995) demonstrated a more or less similar phenomenon where the

overall effect of indigestible feed components resulted in increased rumen fill of approximately 1 kg DM which resulted to a corresponding depression in feed intake of 0.6 kg DM/day. The most probable explanation for this would be a reduction in the rates of clearance of digesta from the rumen, mainly by passage.

2.4.4 Ambient temperature

As ambient temperatures fluctuate, during the course of the year due seasonal changes, or as the day progresses from sunrise to sunset, animals respond to these changes to different extents. Temperatures that might lead to severely altered physiological processes would result in changes in rates of passage of fluid and solid through the rumen. These include temperature ranges above and below the thermo-neutral zone for ruminants (Varga and Prigge 1982).

Warm-blooded animals mainly respond to high environmental temperatures by sweating, panting, and licking (Toole and Toole 2006) to cool their bodies through heat loss via body fluids by evaporation. Increasing plasma volume to increase heat dissipation (Chaiyabutr *et al.* 1986) possibly via radiation may occur. Under extremely high temperatures animals become reluctant to eat thus dry matter intake is reduced (Kennedy and Murphy 1988) to cut down on heat production and heat increment due to feeding. In response to rather low environmental temperatures, warm-blooded animals shiver (Toole and Toole 2006), increase movements of body parts to generate heat energy internally and generally tend to increase dry matter intake (Kennedy and Murphy 1988).

Low ambient temperatures generally lead to increased rates of fluid and solid passage through the rumen. Kennedy (1985) reported a 21% decrease in mean retention time of solid digesta in the rumen as ambient temperature decreased from 21°C to 0°C. This increase in the rate of passage may be attributed to occurrence of shivering and increased movements of various body parts (Kennedy and Murphy 1988). Contraction and expansion of muscles and organs in close association with the rumen may exert pressure on the rumen wall causing it to contract and decrease in size momentarily. Thus exertion of some pressure on the rumen and its contents may force out rumen fluid and solid passage from the rumen at a much faster rate. Extents to which such an occurrence affect rates of passage of fluid through the rumen is virtually undocumented and may require further study. Increased rumen movement has been documented at low environmental temperatures (Kennedy and Murphy 1988), probably as a result of movement of organs in close proximity to the rumen. Such movements of the rumen are accompanied by increased power of ruminal wall contraction (Kennedy and Murphy 1988), which may squeeze rumen digesta resulting in it escaping from the rumen at a more rapid rate.

Increased dry matter intake (similar to level of feeding) on exposure of animals to low environmental temperature (Bernard and Montgomery 1997), is also assumed to have an effect of increasing passage rate of fluid through the rumen due to a push effect.

In extremely high ambient temperatures slower rates of fluid passage through the rumen are due to a decrease in the pushing effect on the ruminal fluid as a result of low intake. Contrary to that, Chaiyabutr *et al*. (1987) observed that higher ambient temperatures resulted in an increase in the rate of fluid passage through the rumen even when a decrease in feed intake occurred.

As indicated in Table 2.3, rates of passage of fluid from the rumen increased by almost double from an ambient temperature that is within the thermo-neutral zone of cattle to a temperature slightly above the thermo-neutral zone. The observed increase in blood and plasma volumes indicated that animals responded to heat stress dissipating heat via evaporation and radiation through the skin thus cooling their bodies using blood water as a medium. Water has a high specific heat capacity with reference to biological systems, hence is mainly used to dissipate heat (Toole and Toole 2006) in most animals.

Table 2.3 Effect of heat stress on blood volume, plasma volume and fluid passage rate through the rumen of Swamp buffalo (Chaiyabutr et al. 1986)

Environmental temperature	26°C	41°C
Rate of flow (l/h)	1.82	3.12
Rumen retention time (h)	18.7	13.5
k_1 (per hour)	0.06	0.086
Blood volume (ml/kg)	63.95	68.08
Plasma volume (ml/kg)	47.45	50.83

The rumen acts as a water reservoir (Fuller *et al*. 2004). Water that contributed to an increase in plasma levels may have been from two sources, water intake and rumen, or both. Water may either enter blood through flowing across the ruminal wall (Chaiyabutr *et al*. 1987); however, proportions that go through this route are minute (Parthasarathy and Phillipson 1953) or diffusion into the blood stream through the intestines (Kamal and Shabaita 1968). Assuming that water was rapidly mobilized from the intestines into the blood, the capability of the intestines to provide large amounts of water is unlikely. Since the rumen acts as a fluid reserve it is likely that water would pass from the rumen into the intestines for absorption into the blood. As water from the intestines is lost into the blood, a high water concentration gradient between the rumen and the intestines is created. Suction power for water from the intestines

was high resulting in an increased flow of fluid through the rumen into the intestines (Chaiyabutr *et al*. 1987). Further research is needed to test this hypothesis. Most studies have reported contradictory results to those of Chaiyabutr *et al*. (1987) on the effect of high temperature on fluid passage rates thus making this appear as a special adaptation strategy of Swamp buffalo (*Bubalus bubalis*).

Warren *et al*. (1974) observed increased levels of water intake with increasing ambient temperature. A study by Wybright and Varga (1991) showed increased fluid passage rates of up to 64% in water infused rumen. Infusion or increase in water levels in the rumen leads to an increased osmotic pressure (Wybright and Varga 1991) on the ruminal wall. Tactile stimulation of the distended rumen wall triggers relaxation of the reticulo-omasal orifice and contraction of the rumen wall resulting in rapid flow and passage of fluid and particulate matter through the rumen (Reid and Titchen 1984). Studies by Warren *et al*. (1974) stated that mean retention time was directly related to or affected by ambient temperature rather than feed intake as influenced by temperature. Desert species are expected to have faster rates of passage compared to species of similar rumen physiology from temperate regions (Clauss *et al*. 2005). The study by Warren *et al*. (1974) used Holstein cattle which is adapted to temperate climates, hence it is expected that a temperate breed would respond to high environmental temperatures of above 32°C to a great extent. Cattle breeds that are well adapted to high environmental temperatures in tropical and sub-tropical climates may respond to temperatures of 32°C and above in a different way and probably to a lesser extent when compared to temperate breeds. More research needs to be conducted on effects of differences in thermal resistance and/or thermal tolerance levels on passage rates in ruminant animals in the tropics.

2.4.5 Feed additives and diet type

Grazing animals in most of Africa's grasslands usually suffer from protein and mineral deficiency. During spring and early summer, phosphorus is deficient in pastures in Southern Africa (Smaling *et al*. 1997). Animals get regular urea and phosphorus supplementation in the form of licks (Marston *et al*. 1998). Urea and minerals have hydrophilic properties (Chizzotti *et al*. 2008). Mineral concentration in the rumen may affect the osmotic pressure in the rumen seemingly affecting the rate of fluid flow in the rumen (Harrison *et al*. 1975).

In the development of mathematical models to predict the rates of fluid passage in the rumen, Seo *et al*. (2005) suggested that factors that influence the osmotic pressure in the rumen should be included in these equations. Rogers *et al*. (1979) and Estell and Galyean (1985) showed that presence of osmotically active compounds such as ash and urea in the rumen

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increased the fluid dilution rate. Cappellozza *et al*. (2013) showed that urea altered osmolality of rumen fluid. Urea readily dissolves in water forming a hypertonic solution (Cappellozza *et al*. 2013). Increased concentrations of urea and minerals in the rumen cause the rumen fluid to be hypertonic with respect to other interstitial fluids. This may result in net movement of water from the interstitial spaces into the rumen by osmosis. An increase in osmotic pressure on the ruminal wall occurs due to the influx of water (Lopez *et al*. 1994). Pressure receptors on the rumen wall may cause relaxation of the reticulo-omasal orifice due to increased pressure, to allow flow of fluid out of the rumen (Reid and Titchen 1984), increasing rates of passage of solid as well. Pressure receptors send signals to the hypothalamus that initiates contraction of the rumen wall, thus expelling fluid and solids from the rumen at an increased flow rate (Fioramonti and Bueno 1988; Carter and Grovum 1990). Liquid and particulate matter is forced to escape from the rumen at a fast rate to relieve pressure on the rumen wall thus resulting in an increased flow of fluid and solid out of the rumen.

However, effects of minerals on increasing passage rate of fluid through the rumen may be questioned. Nsahlai *et al*. (1999) showed passage rates of liquid through the rumen for rapeseed meal (3.60 l/h) to be greater than for fish meal (3.43 l/h). Although both meals were protein concentrates (McDonald *et al*. 2010), the source of protein may have influenced the passage rate. These results are interesting in the sense that, fish meal contains a high mineral content than rapeseed meal (McDonald *et al*. 2010) and thus may be expected to induce much higher fluid passage rates. Effects of increased osmotic pressure in the rumen due to influx of water, ultimately causing an increased passage rate may be overshadowed, perhaps by constituents of rapeseed meal. According to McDonald *et al*. (2010), rapeseed meals may contain large amounts of polyphenolic compounds. This may help explain the higher fluid passage rates through the rumen observed by Nsahlai *et al*. (1999) for rapeseed meal. Silanikove *et al*. (2001) observed increased fluid passage rates through the rumen due to tannins. Summing up it may well be that polyphenolic compounds affect the rate of passage through the rumen to a much greater extent than minerals. This assumption needs to be studied to clarify the gaps in knowledge.

Interesting observations by Koster *et al*. (1996) suggest that protein supplementation may have an effect on fluid passage rates. Linear increases in microbial nitrogen outflow from the rumen with increased quantities of degradable intake protein were observed. Furthermore, increases in provision levels of degradable intake proteins resulted in increased fluid dilution rates in the rumen. Therefore, increased fluid passage may be greatly influenced by the proportion of degradable protein in the diet. However, protein supplementation had very little

effect on rumen dry matter pool size in ruminants fed good quality forage (McCollum and Galyean 1985; Nsahlai 1991).

2.4.6 Stage of reproductive cycle and physiological state

The reproductive cycle may be subdivided into the lactational and non-lactational period, pregnancy stage, non-pregnancy stage and the number of days an animal is on the gestation calendar. During the productive cycle, animals undergo structural and functional changes during gestation and lactation (Coffey *et al*. 1989). Behavioural changes like loss or gain of appetite, increased or decreased water intake may be observed during these stages (Bernard and Montgomery 1997; Lunn 2004). Rate of passage of liquid and solid material through the rumen may be altered by these changes. Gunter *et al*. (1990) showed that rates of particulate and liquid passage through the rumen were higher for pregnant than non-pregnant animals, higher in lactating animals than their non-lactating counterparts, but lower during the late than the early stages in gestation (Table 2.4 and 2.5). Helander *et al*. (2014) suggested that different fractional solid and liquid passage rates should be used when formulating diets for pregnant and lactating ruminants.

During pregnancy, nutrient requirements for pregnant animals are higher than for non-pregnant animals (Kennedy and Murphy 1988). This is due to high demand for protein and energy required for foetal growth (Hutjens 2005) and development. Rumen fluid contains dissolved protein (Fox *et al*. 2004), short chain fatty acids (Lopez *et al*. 2003), and microbial protein. Because of increased demand for the above mentioned nutrients, an increase in rates of passage of fluid through the rumen is observed as a physiological response to meet the increased demand for nutrients in pregnant animals (Lunn 2004).

Table 2.4 Gut fill levels, and rumen liquid and solid passage rates in pregnant, non-pregnant, lactating, and non-lactating ewes (Gunter *et al*. 1990)

Phase	Parameter	Lactating	Non-lactating	Non- pregnant	Pregnant
liquid	Outflow rate (l/h)	0.7	0.5	0.4	0.5
liquid	Rate of passage (%/h)	11.1	8.1	10.9	13.9
liquid	Turnover (h)	9.3	12.7	9.5	7.5
liquid	Rumen Volume (l/kg BW)	0.07	0.08	0.05	0.04
solid	Rate of passage (%/h)	4.6	4.3	4.9	6.8
solid	Gut fill (g/kg BW)	5.7	7.7	6.8	4.8
solid	Mean Retention Time (h)	26.6	27.9	24.4	18.1

Table 2.5 Influence of gestation stage on rumen fill levels and fluid outflow rate in ewes (Gunter *et al*. 1990)

	Parameter	Phase	d 102 gestation	d 118 gestation	d 132 gestation
Non-pregnant	Gut fill (g/kg BW)		5.6	3.8	5.0
Pregnant	Gut fill (g/kg BW)		6.1	6.6	7.7
	Outflow rate (l/h)	Liquid	0.6	0.4	0.5

During the lactation period, there is high demand for water (Gunter *et al*. 1990; Marston *et al*. 1998), minerals, and soluble protein for the process of milk production (Kennedy and Murphy 1988; Marston *et al*. 1998). All nutrients for milk synthesis are absorbed across foregut walls and small intestines into the blood stream for transportation to the mammary gland. Rumen fluid serves as a water reservoir in ruminant animals and contains dissolved minerals and soluble proteins (Fuller *et al*. 2004). High demand for water in the lower intestines may result in mobilisation of water stored in the rumen. Hence, ruminal fluid passes out of the rumen at a faster rate to meet animal's requirements for water and minerals for milk production. When an animal is non-lactating, there is no demand in water for milk production thus the rate of passage of liquid through the rumen is much lower than in lactation. This is similar to observations by Chaiyabutr *et al*. (1986) that increased water demand in the lower gut might result in increased movement of water out of the rumen to meet demand in the lower tract. Consequently, Faichney and Brown (2004) and Helander *et al*. (2014) observed increases in dry matter intakes of about 20-30% from pregnancy to early lactation, which explains higher rates of liquid and solid passage through the rumen during lactation than during pregnancy (Gunter *et al*. 1990; Larsen *et al*. 2009). Work on sheep revealed increased rumen fluid volume of 15% during lactation compared to fluid volume at pregnancy (Kaske and Groth 1997) supporting the theory of increased water demand during lactation. Contrary to these findings, Hartnell and Satter (1979) showed 10%/h higher fluid dilution rates for grazing non-lactating than lactating cows fed silage, suggesting the necessity of more data on the subject. Hence, investigations of effects of interaction between lactation and/or non-lactation period and diet type on dilution rate need to be done.

The rumen and pregnant uterus are in close proximity in the abdominal cavity (Kaske and Groth 1997). It is therefore common sense to assume that as a foetus increases in size there is likelihood that it exerts a pressure on the ruminal wall (Coffey *et al*. 1989; Van Weyenburg *et al*. 2006). This pressure may at least squeeze the rumen thus forcing out some liquid and solid particles with a much greater rate than prior to pregnancy. Increased occupation of

abdominal cavity space by growing foetus in pregnant ruminants may have an overall effect depressing total rumen volume. Rumen fill would be expected to decrease exponentially in pregnant cows as pregnancy progresses. Dairy cows in early lactation have shown increased incapability of consuming enough feed to meet daily requirements for energy. To a certain extent, diminished rumen volume as a result of squeezing from growing foetus causes a reduction in available space for the rumen to expand in anticipation of increased feed intake. Hence, reduction of rumen fill is a result of pregnancy, due to a decrease in rumen volume. Forbes (1970) reported an approximate decrease of 0.39 l/l in volume of ruminal contents as pregnancy progressed in sheep fed on hay. However, Kaske and Groth (1997) observed increased rumen fill levels from mid pregnancy (60-80 days post conception) to lactation (35-55 days postpartum) with fill levels of 0.946 kgDM and 1.444 kgDM, respectively, in ewes. Percentage dry matter content of digesta increased modestly, mean retention times of liquid and small solid digesta reduced by 20-30% at late pregnancy compared to mid pregnancy, with fluid passage rates being approximately 3 times faster than small solids in sheep (Kaske and Groth 1997). Fluid outflow rate reportedly increased by 20-36% between late pregnancy and lactation (Kaske and Groth 1997). Generally, rumen fill levels are expected to decrease with an increase in passage rates of solid and liquid digesta. Progressive increments in rumen fill levels in the course from mid pregnancy to lactation were suggested to be due to a gradual reduction in sensitivity of mechano-receptors on the rumen wall (Baile and Forbes 1974). Such findings may suggest that reticulorumen volumes during various stages of the reproductive cycle may not depend on availability of space in the abdominal cavity alone. They may depend on numerous factors such as diet quality and nervous system response.

Time spent eating and the number of eating sessions were higher during pregnancy than lactation in ewes (Helander *et al*. 2014). Similarly, Kaske and Groth (1997) showed a 19% increase in chewing frequency from mid-pregnancy to lactation in sheep. Duration of eating periods and perhaps increase in chewing times may have some effect on rates of liquid and solid passage through the rumen. Oshita *et al*. (2008) showed higher fractional rates of liquid passage through the rumen in non-lactating cows grazed on rangeland (13.95% per hour) than those fed fodder ad libitum in the stalls (9.4% per hour). Animals that graze on rangelands spend more time chewing and eating than those confined to pens (Seo *et al*. 2005; Oshita *et al*. 2008). Cows have a greater frequency of rumen contractions during eating than during both rumination and rest (Okine and Mathison 1994). Processes of chewing and rumination stimulated rapid movement of material from the rumen into the reticulum (Kennedy 2005) compared to resting. Typical values for frequency of rumen contractions are 1.4/min at rest,

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2.3/min during ruminating and 2.8/min during grazing (Frandson 1981). Hence, the greater the number of ruminal contractions the greater the fractional rate of liquid and solid passage through the rumen (Okine and Mathison 1991). Thus, animals that spend more time grazing on rangelands have faster fluid and particulate passage rates through the rumen than stall-fed animals. Okine and Mathison (1991) concluded that the major determinant of digesta flow through the rumen is a result of reticular contractions. Distension of reticulorumen wall would stimulate an increase in rumen contractions. Fractional passage rate of NDF out of the rumen increased by about 34% as a result of increased rumen contractions (Dado and Allen 1996). One may tend to wonder the true effect of NDF on rumen fill. Earlier discussions pointed out that high NDF content is associated with increased rumen fill levels.

However, that may not be always the case. From an angle associated with reticulorumen contractions, fibre or NDF is a major contributor to increased tactile stimulation of the rumen wall. It may be argued that high levels of NDF in the rumen would increase the intensity and frequency of rumen contractions through tactile stimulation of the rumen wall. This would result to increased passage of digesta out of the rumen with an overall effect of reducing rumen fill.

Alvarez-Rodriguez *et al*. (2010) observed a phenomenon whereby management or husbandry methods had major effects on rumen fill capacity in lambs. They showed that weaned lambs raised on alfalfa meal consumed more forage than suckling lambs fed on alfalfa. These findings suggest that period of lactation had a major effect on rumen fill capacity of light bodied lambs. As a result, one may hypothesise that early weaned lambs have large rumen fill capacity than lambs weaned at a later stage, regardless of unweaned lambs being given solid feed.

So far, a general trend in results showed higher fluid and solid passage rates in lactating than non-lactating ruminants. However, contrary effects have been reported. Oshita *et al*. (2008) observed 10%/h higher fractional passage rates for fluids in non-lactating than lactating cows when fed off silage. These results raise a question on effects of diet and lactation, and diet and non-lactation interactions on rates of passage. Further research is needed to cover the gap in knowledge on these observations.

2.4.7 Particle size and functional specific gravity

Particulate matter is discriminated from moving out of the rumen at two major points in the gut, which are at the dorsal rumen and at the reticulo-omasal orifice (Kennedy 2005) because of particle size (PS) and functional specific gravity (FSG). The likelihood of particles escaping

from the rumen is strongly determined by particle size and density (Lechner-Doll *et al*. 1991). These two factors are inversely related when fermentation has not occurred (Evans *et al*. 1973), but in the course of fermentation Lirette and Milligan (1989) observed a negative curvilinear relationship between functional specific gravity and particle size. Various work on effects of particle size and FSG on passage rate have reported similar findings. Allen and Mertens (1988) suggested the passage of particulate matter depended on how much particles were present near the reticulo-omasal orifice during the second contraction of the rumen. This would strongly suggested that passage rate of solids depended on density. Functional specific gravity of a particle is defined as a physical measure of the weight of a given volume of a particle in the rumen relative to the same volume of fluid in the rumen (Fuller *et al*. 2004). The FSG is determined mainly from the chemical makeup of the ligno-cellulosic matrix (Sutherland 1988). Lechner-Doll *et al*. (1991) showed a negative correlation between particle density and mean retention time in the rumen. Before fermentation occurs, a solid particle is intact and tends to be heavy (high functional specific gravity) enough to sink to the bottom of the rumen, close to the ventral part of the rumen where its chances of moving out of the rumen through the reticulorumen orifice is increased. So, at this point movement is only prevented by particle size. Hence, particles tend to have differential passage rate where it tends to be higher for unfermented particles.

In the course of fermentation after the lag phase (colonisation of feed particles by bacteria) gas is produced from and stays within feed particles (Kennedy 2005). Gas production within particles increases buoyancy of large particles, and as a result particles tend to float and become entrapped in the floating fibre mat. Probability that these trapped particles are cleared from the rumen through passage is reduced (McDonald *et al*. 2010), as they would remain trapped until fermentation is completed. Thus, the rate of passage is slow for particles undergoing fermentation. Overall, high fermentation rate may depress the functional specific gravity through increased buoyancy thus reducing the rates of passage. Smith *et al*. (1972) showed that grasses containing higher levels of fermentable organic matter than legumes had much higher retention times in the rumen as a result of increased susceptibility of being trapped in the floating fibre mat. This supports a phenomenon where by slower passage rates are associated with high fermentation rates and proportion of degradable matter. Thus Rinne *et al*. (2002) found that clearance of digestible plant cell wall fractions of particulate matter was slower compared to indigestible matter. Bayat *et al*. (2010) also showed faster passage rates for indigestible neutral detergent fibre compared to that of potentially degradable neutral detergent fibre of a smaller particle size (Table 2.6).

Although increased reticulorumen contractions have been shown to increase passage rates of both solid and liquid the rumen, this may directly apply to fermenting solid material because of variable functional specific gravity. Reid and Titchen (1984) and Sutherland (1988) suggested that increasing the intensity of rumen contractions actually decreases the rate of passage of particles with low specific gravity from the rumen because contractions propel particles further away from the exit point, the reticulorumen orifice, before it even opens. Discussions on effects of reticulorumen contractions on passage rate should be specific on which fraction of solid matter and the value of specific gravity of particle is passage rate increased.

The theory of the ability of particles to sink (sedimentation) and/or float (stratification) in the rumen resulting in passage out and/or entrapment in the rumen may be true for species of ruminants (grazers) where stratification occurs. There is overwhelming evidence that stratification does not occur in the rumen of browsing ruminant animals (Clauss *et al*. 1998). Passage of particles out of the rumen in browsers is by mass flow, determined by abundance of digesta in the rumen and is normally a function of the occurrence of reticulorumen contractions (Clauss and Lechner-Doll 2001). Reticulorumen contractions are labelled as one of the most important factors that lead to passage of digesta out of the rumen. More studies have to be done to clarify why browsers characterised by lower occurrences of rumen contractions may have faster passage rates of digesta compared to grazers. Lechner-Doll *et al*. (1991) and Jiang and Hudson (1996) suggested that lack of stratification was responsible and strongly linked to reduced particle retention times in the rumen of browsing ruminants. It is suggested that particulate matter in browsing ruminants flows out of the rumen at a rate that is proportional to fluid flow rate. It thus remains to determine how and to what extent passage rates of fluid affect passage of small solids and vice-versa. Reduction in size of large particles of feed is a prerequisite for particulate flow out of the rumen via the reticulo-omasal orifice and may be an important determinant of rumen fill (Allen 1996). Particle size reduction occurs during rumination or re-chewing of previously swallowed feed (Kennedy 1985). Poppi *et al*. (1980) and Dixon and Milligan (1985) showed that resistance to particulate flow through the rumen increases with an increase in particle size. The rate of passage of particulate matter is inversely related to particle size (Kennedy 2005). There is therefore a critical size that particle should reach for them to pass out of the rumen via the reticulo-omasal orifice (Lechner-Doll *et al*. 1991). There are suggestions that critical particle size ranges from 1-4 mm (Poppi *et al*. 1980; Lechner-Doll *et al*. 1991). Small dense particles tend to fall into the ventral rumen just close to the reticulorumen orifice (Wyburn 1980).

Table 2.6 Effects of particle size and digestibility interactions on mean retention time, rumen fill levels and rates of passage in the rumen (Bayat *et al*. 2010)

Particle size	Parameter	GRASS		RED CLOVER	
		Early	Late	Early	Late
		Rumen digesta (kg)			
large	iNDF	0.88	0.97	1.59	2.36
large	pdNDF	3.20	3.37	1.83	1.68
small	iNDF	1.16	1.41	1.36	2.41
small	pdNDF	2.34	2.61	1.36	1.46
		Mean Retention Time (h)			
large	iNDF	28.7	24.3	49.8	37.6
large	pdNDF	13.9	14.8	13.4	11.0
small	iNDF	23.8	24.6	29.0	29.8
small	pdNDF	15.2	14.9	17.9	16.2
		potentially degradable NDF			
large	k_p	0.0034	0.0038	0.0041	0.0039
small	k_p	0.0280	0.0271	0.0242	0.0252
		indigestible NDF			
large	k_p	0.0050	0.0062	0.0046	0.0049
small	k_p	0.0428	0.0424	0.0356	0.0343

iNDF: indigestible neutral detergent fibre; pdNDF: potentially degradable neutral detergent fibre; k_p: fractional passage rate of particles

These small particles are capable of passing out of the rumen at the occurrence of the reticular contractions (Midasch *et al*. 1994) because they would have reached a size that permits passage. Large particles that have a high density are prevented from passing out of the rumen (Poppi *et al*. 1985) because of sedimentation of these particles at the bottom of the rumen (Kaske *et al*. 1992). These particles would still be large and hence are unlikely to pass out of the rumen. The theory of critical particle size as a prerequisite for particulate passage out of the rumen may be questionable because larger particles than this are prevalent in faeces. Welch (1986) and Kaske and Midsach (1997) showed that reticulorumen contractions were accompanied by drastic increases in outflow of solid particles termed to be large particles (particles greater than 5 mm). McBride *et al*. (1983) argued on how the so called large particles are prevented from leaving the rumen yet the diameter of the reticulorumen orifice opening of 35 mm (Bueno 1975) is 7-fold greater than the critical particle size. Kaske *et al*. (1992) revealed that when sedimentation was prevented in the rumen of sheep, outflow of 10 mm sized particles was 40% of the outflow of 1 mm size particle, which shows that a great fraction of large

particles do leave the rumen. An argument that can be raised is whether or not particle size is an important factor that leads to increased mean retention times in the rumen or it's the effectiveness of the floating mat in entrapment and sedimentation of large particles that determine passage rates to a greater extent than particle size.

Rates and extents to which solid particle size may be reduced depend on fragibility of particles. Now, inclusion of particle fragibility as a factor that influences passage rate and ultimately rumen fill opens a new dimension to the current discussion. As noted earlier, high chewing frequencies have an overall effect of increasing passage rates through stimulation of reticular contractions. Chewing also reduces time for particle size reduction ensuring that particles reach a critical size that allows them to pass through the reticulo-omasal orifice swiftly. It can be hypothesised that highly fragile particles pass out of the rumen much faster than less brittle particles. This may be supported by the fact that brittle particles take a much shorter time to undergo particle size reduction, and thus would have a shorter retention time in the floating mat than less fragile particles. This gives more fragile particles a faster passage rate than less fragile particles. Egan and Doyle (1985) where a faster passage rate of indigestible fibre components such as lignin may be explained by this phenomenon. Taking a closer look at possible causes of particle fragibility, a contrary effect of fragibility on passage rate is developed. Increased fragility of plant fibre is caused by high lignin content. As a result degradation rate of high lignin containing particles is reduced, hence more time is required by microbes to colonise and ferment digestible components of fibre. This would result in increased retention times of high lignin particles in the rumen for efficient fermentation. Hence, these particles are likely to be retained for a much longer time in the floating raft. This phenomenon may be aggravated when there are large sized particles with high lignin content, whereby particles would be restricted by size from flowing out through reticulo-omasal orifice, resulting to reduced passage rates.

2.5 Summary

Implicit from the above discussion, countless factors influence passage rates. Research have not considered effects of various combinations of factors on rates of passage of solid and fluid through the rumen. Mathematical models that seek to accurately predict passage rates, rumen fill levels and ultimately roughage intake should incorporate not one of the factors that affect these parameters but increase understanding of why part of the variation is not explained. Few studies focussing on determination of solid and fluid passage rates, rumen fill levels and roughage intake have ever documented feeding behaviour attributes of ruminant species at the

same time. Chewing time, rumination time, duration and frequency of feeding bouts, frequency and amplitude of rumen contractions need to be documented in all studies that measure passage rates. This would ensure a better understanding of these factors in influencing passage kinetics and roughage intake in ruminant animals.

Animal and feed compositional attributes are the major factors to be included into passage rate prediction models. The role of animal physiology in influencing digesta passage rate is critical. Accounting for the influence of various physiological changes in ruminants; feeding level, stage of pregnancy and lactation, and growth in passage rate models can be done by computation of the feeding level based on total net energy requirements relative to net energy requirement for maintenance (animal production level, APL). It is evident that there are still discrepancies on how ambient temperature and particle density (buoyancy) affect the passage rate of digesta in the rumen. Indexing for buoyancy in solid passage rate prediction models would likely involve determination of the extent of degradability of a particle taking into account the time available for digestion. This value of would give the potential degradability at a time equal to the half-life (PD $\frac{1}{2}$ life) of a particle during digestion. PD $\frac{1}{2}$ life would be directly proportional to the amount of gas produced during digestion of a particle that is responsible for buoyancy or floatation of solid particles.

Chapter 3
Modelling of digesta passage rates in grazing and browsing domestic and wild ruminant herbivores

Abstract

Utilisation of poor quality feeds in ruminants is governed by rates of digestion and of passage through the rumen. The passage rate of feed material determines the degree of bypass nutrients and the efficiency of synthesis of microbial protein in the rumen, making modelling of passage rate important. Artificial neural networks were used to develop models of liquid and solid passage rates. Factors that affect rates of passage in all included studies were identified, which included animal and feed factors. The database was composed of observations of domestic and wild ruminants of variable body mass (1.5 to 1238 kg) from 74 studies and 17 ruminant species from different climatic regions. Observations were randomly divided into two data subsets: 75% for training and 25% for validation. Developed models accounted for 66 and 82% of the variation in prediction of passage rates for solid and liquid, respectively. On validation using an independent database, these models attained 42 and 64% of precision in predicting passage rates for solid and liquid, respectively. Liquid and solid prediction passage rate models had no linear and mean bias in prediction. The study developed more précise prediction models for solid and liquid passage rates for ruminants fed on a variety of diets and/or feeds from different climatic regions.

Additional keywords: Artificial Neural Networks, intake, mean retention time, prediction equation, rumen.

3.1 Introduction

Digesta in the rumen exists as liquid or solid, with both phases intermingled together. Fluid and solid passage rates through the rumen are important as they influence digestion of soluble food nutrients (Illius and Gordon 1991), amount of short chain fatty acids absorbed in the rumen and that pass out of the rumen (Lopez *et al.* 2003), affects the amount of by-pass protein of dietary origin (Fox *et al.* 2004) and the amount of microbial protein available to the host as a protein source (Dijkstra *et al.* 2007). Outflow rates of particulate (k_P) and liquid (k_l) digesta from the rumen are influenced by a lot of factors, some of which are tedious and impractical to study (Allen 1996). There exists a wide variation among factors that influence passage rates among studies leading to differences in passage rate data collected in studies on the same or similar research topic (St-Pierre 2007). In a large number of studies, there are treatment effects that have very little influence on the passage rate variables being evaluated (Sauvant *et al.* 2008).

Attempts have been made to develop equations that predict passage rate based on feed chemistry (Nsahlai and Apaloo 2007), animal characteristics (Seo *et al.* 2006; Krizsan *et al.* 2010) and chewing time (Coleman *et al.* 2003) for various classes of ruminants. Illius and Gordon (1991) predicts passage as a function of body weight, though its validity has been questioned by Nsahlai and Apaloo (2007). These studies yielded modest levels of precision in predictions. Evidence suggests that ruminants at different physiological stages fed on a wide range of diets differ in rates of passage of digesta (Nsahlai and Apaloo 2007). Prediction of passage rates using a combination of animal, environmental and feed factors offers a more practical approach.

Artificial neural networks (ANN) have been used to model rumen fermentation patterns in dairy cows (Craninx *et al.* 2008), in vitro methane gas production (Dong and Zhao 2014), rumen fill (Adebayo 2015) and growth patterns in sheep (Ganesan *et al.* 2014). Little emphasis has been put into the use of mathematical modelling methods in ruminant digesta passage kinetics. Few studies, if any, have used ANN to model biological processes of passage rates of digesta through the rumen and ultimately predict roughage intake. Modelling of passage rate enables easy calculation of digesta passage rates, independent from the use of expensive rare earth elements as external markers. Passage rate prediction equations may find application in studies that seek to predict microbial protein synthesis, roughage intake and rumen fill levels. The objective of the current study was to develop robust liquid and solid passage rate prediction models for grazing and browsing ruminants using Artificial Neural Networks.

3.2 Materials and methods

Data were collected from studies that reported at least average values or ranges for body weights of animals used, measured fractional passage rates and/or mean retention times in the reticulo-rumen. A dataset was created bearing passage rates from wild and domesticated ruminants. Factors that affect passage rates were identified in each of these studies. Qualitative factors that affect passage rates were coded with numerical weightings. These were (factor = code/weighting): animal management (grazing = 1 or indoors = 0), feed class (silage = 1 or non-silage = 0), tannin content (feeds that were classified to be tannin rich were millet, sorghum, carob leaves, red clover and browse leaves = 1 and all other feeds with minute tannin levels = 0), and feeding regime (ad-libitum = 1 or restricted = 0). Physiological status (day of pregnancy and lactation), animal production level, amount of urea in the diet, animal body mass (kg) and mature body mass (kg) were also included.

Feed variables were chemical composition (DM, NDF, ADF, CP and ash contents all in g/kg DM), particle size (small = 1, medium = 2, large = 3, mixed sizes = 0) and in-sacco degradability parameters (a – soluble fraction, b – slowly degradable fraction, c – rate of degradation, PD – potential degradability and $PD\frac{1}{2}$life - potential degradability at half-life). Instead, the half-life of a solid matter in the rumen was calculated using rates of degradation (c) according to Grovum and Phillips (1973), where: $t\frac{1}{2}$ life = $(0.693 \div c)$. Degradation models used in computing dry matter loss from each study were identified. $PD\frac{1}{2}$life was calculated using the following formulae: $PD\frac{1}{2}$life $= a + b \times [1 - \exp(-c \times t\frac{1}{2}\text{life})]$ (no time lag model) or $PD\frac{1}{2}$life $= a + b \times [1 - \exp -c(t\frac{1}{2}\text{life} - L)]$ (model accounting for time lag, where L – lag).

Dimensions of particles moving through the rumen were classified into three main groups according to their diameter: large (> 1 mm), medium (0.5 – 1 mm), and small (0.04 – 0.5 mm). The degree of maturity which is correlated to the physiological age (PA) was calculated using the following formulae: PA = (body mass ÷ mature body mass). Ruminants were separated into three main feeding types according to the classification by Hofmann (1989) as: grazers or roughage selectors (cattle, antelope-addax, buffalo, mouflon, muskoxen, nilgai, sheep and blackbuck = 1), browsers or concentrate selectors (moose, okapi, roe deer, dik-dik, duikers and mouse deer = 2), and intermediate feeders (goats, anoa, reindeer, gazelle and ibex = 3). Net energies for maintenance (NE_m), fattening (NE_f), lactation (NE_l), conception (N_c) and production (NE_p) were calculated according to AFRC (1993). Since these formulae were

developed for cattle, sheep and goats only; wild ruminants in our database were categorised into either of the formulae for cattle, sheep and goats using their body weights or mature size, and feeding habits. Animals were assigned to the formulae for (1) cattle (cattle, muskoxen, anoa, antelope-addax, buffaloes, moose, mouflons, nilgai, okapi, reindeer and roe deer), (2) sheep (sheep, blackbucks, and gazelles), or (3) goats (goats, dik-dik, duikers, mouse deer and ibex).

Few studies reported final body weights of animals at the end of the trial, and these were used to compute respective NE_f. For studies that did not measure final body weight of experimental animals, it was assumed that all animals were at maintenance level throughout the trial. All values for net energy were computed in MJ/kg per day. Days in milk reported as early and late lactation were taken to be 60 and 290 days, respectively, for cows. Three studies did not report the milk composition for sheep, ibex and cows, and in order to calculate the energy value for milk, an average butter fat content for sheep, ibex (Raynal-Ljutovac et $al.$ 2008) and cow (Lock and Garnsworthy 2003) milk of 3.2, 3.5 and 3.8%, respectively, were used. Milk content for ibex was assumed to be equivalent to that of goats. The sum of these NE values was used to calculate the total net energy requirements (TNE_R). Animal production level (APL) was calculated (APL = $TNE_R \div NE_m$).

Studies in which feed composition and degradation were not reported but had the type of feed or diet reported feed composition attributes and degradability parameters were looked up in journal articles. These included Hummel et $al.$ (2006), Abdou (2016), Stanton and LeValley (2014), Beefmagazine (2015) and Feedipedia (2016). Feeds and/or diets that did not have any one of ADF or NDF had these compositional attributes calculated using a regression equation derived from the dataset. The equation for acid detergent fibre (Y) and neutral detergent fibre (X) (g/kg DM) was Y = 36.04 ($\pm$ 11.420) + 0.551 ($\pm$ 0.02086) X (n = 360, RMSE = 61.55, R^2 = 0.66, CV = 18.9%).

Where animals were fed a concentrate diet alone, the ash content was taken to be 10%. Passage rates reported as mean retention time in the rumen (MRT_R) were converted to fractional passage rate (FPR) by taking the inverse of mean retention time: FPR = 1 $\div$ MRT. Mature body mass of each ruminant species was looked up from various publications and databases. These included Frandsen (1992), Estes (1993), Jenkins et $al.$ (1993), Schoeman (1996), Lewis et $al.$ (2004; 2010), Wund and Myers (2005), Cillie (2009), ADW (2014), Arkive (2016) and AWF (2016). Data from studies that failed to specify the animal species were eliminated. Most studies that reported solid passage rates did not measure fluid passage rates, and vice-versa. Therefore, two datasets were collated for solid and liquid passage rates.

Although publications collected for the creation of these datasets might not include all published literature, studies used to build these datasets were readily available.

In the present work, two Artificial Neural Network models were programmed on the 32 bit Visual Basic Ver 6.0 to predict the liquid and solid passage rates. Each dataset was used separately. Observations from each dataset were randomly separated into two sub-subsets: 75% of the dataset for model development or training and 25% for model validation. Since different variables span over wide ranges, normalisation (within the interval $(-1, 1)$) of input and output data was done. For modelling, a three layer Levenberg–Marquardt BP neural network which generally includes one input layer, one hidden layer and one output layer was adopted; thus network topologies of 23-23-1 and 17-17-1 corresponding to the numbers of neurons of input, hidden and output layers for solid passage and liquid passage rates, respectively, were adopted (Figure 3.1). Training was carried out using backpropagation algorithm. Both models were trained for 3200 and 3600 epochs at learning rate of 0.05, momentum of 0.8 and the net errors were reduced to 0.00018 and 0.00011 on validation data for solid passage and liquid passage rate, respectively.

The correlation procedure of SAS 9.3 software (SAS Institute Inc., Cary, NC, USA) was used to establish the Pearson correlation coefficients of any two input predictor variables. For all evaluations, regression analyses of observed against predicted passage rates, residuals against observed passage rate and residuals against predicted passage rates were carried out using the linear regression procedure. Coefficients of determination were used to evaluate the precision of regression lines in approximating real data points of models. Root mean square error (RMSE) was used to determine accuracy of these models. To evaluate the linear and mean biases in model predictions, the residuals (observed minus predicted passage rates) were regressed against predicted passage rates. The intercept and slopes of these regression lines were tested against 0 and 1, respectively, to determine any linear or mean bias (St-Pierre 2003). Residual plots against observed passage rates were used to determine how close the predictions were from the real datasets. The process models developed in this study have been deposited into the Repository of Intelligent Models (REDIM 2016) with accession number PRDA001762 and PRCN001814 for solid and liquid passage rate models respectively as indicated at http://www.redim.org.za/?search=PRDA001762 and http://www.redim.org.za/?search=PRCN001814.
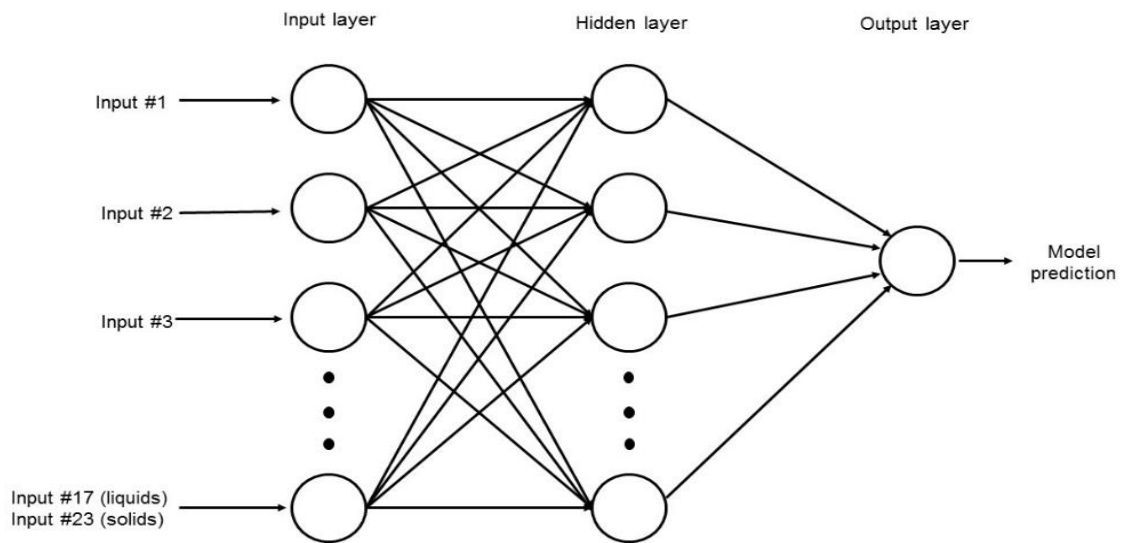
Figure 3.1 The basic structure of Levenberg–Marquardt back propagation (LM-BP) neural network for modelling

3.3 Results

Numbers of observations in the database were unevenly distributed among the ruminant feeding types (67-78% were grazers, 10-12% were browsers and 9-19% were intermediate feeders). In predicting liquid passage rate, 12 observations were on pregnant and lactating animals (6 lactating and pregnant cattle, 3 lactating cattle, 2 lactating sheep and 1 pregnant sheep). Out of 87 observations used for validation, seven (7) observations were on pregnant and lactating animals (2 lactating and pregnant cattle, 1 lactating cow and 4 pregnant sheep). All other classes of ruminants were neither lactating nor pregnant. For solid passage rates, 102 observations were on pregnant and lactating animals (7 pregnant cattle, 83 lactating cattle, 2 lactating sheep, 5 pregnant sheep and 5 lactating ibex). Thirty three (33) observations on pregnant and lactating animals (1 pregnant cattle, 25 lactating cattle, 3 lactating ibex, 2 lactating sheep and 2 pregnant sheep) were used for validation. All other classes of ruminants were neither lactating nor pregnant. Table 3.1 and 3.2 give the animal and diet compositional attributes used in model development, respectively.

Correlation coefficients of the predictor variables used in model development for liquid passage rates were <0.5 and significant, except for correlations >0.5 between APL and days into lactation, body mass and mature body weight, ADF and NDF, body mass and physiological age, and days in lactation and days in pregnancy, which were expected (Table 3.3). Correlation coefficients of predictor variables used in model development for solid passage rates were <0.5

yet significant. As expected, correlation coefficients were >0.5 between APL and days in lactation, body mass and mature body weight, ADF and NDF, body mass and physiological age, and days in lactation and body mass, PD and b, CP and rate of degradation, DM and silage, CP and ADF, CP and NDF, APL and BM, APL and physiological age, mature body mass and feeding type, PD at half-life and "a", PD at half-life and PD. However, a correlation coefficient of >0.5 between body mass and silage was unexpected (Table 3.3).

Table 3.1 Summary of animal attributes used in prediction (Pred) and validation (Valid) of passage rates

	Liquid model			Solid model		
	Pred	Valid		Pred	Valid	
No. of species	17	12	FPR (per h)	15	11	FPR (per h)
Mass (kg)	1.5–890	2.1–890		1.5–1238	1.5–1238	
Grazers	201	72		300	103	
Cattle	115	42	0.091 ± 0.031	202	62	0.031 ± 0.020
Sheep	62	21	0.074 ± 0.035	92	35	0.035 ± 0.015
Buffaloes	6	3	0.058 ± 0.020	2	0	0.024 ± 0.0002
Antelopes	4	4	0.056 ± 0.017	5	3	0.024 ± 0.004
Mouflons	1	0	0.026	0	0	-
Muskoxen	11	2	0.050 ± 0.032	7	4	0.032 ± 0.031
Nilgai	1	0	0.019	0	0	-
Blackbucks	1	0	0.017	0	0	-
Browsers	36	8		39	16	
Moose	14	3	0.039 ± 0.008	9	3	0.022 ± 0.006
Okapi	7	1	0.062 ± 0.014	11	5	0.045 ± 0.010
Roe deer	0	1	0.045	0	0	-
Dik-dik	8	2	0.076 ± 0.014	6	4	0.04 ± 0.016
Duikers	4	1	0.048 ± 0.010	3	2	0.039 ± 0.008
Mouse deer	4	0	0.051 ± 0.006	3	1	0.046 ± 0.004
Intermediate feeder	24	7		85	23	
Anoa	4	0	0.081 ± 0.011	4	0	0.039 ± 0.008
Reindeer	5	3	0.045 ± 0.014	4	0	0.020 ± 0.0004
Gazelles	6	0	0.100 ± 0.015	6	0	0.056 ± 0.012
Goats	8	4	0.100 ± 0.034	53	16	0.027 ± 0.007
Ibex	0	0	-	17	7	0.054 ± 0.021

FPR: fractional passage rate; Pred: prediction; Valid: validation

Correlation coefficients of <0.5 indicate that input variables did not strongly influence each other in liquid and solid passage rate prediction.

The regression relationship between the observed (Y) and predicted (X) liquid passage rates (per h) in model development was: $Y = -0.0013 (\pm 0.0024) + 1.004 (\pm 0.0295) X$ (n = 261, RMSE = 0.0142), accounting for 82% of the variation in prediction. The intercept ($P = 0.5863$) and slope ($P = 0.8818$) were not different from 0 and 1, respectively (Fig 3.2.a). A plot of residual liquid passage rate against predicted liquid passage rate assessing the mean bias (intercept) and linear bias (slope) of the model in predicting liquid passage rate (Fig 3.2.b) is given in this equation: $Y = -0.0031 (\pm 0.00241) + 0.0044 (\pm 0.02948) X$ ($R^2 = 0.0001$, RMSE = 0.01422). The intercept ($P = 0.5863$) and slope ($P = 0.8818$) from the residual plot were not different from zero. It can be observed from the plot that with the exception of six outliers, residuals showed no obvious pattern on the horizontal axis. A plot of residual liquid passage rate against observed liquid passage rate assessed the goodness of predictions (Fig 3.2.c) showing that residual liquid passage rate increased with increasing liquid passage rate. The regression relationship between the observed (Y) and predicted (X) liquid passage rates (per h) in model validation using unseen data was: $Y = 0.02301 (\pm 0.00557) + 0.767 (\pm 0.06178) X$ (n = 87, RMSE = 0.02105). This equation accounted for 64% of the variation in unseen data. The intercept and slope were significantly different from 0 ($P = 0.0001$) and 1 ($P = 0.0003$), respectively (Fig 3.2.d).

Table 3.2 Summary statistics of feed and animal attributes used in both prediction (Pred) and validation (Valid) of passage rates

	Solid passage rate model					Liquid passage rate model				
	N	Max	Min	Mean	SD	N	Max	Min	Mean	SD
Urea (g/kg)	566	9.4	0	0.275	1.25	348	7	0	0.13	0.85
DM (g/kg)	566	966	70	742	265	348	957	154	746	263
NDF (g/kg)	566	913	110	556	162	348	874	110	528	157
ADF (g/kg)	566	603	55	352	92	348	654	33.8	327	107
CP (g/kg)	566	295	25.7	130	57	348	710	19.4	142	79
ASH (g/kg)	566	138	20	76	18.3	348	197	20	81.6	26
DP (days)	566	138	0	1.7	12.3	348	138	0	3	15
DL (days)	566	290	0	17.8	45.9	348	233	0	5	29
MBM	566	1100	2	374	286	348	900	2	411	283
PhyA	566	1.5	0.07	0.629	0.315	348	1.5	0.125	0.58	0.26
APL	566	3.28	0.87	1.28	0.53	348	2.4	1	1.09	0.26
FPR (per h)	566	0.091	0.0007	0.033	0.0181	348	0.183	0.017	0.078	0.034
a (g/kg)	566	647	2	202	105					
b (g/kg)	566	853	38	528	142					
c (per h)	566	0.174	0.010	0.049	0.026					
$PD_{1/2 \text{ life}}$ (g/kg)	566	789	50	452	115					
PD (g/kg)	566	964	69	704	169					

DP: days pregnant; DL: days in lactation; MBM: mature body mass; PhyA: physiological age; APL: animal production level; FPR: fractional passage rate; $PD_{1/2}$ life: potential degradability at half-life.

The regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) in model development was: Y = -0.0014 (± 0.00128) + 1.005 (± 0.0348) X (n = 424, RMSE = 0.01047), accounting for 66% of the variation in prediction. The intercept ($P = 0.2753$) and slope ($P = 0.8823$) were not different from 0 and 1, respectively (Fig 3.3.a). A plot of residual solid passage rate against predicted solid passage rate assessing the mean bias (intercept) and linear bias (slope) of the model in predicting solid passage rate (Fig 3.3.b) had the equation: Y = -0.0014 (±0.00128) + 0.00516 (±0.03482) X ($R^2 = 0.0001$, RMSE = 0.01047). The intercept ($P = 0.2753$) and slope ($P = 0.8823$) of the residual plot were not different from zero. It can be observed from the plot that residuals formed a cone shaped cluster on the horizontal axis. A plot of residual solid passage rate against observed solid passage rate assessed the goodness of the predictions (Fig 3.3.c). The residual solid passage rate increased with increasing solid passage rates. The regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) in model validation was: Y = 0.00476 (± 0.00323) +

0.888 (± 0.08763) X (n = 142, RMSE = 0.01375), accounting for only 42% of the variation in unseen data. The intercept and slope were not different from 0 ($P = 0.1429$) and 1 ($P = 0.2049$), respectively (Fig 3.3.d). Three outliers were observed for muskoxen in validation.

3.4 Discussion

Passage rates are affected by a wide variety of factors that have varying or similar effects. It has been reported that passage rate is a function of animal species (Lechner *et al*. 2010), level of feeding (Seo *et al*. 2006; Mazzenga *et al*. 2009), forage to concentrate ratio (Bartocci *et al*. 1997), feeding behaviour (Okine *et al*. 1998), environmental temperature (Chaiyabutr *et al*. 1987; Bartocci *et al*. 1997), buffer content (Cappellozza *et al*. 2013), ionophores (Schelling 1984), water intake (Varga and Harpster 1995), roughage quality (Vaga and Poppi 1997), animal reproductive state (Larsen *et al*. 2009), particle size and functional specific gravity (Poppi *et al*. 1980; Lechner-Doll *et al*. 1991), tannin content in diet (Silanikove *et al*. 2001; Al-Kindi *et al*. 2016) and diet or feed compositional attributes (Nsahlai *et al*. 1999). Ideally, passage rate prediction equations should be low input, easy to use models that incorporate easy to measure predictor variables. However, limiting input variables may result to lower accuracy in predicting passage rates for diverse classes of ruminants. Developed models in this study are not low input models; however input variables are fairly easy to compute.

All models developed in this study had slopes equal to 1 and intercepts at 0. Coupled with high precision, all prediction models accounted for large amounts of variation in unknown observations. Very few, if any models developed thus far have achieved such high precision in predicting both solid and liquid passage rates for 17 different ruminant animal species (wild and domesticated) from a wide range of climatic regions using a single model. In all model predictions and validations, all classes of ruminants were clustered along the ideal prediction line. A couple of sporadic outliers in prediction and validation of the solid passage rates from ibex and muskoxen, respectively, are clearly identifiable. For both ruminant species, passage rate was grossly under predicted by these models, particularly as these animals inhabit the cold climate. Ambient temperature ranges outside the thermo-neutral zone lead to physiological responses which alter passage of fluid and solid through the rumen. Lowering temperatures to freezing increased passage rate of solid by 21% (Kennedy 1985) and increased temperatures doubled passage rates of liquid (Chaiyabutr *et al*. 1987). The degree of change in passage rates as a result of temperature fluctuations is exceedingly high and the direction of change is unpredictable. These suggest that studies need to consider season and place of study to index environmental temperature.

Most studies have developed passage rate prediction equations with good coefficients of determination (R^2 value) that accounted for a greater portion of the variation using intake (of dry matter or neutral detergent fibre) as major predictor variables. However, given that the main application of passage rate equations would be to predict dry matter intake and microbial yields, inclusion of intake when developing passage rate models may be questionable. To eliminate this bias, both prediction models developed in this study did not incorporate feed intake as a predictor variable.

Unlike models developed by Seo *et al*. (2006), models for predicting passage rates for liquid in this study had very few lactating and pregnant cattle and sheep, and other ruminants had no pregnant or lactating animals. This may limit the use of models developed in this study in predicting passage rates for pregnant and/or lactating dairy cows and other ruminants. Since most studies did not report body weight changes for studied animals, assumptions that animals in those studies were at maintenance level may be biased. Obtaining body weight changes in those studies and computing animal production level (APL) would have accounted for some variation in model development.

Seo *et al*. (2006) excluded observations from wild ruminants and animals of body mass less than 100 kg, and datasets from animals that had dry matter intakes of less than 10 g/kg body weight, thus limiting the conditions to which their equations can be applied. Similarly, models by Krizsan *et al*. (2010) made use of passage rate observations from trials done in Europe and the United States alone. These models may be applicable for ruminants from temperate areas but not to those from tropical regions. However, model development in this study made use of a wide range of ruminant species of differing body mass, from the smallest ruminant in the world (mouse deer averaging 1.6 kg in body mass) to large ruminant animals averaging over 1238 kg in body mass. The implication is that the models developed in this study can be used to predict passage rates for any size, class and type of ruminant animal under any climatic condition with considerable precision.

Table 3.3 Pearson correlations between input factors used in solid (top-right hand side) and liquid (bottom-left hand side) model development

	Tan	Sil	FTyp	Gr-In	Ad-R	Urea	DM	NDF	ADF	CP	Ash	DayP	DayL	BM	MBM	PhAg	APL	FPR	PS	$PD_{1/2}$	c	b	a	PD	
Tan		0.04 (0.29)	0.16 (0.00)	0.36 (0.00)	-0.11 (0.01)	-0.09 (0.03)	-0.33 (0.00)	-0.30 (0.00)	-0.23 (0.00)	0.28 (0.00)	0.25 (0.00)	-0.06 (0.16)	-0.06 (0.17)	-0.06 (0.17)	-0.05 (0.22)	-0.01 (0.87)	-0.03 (0.45)	-0.01 (0.90)	-0.06 (0.18)	-0.46 (0.00)	0.27 (0.00)	-0.33 (0.00)	-0.18 (0.00)	-0.33 (0.00)	Tan
Sil	0.03 (0.60)		-0.23 (0.00)	-0.10 (0.02)	0.05 (0.20)	-0.09 (0.03)	-0.66 (0.00)	-0.24 (0.00)	-0.14 (0.00)	0.06 (0.13)	0.06 (0.15)	-0.06 (0.16)	0.45 (0.00)	0.60 (0.00)	0.41 (0.00)	0.45 (0.00)	0.47 (0.00)	-0.01 (0.84)	0.24 (0.00)	0.02 (0.62)	0.31 (0.00)	-0.40 (0.00)	0.25 (0.00)	-0.12 (0.00)	Sil
FTyp	0.38 (0.00)	-0.85 (0.11)		0.06 (0.15)	-0.07 (0.12)	-0.13 (0.00)	0.12 (0.01)	-0.11 (0.01)	-0.10 (0.01)	0.13 (0.00)	0.02 (0.63)	-0.09 (0.04)	-0.20 (0.00)	-0.48 (0.00)	-0.50 (0.00)	-0.40 (0.00)	-0.25 (0.00)	0.05 (0.28)	-0.23 (0.00)	-0.01 (0.91)	-0.13 (0.00)	0.18 (0.00)	-0.09 (0.03)	0.15 (0.00)	FTyp
Gr-In	0.25 (0.00)	-0.12 (0.03)	0.04 (0.42)		0.03 (0.47)	-0.05 (0.21)	-0.12 (0.00)	-0.07 (0.09)	-0.12 (0.01)	0.17 (0.00)	0.17 (0.00)	0.00 (0.10)	-0.09 (0.03)	-0.07 (0.08)	-0.09 (0.03)	0.05 (0.24)	-0.13 (0.00)	0.09 (0.04)	-0.09 (0.03)	-0.09 (0.03)	0.10 (0.02)	0.05 (0.22)	0.00 (0.95)	-0.00 (0.96)	Gr-In
Ad-R	0.32 (0.56)	0.06 (0.25)	0.03 (0.53)	0.15 (0.00)		0.03 (0.51)	-0.07 (0.12)	0.20 (0.00)	0.19 (0.00)	-0.24 (0.00)	-0.04 (0.31)	0.02 (0.67)	0.05 (0.24)	0.07 (0.08)	0.10 (0.02)	0.05 (0.23)	0.04 (0.29)	0.04 (0.34)	0.05 (0.26)	-0.03 (0.50)	-0.04 (0.40)	0.03 (0.50)	-0.02 (0.63)	-0.01 (0.85)	Ad-R
Urea	-0.08 (0.14)	-0.04 (0.52)	-0.08 (0.15)	-0.09 (0.11)	0.04 (0.40)		0.14 (0.00)	0.24 (0.00)	0.22 (0.00)	-0.06 (0.18)	-0.13 (0.00)	-0.03 (0.46)	-0.08 (0.06)	-0.03 (0.53)	0.00 (0.96)	-0.01 (0.79)	-0.11 (0.01)	-0.09 (0.04)	-0.04 (0.38)	-0.06 (0.18)	-0.00 (1.00)	-0.07 (0.08)	0.00 (0.91)	-0.09 (0.04)	Urea
DM	-0.37 (0.00)	-0.26 (0.00)	-0.05 (0.33)	-0.35 (0.00)	-0.00 (0.88)	0.11 (0.03)		0.30 (0.00)	0.22 (0.00)	-0.15 (0.00)	-0.09 (0.03)	-0.00 (0.94)	-0.27 (0.00)	-0.47 (0.00)	-0.43 (0.00)	-0.31 (0.00)	-0.37 (0.00)	-0.03 (0.54)	-0.18 (0.00)	0.06 (0.14)	-0.39 (0.00)	0.28 (0.00)	-0.17 (0.00)	0.05 (0.28)	DM
NDF	-0.13 (0.01)	-0.17 (0.00)	-0.25 (0.00)	-0.00 (0.99)	0.23 (0.00)	0.12 (0.02)	0.30 (0.00)		0.81 (0.00)	-0.66 (0.00)	-0.06 (0.16)	0.028 (0.50)	-0.21 (0.00)	-0.18 (0.00)	-0.05 (0.22)	-0.15 (0.00)	-0.24 (0.00)	-0.17 (0.00)	-0.01 (0.74)	-0.14 (0.00)	-0.37 (0.00)	0.23 (0.00)	-0.29 (0.00)	0.01 (0.74)	NDF
ADF	-0.00 (0.96)	-0.29 (0.00)	-0.11 (0.04)	0.00 (0.96)	0.15 (0.01)	0.17 (0.00)	0.33 (0.00)	0.81 (0.00)		-0.51 (0.00)	-0.01 (0.84)	-0.01 (0.91)	-0.04 (0.31)	-0.04 (0.35)	-0.01 (0.90)	0.00 (0.94)	-0.04 (0.39)	-0.17 (0.00)	0.11 (0.01)	-0.29 (0.00)	-0.20 (0.00)	0.19 (0.00)	-0.43 (0.00)	-0.10 (0.02)	ADF
CP	0.11 (0.03)	-0.02 (0.76)	0.10 (0.08)	-0.04 (0.52)	-0.09 (0.09)	0.13 (0.01)	-0.01 (0.91)	-0.33 (0.00)	-0.26 (0.00)		0.23 (0.00)	-0.00 (0.93)	0.13 (0.00)	0.00 (1.00)	-0.17 (0.00)	0.08 (0.06)	0.16 (0.00)	0.28 (0.00)	-0.06 (0.15)	0.01 (0.89)	0.56 (0.00)	-0.17 (0.00)	0.10 (0.02)	-0.13 (0.00)	CP
Ash	0.10 (0.06)	-0.24 (0.00)	-0.17 (0.00)	0.29 (0.00)	-0.04 (0.43)	-0.07 (0.18)	-0.17 (0.00)	0.17 (0.00)	0.03 (0.57)	0.11 (0.05)		0.04 (0.29)	-0.02 (0.65)	-0.02 (0.69)	-0.14 (0.00)	0.09 (0.04)	0.08 (0.07)	0.05 (0.22)	-0.07 (0.09)	-0.14 (0.00)	0.28 (0.00)	-0.01 (0.91)	-0.13 (0.00)	-0.19 (0.00)	Ash
DayP	-0.09 (0.10)	-0.04 (0.47)	-0.09 (0.11)	0.00 (0.92)	0.05 (0.35)	-0.03 (0.61)	-0.13 (0.01)	-0.01 (0.86)	-0.05 (0.39)	0.06 (0.30)	0.05 (0.38)		-0.06 (0.19)	-0.03 (0.53)	-0.08 (0.05)	0.29 (0.00)	-0.06 (0.15)	0.02 (0.62)	-0.05 (0.21)	0.02 (0.71)	0.01 (0.82)	-0.02 (0.62)	0.05 (0.26)	0.03 (0.43)	DayP
DayL	-0.08 (0.13)	0.017 (0.76)	-0.08 (0.13)	0.09 (0.11)	0.05 (0.38)	-0.03 (0.63)	-0.32 (0.00)	-0.07 (0.21)	-0.15 (0.01)	0.12 (0.03)	0.08 (0.14)	0.58 (0.00)		0.51 (0.00)	0.30 (0.00)	0.45 (0.00)	0.80 (0.01)	0.10 (0.00)	0.26 (0.00)	0.07 (0.09)	0.07 (0.10)	-0.28 (0.00)	0.25 (0.00)	-0.03 (0.53)	DayL
BM	-0.22 (0.00)	0.28 (0.00)	-0.36 (0.00)	0.06 (0.27)	-0.03 (0.57)	0.13 (0.02)	-0.38 (0.00)	0.03 (0.53)	-0.06 (0.23)	-0.11 (0.04)	-0.07 (0.23)	0.08 (0.12)	0.29 (0.00)		0.82 (0.00)	0.71 (0.00)	0.59 (0.00)	-0.05 (0.28)	0.41 (0.00)	0.09 (0.03)	0.24 (0.00)	-0.30 (0.00)	0.29 (0.00)	0.06 (0.16)	BM
MBM	-0.08 (0.12)	0.24 (0.00)	-0.33 (0.00)	0.07 (0.19)	-0.06 (0.25)	0.03 (0.53)	-0.35 (0.00)	0.11 (0.03)	0.041 (0.44)	-0.16 (0.00)	0.04 (0.43)	-0.03 (0.58)	0.14 (0.01)	0.79 (0.00)		0.36 (0.00)	0.38 (0.00)	-0.11 (0.01)	0.29 (0.00)	0.11 (0.05)	0.08 (0.00)	-0.20 (0.00)	0.26 (0.00)	0.13 (0.00)	MBM
PhAg	-0.20 (0.00)	0.09 (0.08)	-0.17 (0.00)	0.06 (0.26)	0.01 (0.88)	0.16 (0.00)	-0.13 (0.02)	0.03 (0.57)	-0.06 (0.30)	-0.08 (0.13)	-0.17 (0.00)	0.33 (0.00)	0.22 (0.00)	0.50 (0.00)	0.03 (0.58)		0.52 (0.00)	0.00 (0.95)	0.34 (0.00)	-0.03 (0.47)	0.28 (0.00)	-0.32 (0.00)	0.18 (0.00)	-0.04 (0.40)	PhAg
APL	-0.07 (0.19)	0.10 (0.07)	-0.02 (0.74)	0.02 (0.75)	0.07 (0.18)	-0.06 (0.31)	-0.19 (0.00)	-0.07 (0.17)	-0.22 (0.00)	0.11 (0.04)	0.05 (0.34)	0.34 (0.00)	0.69 (0.00)	0.24 (0.00)	0.21 (0.00)	0.09 (0.10)		0.06 (0.14)	0.44 (0.00)	-0.11 (0.01)	0.17 (0.00)	-0.39 (0.00)	0.12 (0.00)	-0.17 (0.00)	APL
FPR	-0.22 (0.00)	0.00 (0.96)	-0.11 (0.04)	0.06 (0.30)	0.05 (0.33)	0.09 (0.09)	0.02 (0.68)	-0.01 (0.77)	-0.03 (0.54)	0.21 (0.00)	0.03 (0.56)	0.24 (0.00)	0.30 (0.00)	0.21 (0.00)	0.13 (0.02)	0.17 (0.00)	0.37 (0.00)		-0.38 (0.00)	0.07 (0.08)	0.19 (0.00)	0.02 (0.72)	0.06 (0.12)	-0.01 (0.78)	FPR
	Tan	Sil	FTyp	Gr-In	Ad-R	Urea	DM	NDF	ADF	CP	Ash	DayP	DayL	BM	MBM	PhAg	APL	FPR		-0.06 (0.17)	0.04 (0.39)	-0.24 (0.00)	0.07 (0.10)	-0.10 (0.02)	PS
																					-0.21 (0.00)	0.38 (0.00)	0.78 (0.00)	0.76 (0.00)	$PD_{1/2}$
																						-0.10 (0.02)	-0.16 (0.00)	-0.21 (0.00)	c
																							-0.23 (0.00)	0.67 (0.00)	b
																								0.40 (0.00)	a
																									PD

Tan: tannins; Sil: silage; F-Typ: feeding type; Gr-In: grazing or indoors; Ad-R: ad libitum or restricted; DayP: days pregnant; DayL: days in lactation; MBM: mature body mass; PhAg: physiological age; APL: animal production level; FPR: fractional passage rate; PS: particle size; $PD_{1/2}$: potential degradability at half-life.
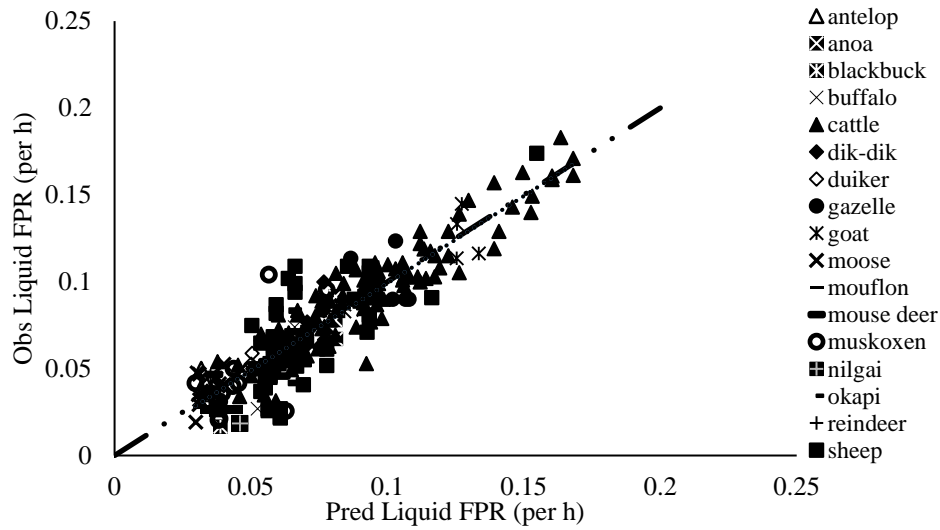
Figure 3.2. a Relationship between the observed (Obs) and predicted (Pred) liquid passage rates (k_1) for model development.
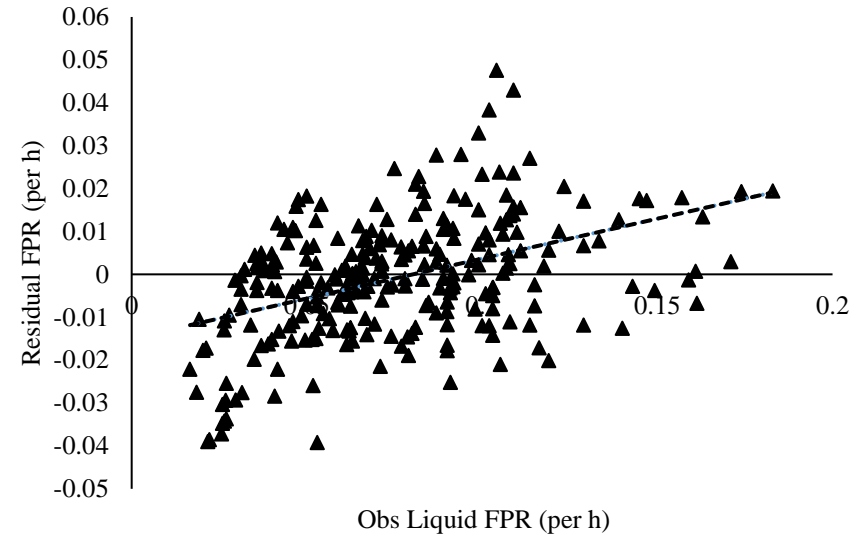
Figure 3.2. c Residual (Observed – Predicted) plot against observed (Obs) liquid FPR.
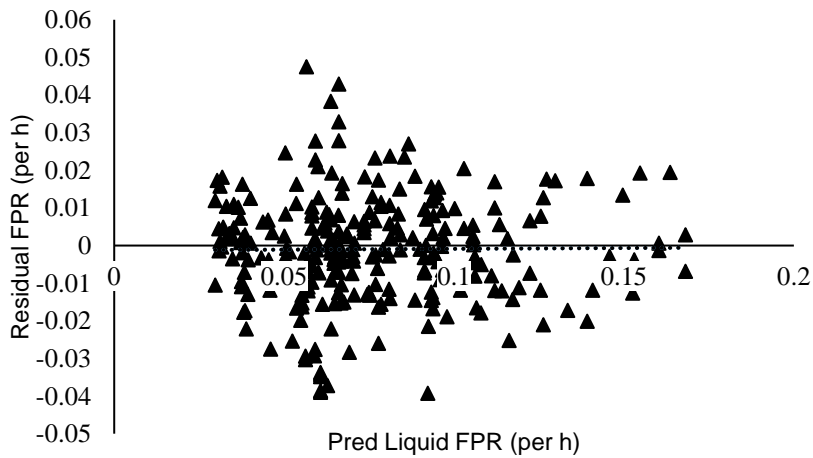
Figure 3.2. b Residual (Observed – Predicted) plot against predicted (Pred) liquid FPR to test model bias in prediction.
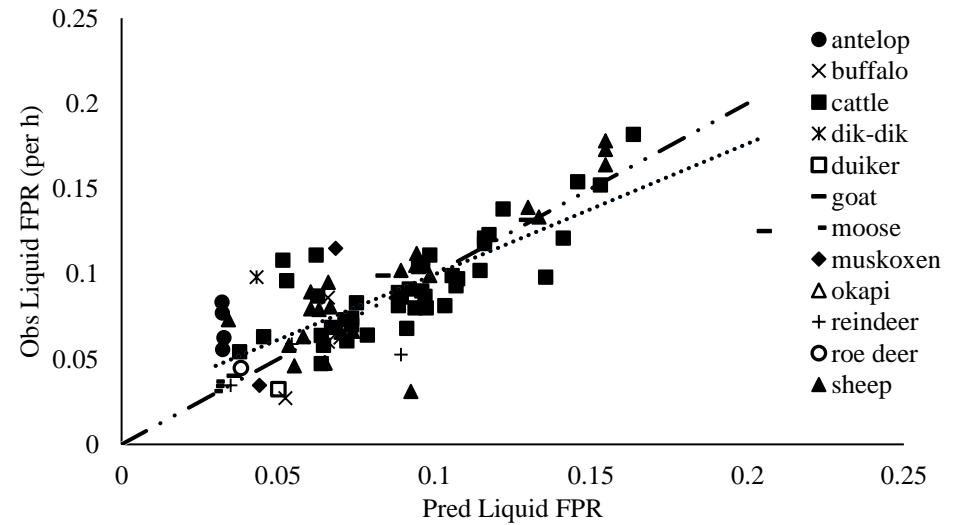
Figure 3.2. d Relationship between the observed (Obs) and predicted (Pred) liquid passage rates (k_1) for model validation.

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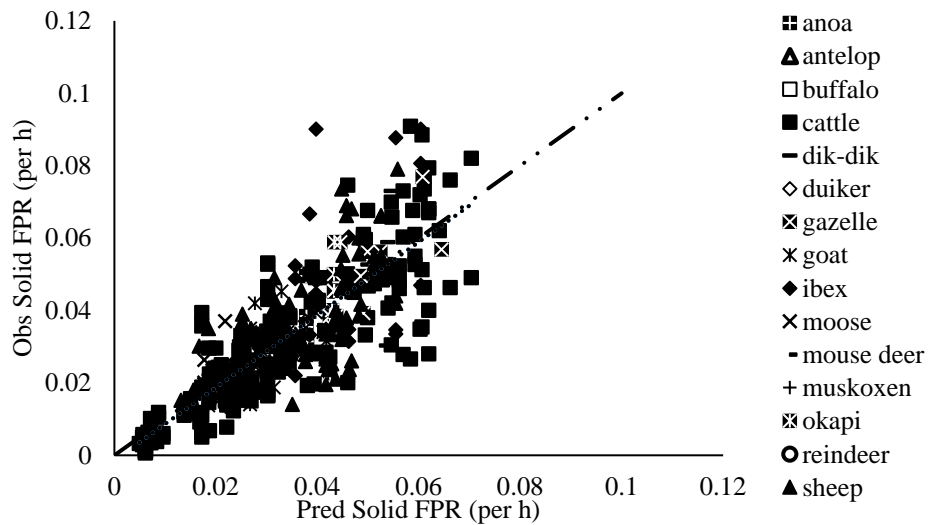
Figure 3.3. a Relationship between the observed (Obs) and predicted (Pred) solid passage rates (k_P) for model development
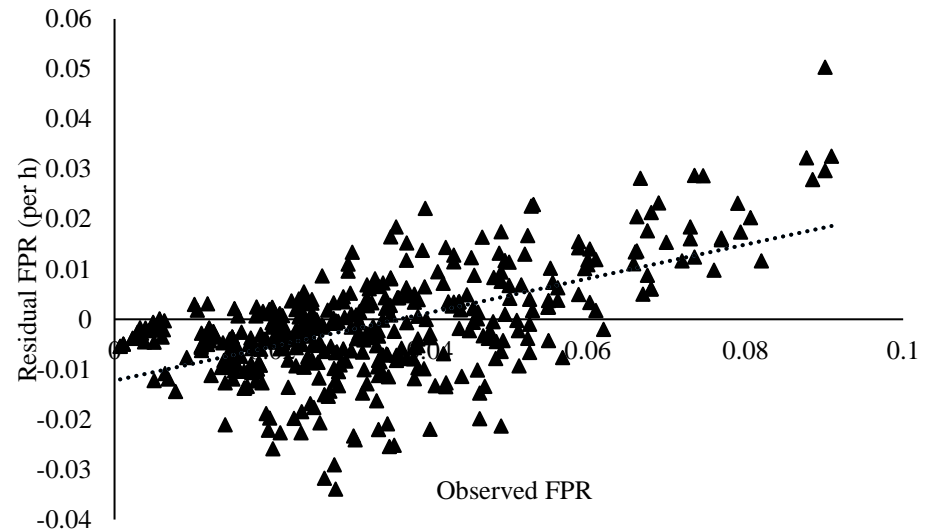
Figure 3.3. c Residual (Observed – Predicted) plot against observed (Obs) solid FPR
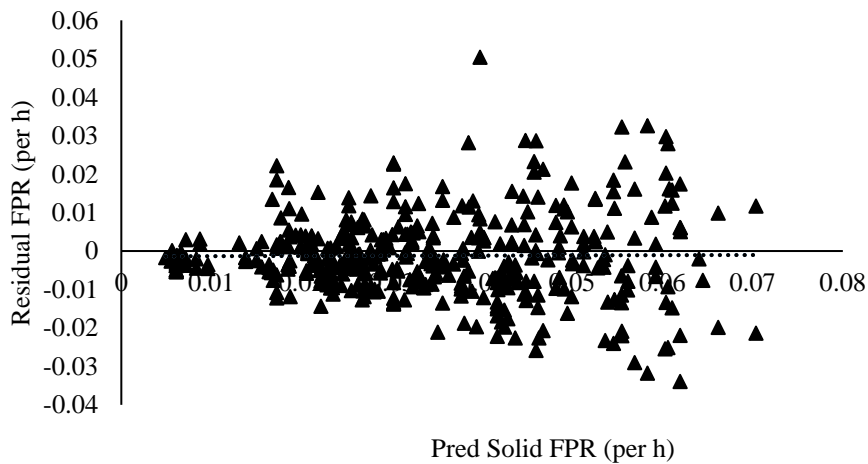
Figure 3.3. b Residual (Observed – Predicted) plot against predicted (Obs) solid FPR to test model bias in prediction
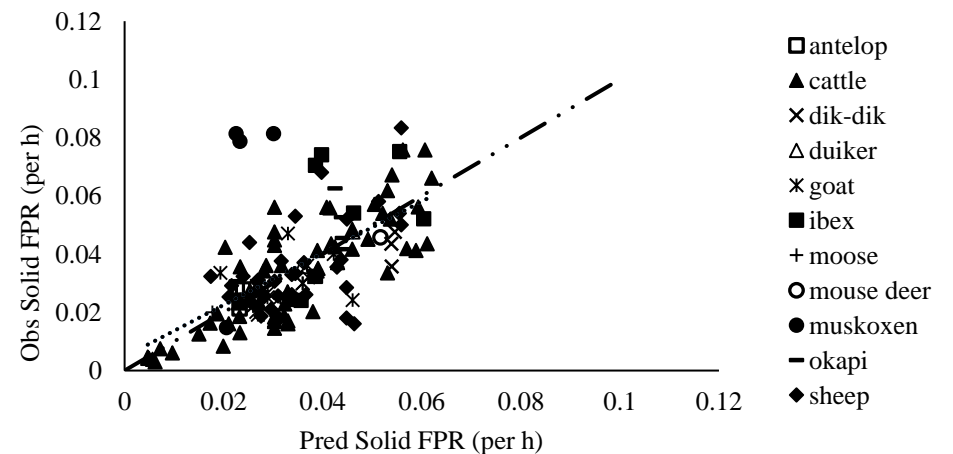
Figure 3.3. d Relationship between the observed (Obs) and predicted (Pred) solid passage rates (k_l) for model validation

Particle density is one of the major factor affecting solid particle passage out of the rumen (Hristov *et al*. 2003). It was assumed that high potential degradability at half-life would increase gas production within solid particles rendering them buoyant. This propels them away from the reticulo-rumen orifice, reducing passage. However, correlation results showed that passage rates of solids tended to (P <0.08) increase with degradability at half-life, defeating the use of this variable. Thus, rapid reduction in particle size overshadows the effect of buoyancy in reducing passage rates. This may show some limitations in use of Artificial Neural Networks in capturing biological phenomena.

Based on coefficients of determination, models for predicting liquid passage rates accounted for 94% (Seo *et al*. 2006), 84% and 83% (Seo *et al*. 2007) of the variation in prediction. Residual plots (residuals against predicted passage) of the liquid prediction model, together with that of Seo *et al*. (2006) revealed that models from both studies had no linear or mean bias in prediction of liquid passage rates. Although the model for liquid passage in this study accounted for less variation than models of Seo *et al*. (2006), it performed better in model validation using an independent dataset by accounting for 3 times more variation. Even though the liquid model in this study accounted for less variation in validation compared to that of Seo *et al*. (2009) (R^2 = 0.81), the latter study showed a linear bias in prediction of liquid passage rates.

A comparison between the coefficients of determination from this study (mathematical modelling) and those from other studies (mainly statistical modelling) showed more or less similar results. Seo *et al*. (2006) developed passage rate prediction equations for different ruminant types using dry matter intake of forage, and dry matter intake of forages and concentrates per unit of body mass. Their equations for predicting solid passage rate explained +21% (for forages) and +29% (for concentrates) more variation than the model developed in this study. However, the solid passage prediction model developed in this study explained more variation compared to other models which accounted for only 37% (Nsahlai and Apaloo 2007), 53% for forages (Cannas *et al*. 2004) and 65% for concentrates (Cannas *et al*. 2004), of observed variation. On validation using independent datasets, models only managed to account for 39% (forages) and 40% (concentrate) of the variation (Seo *et al*. 2006), which is lower than findings in this study for the solid passage rate prediction model evaluated.

On the contrary, evaluation of two prediction equations developed for forages from Seo *et al*. (2009), models explained more variation (66 and 86%) than the solid passage prediction model in our study, although RMSE in validation were similar to those of this study.

Models by Seo *et al*. (2009) had superior coefficients of determination for both liquids and solids compared to models in this study when evaluated using an independent dataset. Firstly, models of Seo *et al*. (2009) accounted for one of the most critical but neglected factor that influences passage rates i.e. feeding behaviour. This study did not include feeding behaviour as an input variable for passage rate predictions due to unavailability of information on feeding behaviour in all studies. Based on the influence of feeding behaviour on frequencies and amplitudes of reticulo-rumen contractions, it seems possible to develop prediction models for feeding behaviour; and then to input feeding behaviour variables into the solid and liquid passage rate prediction equations (Sauvant *et al*. 1996; Seo *et al*. 2007; 2009). However, this warrants a further study. Secondly, higher coefficients of determination of models by Seo *et al*. (2009) in evaluation may have been due to limited ruminant classes and limited intake level used in the evaluation as compared to the wide range of ruminant animals used in this study.

Ruminant animals grazing on tropical grasslands of Africa are subjected to feed shortages during the dry seasons due to droughts as a result of climate change. It is thought that ruminants exposed to starvation may retain digesta for long durations in the rumen to render digestion efficient. Hence, these ruminants generally elicit slower rates of passage of both solid and liquid in the rumen, and high rumen fill levels (Nsahlai *et al*. 1996) than temperate ruminants. Due to the impending feed shortages consequent upon drought, models developed for use in the future should consider accounting for hunger in prediction so as to accommodate changes in environmental conditions. Increased precision in prediction of passage rates of digesta for ruminant animals can be further improved by considering factors such as degree of hunger, water intake, feeding behaviour and climatic conditions.

3.5 Conclusion

Both solid and liquid passage rate prediction models achieved good accuracy in prediction as all ruminants were clustered along the ideal prediction line. The study developed more precise prediction models for solid and liquid passage rates for ruminants fed on a variety of diets and/or feeds from different climatic regions. There is still more work to be done to refine current prediction models so as to achieve precise prediction of passage rates of digesta in the rumen. The success of artificial neural networks in the prediction of solid and liquid passage rates in this study may pave a way for predicting roughage intake for diverse ruminant herbivores from different climatic regions using one prediction model.

Chapter 4

Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of Merino and Damara sheep, and Nguni goats under subtropical conditions

Abstract

Diurnal feeding behaviour is not usually used in predicting feed intake. The current study investigated the effect of tropical roughage and diet quality on dry matter intake, duration and number of daytime and night time eating bouts, idling sessions and ruminating activities in small ruminants. In Exp 1 and 2, roughage quality was improved by urea treatment of veld hay, while diet quality was improved by supplementing with lucerne hay (Exp 3), sunflower meal and lespedeza (Exp 4), fish meal (Exp 5a) and sunflower meal (Exp 5b). In all experiments goats and sheep were randomly allocated to experimental diets. Day-time (0600–1800 h) and night time (1800–0600 h) feeding behaviour activities of these animals were recorded. Roughage and diet quality had significant effects on rumination index in Exp 1, but not in Exp 2, 3 and 5. Time spent eating was significantly affected by roughage or diet quality (Exp 1, 3 and 4), period of the day (all experiments) and their interaction (Exp 1). Roughage or diet quality (Exp 1 and 5a), period of the day (all experiments) and their interactions (Exp 1) significantly affected the time spent ruminating. Surprisingly, intake rates (g/bout and g/min) were not affected by diet and roughage qualities in all experiments. Period of day had an effect on duration of rumination sessions (Exp 1, 2 and 3), however, diet or roughage quality affected the duration of eating bouts (Exp 3) and rumination sessions (Exp 1 and 2). Diet or roughage quality had a significant effect on the duration eating sessions in Exp 3 only, whilst period of day significantly affected this same behaviour in Exp 2 and 3. Diet quality and period interaction affected idling time whilst lying and on the duration of rumination bouts in Exp 1. Generally, goats and sheep fed on roughage alone ruminate at night and eat more during the day but those fed a roughage and supplemented with lucerne hay spent more time ruminating than eating. Time spent eating and ruminating had positive correlations to feed intake. Intake rates (g/min and g/bout) had strong positive correlations to intake, which were significant. There is a potential of using feeding behaviour to predict intake.

Additional keywords: Intake, Poor quality roughage, Daily feeding activities, Rumination, Small ruminant

4.1 Introduction

Small ruminants, sheep and goats, are becoming the most important livestock species for African pastoralist communities in semi-arid and arid areas of tropical Africa (Degen 2007) because they can survive in harsh conditions. Due to fluctuations in rainfall patterns, occurrence of droughts, desertification, limited crop cultivation and overgrazing, goats and sheep are increasingly facing feed shortages, especially during the dry seasons (Ben Salem and Smith 2008). The major constraint to ruminant production in semi-arid and arid areas of sub-Saharan Africa is poor nutrition due to abundance of feeds of low nutritional value, poor digestibility and scarcity of feeds (Osuji *et al*. 1995). Low levels of productivity in ruminants that graze on poor quality roughages may be a result of low feed intake. Due to the bulkiness of tropical roughages, ruminant animals fail to eat enough to meet their nutritional needs. Ruminants grazing on poorly digestible roughages may spend more time rechewing ingesta to render degradation more efficient, which may be viewed as an essential adaptation. However, spending more time rechewing ingesta would increase energy demand for maintenance and reduced time spent eating, resulting in animals failing to eat enough to meet requirements for maintenance and growth.

Diurnal feeding behaviour describes and encompasses activities such as time spent eating, ruminating, and idling, and the number of feeding and ruminating sessions ruminant herbivores partake on a normal circadian cycle. Duration of feeding behaviour measures may vary between individual ruminants of the same feeding type, physiological state, species, forage type, roughage quality, amount of feed allocated and probably the period of day (Emmans and Kyriazakis 2001). Influences of idling, rumination and eating/grazing on frequency and amplitudes of reticulo-rumen contractions which in turn affect fluid and solid passage rates may influence nutrient supply, microbial protein yields and roughage intake in ruminant herbivores.

In the dry seasons, small ruminants mainly depend on poor quality crop residues such as maize stover to supplement grazing. A number of technologies have been developed to improve nutritional status of animals during the dry season, but the rate of adoption by small-scale farmers is poor. These technologies include the use of cactus plant species as winter supplements, protein concentrate supplementation, treatment of hay or crop residues using lime, urea, ash or animal urine (non-protein nitrogen sources), chopping and soaking crop residues in water before offering to livestock (Ben Salem and Smith 2008). Urea treatment of poor quality hay or crop residues has been shown to increase digestibility by up to 5% more

than concentrate supplements, increases crude protein and energy values of forages, and generally improves the nutritional status of animals (Abdou *et al*. 2011).

Improvement of nutritional status in goats and sheep kept by pastoralist communities' would reduce live weight loss during the dry season necessitating increased feed intake. Reduction in live weight loss translates to a reduction in mortality of livestock, which may be viewed as a great achievement in drought stricken areas. The increased importance of goats and sheep in pastoral communities has necessitated the need for knowledge on how small ruminant production can be improved. The effects of feed intake on ruminant production are dictated by knowledge on feeding behaviour. There are no studies that determine how roughage intake and improvement of dietary roughage quality influences diurnal feeding behaviour in goats and sheep fed on non-supplemented urea-treated tropical veld hay, except for two studies by Chermiti *et al*. (1994) and Trach *et al*. (2001) in cattle fed on supplemented urea treated wheat and rice straw, respectively. Few studies, if any, done in subtropical and tropical Africa have evaluated all three major feeding behaviours during the day and at night at once. It is possible that diet and roughage quality affects feeding behaviour, and feeding behaviour would affect intake, so feeding behaviour should be included in mathematical models that seek to predict roughage intake in ruminant animals (Sauvant *et al*. 1996). The objective of the present study was to determine (1) how improvement of hay and diet quality influences feeding behaviour and intake in goats and sheep, (2) how day-time and night-time feeding behaviour patterns vary with diet and roughage quality, and (3) whether or not there is a link between feeding behaviour patterns and feed intake. The study tested the hypothesis that improvement of roughage and diet quality has an effect on diurnal feeding behaviour patterns and intake in goats and sheep.

4.2 Materials and methods

4.2.1 Study site

These experimental trials were conducted with the approval of the University of KwaZulu-Natal Ethics Committee; the Animal Ethics Subcommittee (ref. AREC/072/2015M) at the University of Kwazulu-Natal's Ukulinga Research Farm, Pietermaritzburg, in the subtropical hinterland of KwaZulu-Natal Province, South Africa. It lies at 30°24'S, 29°24'E at an altitude of 700m. Mean annual rainfall in the study site is approximately 735 mm, falling mostly in summer, between October and April. Maximum and minimum mean annual temperatures are

25.7 and 8.9°C, respectively. In extreme cases, summer temperatures may reach highs of above 36°C with minimum temperatures as low as 3°C at night in winter.

4.2.2 Animals, housing, feeds, diets and feeding

In Exp. 1, seven adult Merino wether sheep (average initial body mass of 56 ± 3.60 kg) were used. In one dietary treatment, roughage quality was enhanced by treating veld hay with 4% urea for 40 days to give hay of improved roughage quality (IRQ) and the other treatment was untreated veld hay with poor roughage quality (PRQ) (Table 4.1). Sheep were randomly allocated to either IRQ (n = 4) or PRQ (n = 3) and given approximately 2 kg DM of either IRQ or PRQ veld hay at 1000 h and 1500 h daily for the whole duration of the trial. In Exp. 2, 18 Nguni goats were divided into two groups that comprised of 9 light mass (average initial body mass of 16.94 ± 2.51 kg) and 9 heavy mass (average initial body mass of 33.6 ± 5.00 kg) goats. In one dietary treatment, roughage quality was enhanced by treating veld hay with 4% urea for 20 days to give hay of improved roughage quality (IRQ), in the second treatment, veld hay was sprayed with 4% urea before feeding to give semi-improved roughage quality (SIRQ), and the third treatment was untreated veld hay with poor roughage quality (PRQ) (Table 4.1). Each group was randomly allocated to either IRQ, SIRQ or PRQ making six goats/feed type and given approximately 2 kg DM/day of either IRQ, SIRQ or PRQ at 0800 h and 1500 h daily for the whole duration of the trial.

In Exp. 3, 25 Merino sheep (average initial body mass of 43.6 ± 11.5 kg) were blocked by body weight into 5 groups. Sheep in each group were randomly assigned to 5 dietary treatments in a completely randomised block design. These 5 diets were designed to provide a range of diet qualities that consisted of veld hay and lucerne hay only, mixed in varying proportions (Table 4.1). Final body mass was not determined because the trial duration was 7 days only, hence body mass changes were not reported. In Exp. 4, 12 Damara sheep (average initial body mass of 27.54 ± 3.68 kg) were randomly assigned to 4 different dietary treatments composed of varying levels of any one of three roughage sources: maize stover at milk stage, maize stover at dry stage and grass hay. Diet qualities were varied by mixing the roughage with any one of two protein sources: cottonseed meal and lespedeza (Table 4.1) in a completely randomised design. In Exp. 5, 64 Merino lambs (average initial body mass of 22.4 ± 3.65 kg) were randomly allocated to *Themeda triandra* hay offered *ad libitum*. Diet quality was improved by supplementing hay with 600 g of air-dried concentrates (Table 4.1). The concentrate portion of the diet was offered in two equal portions daily between 0800 to 0830 h

and between 1500 and 1530 h while the hay component was given after the allocated concentrate was completely consumed.

In all experiments, sheep and goats were allowed 14-day adaptation period to experimental diets and had > 3 days to adapt to conditions in the individual crates before feeding behaviour was recorded. Sheep and goats in each study were housed in individual crates (70 cm wide, 150 cm long and 90 cm high) with slatted wooden floors, and allowed ad libitum access to both roughage and water. Hay and maize stover were milled to pass through a 12 mm screen using a hammer mill (Scientec hammer mill 400, Lab World Pty Ltd, Johannesburg, RSA). Feed left in feeders was weighed daily before new feed allocation was done. Daily feed intake was calculated by subtracting feed left from feed allocated (Intake = feed in – feed out) in all experiments, except in Exp 4.

4.2.3 Behavioural assessment

Feeding behaviours assessed in each study were: duration of time spent eating, ruminating, idling whilst standing, idling whilst lying down during the day and at night. Number of feeding bouts and duration of each feeding bout during the day and at night were also determined for each study, in which the daytime period was taken to be from 0600 to 1800 h, and the night-time period was taken to be from 1800 to 0600 h. A circadian assessment of feeding behaviour was conducted for Exp. 1, 2, 3 and 5. In Exp. 1 and 2, five closed circuit television (CCTV) cameras were used to record the feeding behaviour of sheep and goats for 24 hours a day over a 5 and 4 day period, respectively. In Exp. 1 and 2, duration of activities were determined by watching the videos and recording durations and frequencies of each of these behaviours. In Exp. 3, feeding behaviour was recorded on 3 different days for periods of 24 hours at a time. Each 24-hour period was divided into 1 h long periods which in turn were divided into five-minute segments, and the activity of individual sheep observed and recorded. In Exp. 4, an observer positioned on a spot where all sheep could be seen and recorded feeding behaviour without disturbing them. Before any visual observation of sheep commenced, sheep were given feed ad libitum. Use of once-off feeding was adopted so as to have disturbance-free sessions when feeding behaviour was recorded. Activities were recorded at 2-minute intervals for 10 hours for 3 consecutive days. In Exp 5, each 24-hour day was divided into 8 periods of three hours each during which two enumerators (each assigned to specific animals) sat on either sides of the pens and recorded the activity of sheep every two minutes.

Moisture, dry matter, organic matter and ash were analysed using the procedures described by the Association of Official Analytical Chemists (AOAC 1999). Nitrogen content

was determined using the LECO TruSpec nitrogen analyser (LECO FP2000, LECO, Pretoria, South Africa). Crude protein content was calculated by multiplying the nitrogen content by a factor of 6.25 (Crude protein = nitrogen content × 6.25). Neutral detergent and acid detergent fibres were analysed using ANKOM A220 fibre analyser (ANKOM Technology, New York, USA). Hemicellulose content as determined by subtracting acid detergent fibre content from neutral detergent fibre content (Hemicellulose = neutral detergent fibre – acid detergent fibre). Crude fat content was determined using the Soxhlet method on the Soxhlet Buchi 810 fat analyser (Soxhlet Buchi, Switzerland).

Table 4.1 Chemical composition of experimental feeds

	Chemical composition (g/kg DM)						
Experiment 1	DM	CP	NDF	ADF	HEM	Ash	CF
IRQ	923	91	746	417	330	86	12
PRQ	926	40	735	391	344	67	13
Experiment 2							
IRQ	904	76	723	632	91	70	12
SIRQ	920	48	723	592	131	83	11
PRQ	923	20	735	581	154	89	13
Experiment 3							
100% PRQ	916	46	787	527	260	60	27
75% PRQ + 25% Lucerne hay	911	81	758	534	224	66	23
50% PRQ + 50% Lucerne hay	908	116	729	541	188	72	20
25% PRQ + 75% Lucerne hay	904	150	700	549	151	78	16
100% Lucerne-hay	900	185	672	556	116	84	12
Experiment 4							
60% MSM+ 40% SFM	896	192	455	279	176	69	16
60% MSM+ 40% LSP	901	77	544	353	191	68	19
40% MSD + 60% SFM	910	235	456	273	183	69	16
60% GH + 40% SFM	919	179	532	324	209	64	27
Experiment 5 a							
Themeda triandra hay	931	61	733	440	293	40	12
TTH + 16% FM concentrate	902	111	366	203	220	59	31
TTH + 20% FM concentrate	903	134	365	203	219	68	29
TTH + 24% FM concentrate	906	162	382	203	229	72	32
TTH + 28% FM concentrate	907	183	383	203	229	76	36
Experiment 5 b							
TTH + 16% SFM concentrate	908	112	401	210	235	52	32
TTH + 20% SFM concentrate	911	134	422	210	247	60	34
TTH + 24% SFM concentrate	911	157	447	210	261	66	36
TTH + 28% SFM concentrate	916	179	471	210	331	67	38

IRQ: improved roughage quality; PRQ: poor roughage quality; SIRQ: semi-improved roughage quality; MSM: maize stover at milk stage; MSD: maize stover at dry stage; SFM: sunflower meal; FM: fish meal; LP: lespedeza; GH: grass hay; TTH: *Themeda triandra* hay; DM: dry matter; CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; HEM: hemicellulose; CF: crude fat.

4.2.4 Statistical analysis

Effects of roughage and diet quality on intake (except Exp 4) and feeding behaviour were analysed using the General Linear Model (GLM) procedure of SAS 9.3 software (SAS Institute Inc., Cary, NC, USA). The GLM procedure was also used to determine the effect of roughage quality, period of day, and roughage quality and period of day interactions on feeding behaviour parameters (Exp. 1, 2, 3 and 5). The Student-Newman-Keuls (SNK) test was used to separate sample means that were significantly different from each other at *P* <0.05. Initial body mass (BM) was taken as a covariate. The experimental model for feeding behaviour was as follows: $FB_{ijkl} = \mu + R_i + P_j + (R \times P)_{ij} + BM_k + e_{ijkl}$, where: FB = Feeding behaviour (eating time, ruminating time, idling time whilst standing, idling time whilst lying), μ = overall mean, R_i = effect of roughage or diet quality, P_j = effect of period of the day (j = Day; Night), $(R \times P)_{ij}$ = effect of roughage quality and period of day interactions and e_{ijkl} = experimental random error.

4.3 Results

4.3.1 Effect of improving veld hay quality on diurnal feeding behaviour in Merino sheep

In Exp 1, as expected, DM and NDF intake increased by +41% and +43% for sheep fed on IRQ compared to sheep fed PRQ. Time spent ruminating per unit of dry matter and NDF intake were significantly higher by +279 and +387 min/day, respectively, for sheep fed PRQ compared to those fed IRQ. Interestingly, average dry matter intake rates per unit time and feeding bout were similar for these two roughage qualities (Table 4.2). On an average day, sheep fed on IRQ spent 19, 34 and 47% whilst those fed on PRQ spent 13, 45 and 42% of the day eating, ruminating and idling, respectively (Table 4.3). There was great variation in daytime and night-time feeding behaviour patterns between and within each dietary treatment. Daily eating time and time spent idling whilst lying were greater by +86 and +137 min/day for sheep fed on IRQ compared to PRQ, respectively.

However, daily ruminating time and duration of ruminating bouts were higher by +160 and +10 min/day, respectively, for sheep fed PRQ compared to those fed IRQ. Eating and ruminating time were affected by roughage quality, period of day and their interaction (*P*<0.01). Roughage quality had no effect on the daily number and duration of eating bouts, and on the daily number of ruminating bouts and daily time spent idling whilst standing. Sheep fed IRQ spent significantly more time eating during the day (+82 min/day), but less time ruminating during the day (-42 min/day) and night (-119 min/day) compared to those fed on

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PRQ. On the contrary, time spent eating during the night was similar for both dietary treatments. Irrespective of roughage quality, sheep spent significantly more time eating during the day than at night (+170 and +93 min/day for IRQ and PRQ, respectively), but less time ruminating during the day than at night (-117 and -194 min/day for IRQ and PRQ, respectively). Duration of feeding bouts were not affected by roughage quality, period of day or their interaction ($P>0.05$). Roughage quality, period of day and their interaction affected the duration of ruminating bouts. Ruminating sessions were +3 and +12 min longer for sheep fed IRQ and PRQ, respectively, at night than during the day. Day-time (+5 min) and night time (+14 min) duration of ruminating bouts were greater for sheep fed PRQ compared to those fed IRQ.

As expected, the number of ruminating and eating bouts were affected by period of day ($P<0.05$), but not by roughage quality or diet x period of day interactions ($P>0.05$). Number of ruminating bouts was higher at night than during the day (+3 and +2 for IRQ and PRQ, respectively). Sheep visited feeding troughs 3 times more during the day than at night. As anticipated, time spent idling whilst standing was not affected by roughage quality ($P>0.05$), but daytime and night-time idling patterns were different ($P<0.05$).

Sheep spent more time idling whilst standing during the day (+25 and +76 min for IRQ and PRQ, respectively) than at night. During the day, sheep fed PRQ stood idling for +57 min more than those fed on IRQ. Unexpectedly, idling time whilst lying was not affected by period of day ($P<0.05$), but was significantly affected by roughage quality and their interaction. Time spent idling whilst lying was greater at night than during the day by +79 and +33 min for IRQ and PRQ, respectively. At night, sheep fed IRQ spent significantly more time idling whilst lying (+125 min) than sheep fed on PRQ. As expected, chewing time was not affected by period of day ($P>0.05$), but was significantly affected by diet and diet $\times$ period interactions. Sheep fed IRQ chewed less (-74 min/day) than sheep fed PRQ. However, sheep fed PRQ chewed more (+114 min) at night and less (-40 min) during the day than those fed on IRQ. Sheep fed PRQ lost 0.14 kg/day more than those fed on IRQ.

Table 4.2 Effect of improving veld hay quality on diurnal feeding behaviour in Merino sheep (Exp 1, 3 and 5), Nguni goats (Exp 2) and Damara sheep (Exp 4)

	Intake (kg/day)		Rumination time (per day)		DM intake rate		BMC
Experiment 1	DM	NDF	(min/kgDMI)	(min/kgNDFI)	(g/min)	(g/bout)	(kg/day)
IRQ	1.55[a]	1.16[a]	318[b]	426[b]	5.8[a]	148[a]	-0.02[a]
PRQ	1.10[b]	0.81[b]	597[a]	813[a]	6.1[a]	119[a]	-0.16[b]
RMSE	0.0966	0.0725	45.62	61.85	1.2	22.4	0.0494
Experiment 2							
IRQ	0.92[a]	0.83[a]	421[a]	466[a]	3.2[a]	65[a]	-0.012[a]
SIRQ	0.89[a]	0.81[a]	390[a]	424[a]	3.1[a]	72[a]	-0.032[a]
PRQ	0.63[a]	0.58[a]	513[a]	556[a]	2.6[a]	55[a]	-0.071[b]
RMSE	0.2717	0.2482	146.6	159.4	1.025	22.71	0.023
Experiment 3							
100% PRQ	1.09[a]	0.94[a]	546[a]	636[a]	2.97[a]	56.2[a]	NR
75% PRQ + 25% LH	1.25[a]	1.04[a]	492[a]	592[a]	3.90[a]	72.7[a]	NR
50% PRQ + 50% LH	1.41[a]	1.13[a]	442[a]	550[a]	4.59[a]	73.6[a]	NR
25% PRQ + 75% LH	1.37[a]	1.06[a]	502[a]	648[a]	5.42[a]	76.3[a]	NR
100% Lucerne hay	1.59[a]	1.19[a]	370[a]	496[a]	6.20[a]	90.6[a]	NR
RMSE	0.5130	0.4031	157.9	198.8	1.947	30.77	NR
Experiment 5a							
TTH + 16% FM	0.91[a]	0.37[a]	546[a]	1339[a]	4.24[a]	50.0[a]	0.174[a]
TTH + 20% FM	0.92[a]	0.37[a]	619[a]	1520[a]	4.01[a]	50.8[a]	0.199[a]
TTH + 24% FM	0.92[a]	0.39[a]	527[a]	1248[a]	4.13[a]	50.6[a]	0.180[a]
TTH + 28% FM	0.89[a]	0.37[a]	624[a]	1477[a]	3.74[a]	49.7[a]	0.188[a]
RMSE	0.056	0.023	84.60	202.2	0.878	5.397	0.060
Experiment 5b							
TTH + 16% SFM	0.90[a]	0.39[b]	550[a]	1253[a]	4.12[a]	49.7[a]	0.163[a]
TTH + 20% SFM	0.92[a]	0.42[a]	522[a]	1141[a]	4.18[a]	51.6[a]	0.138[a]
TTH + 24% SFM	0.94[a]	0.44[a]	489[a]	1043[a]	4.65[a]	52.1[a]	0.145[a]
TTH + 28% SFM	0.90[a]	0.45[a]	531[a]	1060[a]	4.20[a]	49.6[a]	0.096[b]
RMSE	0.055	0.025	84.79	185.2	1.266	5.063	0.042

IRQ: improved roughage quality; PRQ: poor roughage quality; SIRQ: semi-improved roughage quality; DMI: dry matter intake; NDFI: neutral detergent fibre intake; MSM: maize stover at milk stage; MSD: maize stover at dry stage; SFM: sunflower meal; LP: lespedeza; LH: lucerne hay; TTH: *Themeda triandra* hay; BMC: body mass change.

[a, b] Means in a column with different superscripts are significantly different

4.3.2 Effect of improving veld hay quality on diurnal feeding behaviour patterns in Nguni goats

In Exp 2, unexpectedly, average dry matter intake, NDF intake, ruminating indices (dry matter and NDF) and average dry matter intake rates per unit time and feeding bout were similar for all 3 roughage qualities in goats (Table 4.2). On an average day goats spent 20% eating, 28% ruminating and 52% idling (IRQ), 20% eating, 25% ruminating and 50% idling (SIRQ), but spent 17% eating, 21% ruminating and 62% idling (PRQ) (Table 4.4). Roughage quality had no significant effect on all feeding behaviour parameters except for number of ruminating bouts. Surprisingly, there were no effects of roughage quality and roughage quality × period of the day interactions on all feeding behaviours measured. However, period of day significantly affected all feeding behaviour parameters except for time spent chewing. As expected, goats spent more time eating during the day than at night by +140 min (IRQ), +179 min (SIRQ) and +137 min (PRQ), more time standing while idling during the day than at night by +104 min (IRQ), +120 min (SIRQ) and +155 min (PRQ), and more time ruminating at night than during the day by +179 min (IRQ), +180 min (SIRQ) and +157 min (PRQ). Number of eating bouts were greater during the day than at night (+6 for all roughage qualities), however, the number of ruminating bouts were greater during the night than during the day by +5 (IRQ and PRQ) and +6 (SIRQ). Duration of eating bout was greater during the day than at night across all roughage qualities (+4, +8 and +3 min for IRQ, SIRQ and PRQ, respectively). An opposing trend was observed for the duration of ruminating bout which was longer at night than during the day (+5, +4 and 6 for IRQ, SIRQ and PRQ, respectively). Goats spent more time lying at night than during the day (+69, +122 and +138 min for IRQ, SIRQ and PRQ, respectively). Goats fed PRQ lost -0.06 and -0.04 kg/day more than those on IRQ and SIRQ, respectively.

4.3.3 Effect of varying levels of lucerne hay on diurnal feeding behaviour patterns in Merino sheep

In Exp 3, diet quality had no effect on average dry matter intake, ruminating indices (dry matter and NDF), NDF intake and average dry matter intake rates per unit time and feeding bout (Table 4.2). On an average day sheep spent 25% eating, 39% ruminating and 36% idling (100% PRQ); 23% eating, 42% ruminating and 35% idling (75% PRQ); 21% eating, 38% ruminating and 41% idling (50% PRQ); 18% eating, 40% ruminating and 42% idling (25% PRQ); 19% eating, 37% ruminating and 44% idling (100% LH) (Table 4.5). Diet had an effect on eating and chewing time, time spent idling whilst standing, and duration of eating bouts. Increasing levels of lucerne hay decreased eating time during the day (-32, -45, -77 and -67 min for 25%

LH, 50% LH, 75% LH and 100% LH, respectively) and at night (-7, -20, -34 and -32 min for 25% LH, 50% LH, 75% LH and 100% LH, respectively) relative to 100% PRQ. Similarly, overall chewing times decreased during the day (-1, -17, -46 and -87 min for 25% LH, 50% LH, 75% LH and 100% LH, respectively) and at night (+1, -29, -22 and -20 min for 25% LH, 50% LH, 75% LH and 100% LH, respectively) relative to 100% PRQ. Differences in time spent idling while standing did not follow a consistent trend with increasing lucerne content of diets during the day (-9, +16, +38 and +61 for 25% LH, 50% LH, 75% LH and 100% LH diets, respectively), but increased gradually at night (+1, +14, +29 and +40 for 25% LH, 50% LH, 75% LH and 100% LH diets, respectively) with reference to 100% PRQ. Period of day influenced all feeding behaviours measured, whilst time spent chewing and number of ruminating bouts were significantly affected by diet and period of the day interactions. Sheep spent more time eating during the day than at night (+83, +58, +58, +40 and +48 min for 100% PRQ, 25% LH, 50% LH, 75% LH and 100% LH diets, respectively), surprisingly, spent more time ruminating during the day than at night (+6, +29, +75, +49 and -6 min for PRQ, 25% LH, 50% LH, 75% LH and 100% LH diets, respectively) and less time idling while standing at night than during the day (-28, -18, -30, -37 and -49 min for 100% PRQ, 25% LH, 50% LH, 75% LH and 100% LH diets, respectively). Duration of eating bouts were greater during the day (+7, +7, +6, +2, and +1 min for PRQ, 25% LH, 50% LH, 75% LH and 100% LH diets, respectively) than at night, and so were the number of eating bouts (+1 for all diets). Duration of ruminating sessions were surprisingly greater during the day (+3, +5, +6, +4 and -1, for PRQ, 25% LH, 50% LH, 75% LH and 100% LH diets, respectively) than at night, although the frequency of ruminating bouts was greater at night than during the day. Sheep spent more time lying at night (+118, +107, +162, +126 and +91 for PRQ , 25% LH, 50% LH, 75% LH and 100% LH diets, respectively) than during the day.

4.3.4 Effect of varying levels of lespedeza and sunflower meal on daytime feeding behaviour patterns in Damara sheep

In Exp 4, on an average 10 h daytime period sheep spent 36% eating, 22% ruminating and 42% idling (MSM + 40% SFM); 48% eating, 27% ruminating and 25% idling (40% LSP); 26% eating, 19% ruminating and 55% idling (60% SFM) and 32% eating, 23% ruminating and 45% idling (GH + 40% SFM) (Table 4.6). Type of diet had no effect on times spent ruminating, idling whilst standing, and on the number of eating and ruminating sessions (*P*>0.05). The time spent eating was statistically similar for all diets, except for sheep fed on 40% LSP that ate +134 min longer than those fed on 60% SFM diet. Supplementation with 40% SFM compared

to 40% LSP when MSM was the main roughage source increased chewing time (+104 min). Feeding MSD compared to GH as main roughage in diets supplemented with SFM increased chewing time (+59 min). There was no effect of feeding MSM compared to GH as the main roughage source in a diet with 40% SFM. Feeding MSM compared to MSD in diets fed with SFM significantly lowered chewing time (-79 min). Sheep fed on MSM+LSP diets significantly spent less time chewing compared to those fed MSD+SFM (-183 min) and GH+SFM (-124 min). Except for sheep fed MSM+LSP which spent more time eating per session (+4, +6 and 4 min) compared to other dietary treatments, durations of eating bouts were similar across 3 diets ($P>0.05$). Supplementation with 40% SFM with 40% LSP when MSM was the main roughage source significantly increased duration of ruminating sessions (+3 min).

4.3.5 Effect of varying levels of fish and sunflower meals on diurnal feeding behaviour patterns in Merino sheep

In Exp 5a, diet quality had no effect on intake, rumination indices and intake rates (Table 4.2). On an average day, sheep spent 15-17% eating, 34-39% ruminating and 45-51% idling across all levels of FM supplementation (Table 4.7). As expected, diet quality and diet × period of day interactions had no effects on the duration of eating and ruminating sessions, and the number of eating and ruminating sessions lin sheep fed increasing levels of FM supplement. Duration of eating bouts were +11, +17, +12 and +15 min more during the day than at night for sheep fed on 16, 20, 24 and 28% FM supplement. However, duration of ruminating sessions were greater at night than during the day by +4, +7, +5 and +8 min (16, 20, 24 and 28% FM supplement, respectively). Interestingly, number of ruminating bouts were greater during the day (+7, +5, +6 and +6 for 16, 20, 24 and 28% FM supplementation, respectively) than at night. Sheep supplemented with FM gained on average +0.185 kg/day in body mass.

Generally, sheep spent 15-16% eating, 33-40% ruminating and 44-51% idling across all levels of SFM supplementation (Exp 5b). Diet quality had no effects on all diurnal feeding behaviour parameters in sheep fed increasing levels of SFM supplement (Table 4.7). Period of day affected time spent ruminating and eating, duration of eating and ruminating sessions, and number of ruminating sessions. There was no effect of diet and period of day interactions on all feeding behaviour parameters. Duration of eating sessions were +11, +14, +12 and +12 min more during the day than at night for sheep fed 16, 20, 24 and 28% SFM supplement, respectively. Duration of ruminating bouts were +5, +8, +5 and +5 min more at night than during the day for sheep fed on 16, 20, 24 and 28% SFM supplement. Unexpectedly, the number of ruminating bouts was greater during the day than at night (+6, +7, +6 and +5 for

sheep fed on 16, 20, 24 and 28% SFM supplement, respectively). Generally, sheep spent more time eating during the day (+91, +111, +108 and +105 min for sheep fed on 16, 20, 24 and 28% SFM supplement) than at night, and spent more time ruminating at night (+95, +102, +92 and 110 min for 16, 20, 24 and 28% SFM supplement) than during the day. Times spent idling and chewing were evenly distributed throughout the day and at night. Generally sheep supplemented with SFM on average gained +0.148 kg/day in body mass, however, sheep supplemented with 28% SFM gained 0.053 kg/day below average body weight gain observed in the other dietary treatments.

All feeding behaviours had significant positive correlations to intake (Table 4.8). Time spent chewing and ruminating correlation coefficients ≈0.5 to intake which were significant ($P<0.05$). There was a significant ($P<0.05$) correlation between time spent ruminating and eating ($R>0.5$) to time spent chewing. Time spent eating was positively correlated to time spent ruminating ($R<0.5$; $P>0.05$). Intake rates were positively correlated to intake ($R>0.7$; $P<0.0001$). Surprisingly, the major feed attributes (NDF and ADF) though positively correlated between them ($P<0.001$) had positive correlations to intake which were highly significant ($P<0.005$). Crude protein content had positive but significant correlations to times spent eating and ruminating, and intake rates.

Table 4.3 Effect of improving veld hay quality on duration of day-time and night-time feeding behaviour patterns in Merino sheep (Exp 1)

Behaviour	Feeds						RMSE	Significance of influence		
	IRQ			PRQ				Feed	Period	Feed × Period
	Day	Night	24 h period	Day	Night	24 h period				
Time spent (min)										
Eating	222	52	274^a	140	47	187^b	23.54	*	***	*
Ruminating	188	305	493^b	230	424	654^a	9.624	***	***	***
Chewing	410	357	767^b	370	471	841^a	21.72	*	NS	***
Idling – standing	112	87	199^a	169	93	262^a	26.71	NS	**	NS
Idling – lying	198	277	475^a	185	152	338^b	45.45	*	NS	*
Duration of bouts (min)										
Eating	28	20	26^a	20	19	21^a	5.363	NS	NS	NS
Ruminating	20	23	22^b	25	37	32^a	3.292	***	***	*
Number of bouts										
Eating	8	3	11^a	7	2	9^a	1.296	NS	***	NS
Ruminating	10	13	23^a	10	12	22^a	1.912	NS	*	NS

Idling: any period of time when the animal is not ruminating or eating, and includes behaviours such as licking, fighting, drinking water, scratching and sleeping.

Period: day and night; IRQ: improved roughage quality; PRQ: poor roughage quality

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4.4 Effect of improving veld hay quality on duration of day-time and night-time feeding behaviour patterns in Nguni goats (Exp 2)

Behaviour	Feeds									RMSE	Significance of influence		
	IRQ			SIRQ			PRQ				Feed	Period	F × P
	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h				
Time spent (min)													
Eating	216	76	292	237	58	295	193	56	249	39.90	NS	***	NS
Ruminating	112	291	403	89	269	358	70	227	297	65.99	NS	***	NS
Chewing	328	366	694	326	327	653	263	283	546	71.17	NS	NS	NS
Idling – standing	158	54	212	166	46	212	208	53	261	38.83	NS	***	NS
Idling – lying	231	300	531	225	347	572	246	384	630	78.93	NS	**	NS
Duration of bouts (min)													
Eating	22	18	21	26	18	25	22	19	21	3.221	NS	***	NS
Ruminating	24	29	27	23	27	26	16	25	23	4.886	*	**	NS
Number of bouts													
Eating	10	4	14	9	3	12	9	3	12	1.529	NS	***	NS
Ruminating	5	10	15	4	10	14	4	9	13	2.069	NS	***	NS

Idling: any period of time when the animal is not ruminating or eating, and includes behaviours such as licking, fighting, drinking water, scratching and sleeping.

Period: day and night; IRQ: improved roughage quality; SIRQ: semi-improved roughage quality; PRQ: poor roughage quality; F × P: feed × period interactions.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4.5 Effect of varying veld hay to lucerne hay ratios on duration of day-time and night-time feeding behaviour patterns in Merino sheep (Exp 3)

| | Diets | | | | | | | | | | | | | | | Significance of influence | | |
| | 100% PRQ | | | 75% PRQ + 25% LH | | | 50% PRQ + 50% LH | | | 25% PRQ + 75% LH | | | 100% LH | | | | | |
Behaviour	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h	Day	Night	RMSE	Diet	Period	D × P
TSE (min)	225	142	367	193	135	328	180	122	302	148	108	256	158	110	27.61	***	***	NS
TSR (min)	282	276	558	314	285	599	312	237	549	314	265	579	263	269	30.99	NS	**	*
TSC (min)	508	209	717	507	210	717	491	180	671	462	187	649	421	189	27.87	**	***	*
TSIS (min)	82	54	136	73	55	128	98	68	166	120	83	203	143	94	28.44	***	***	NS
TSIL (min)	130	248	378	139	246	385	131	293	424	138	264	402	157	248	42.36	NS	***	NS
DEB (min)	22	15	19	23	16	19	19	13	16	15	13	13	15	14	3.172	***	***	NS
DRB (min)	26	23	24	29	24	27	26	20	23	27	23	24	22	23	2.827	*	***	*
NEB	10	9	19	9	8	17	10	9	19	10	9	19	10	8	1.459	NS	*	NS
NRB	11	12	23	11	12	22	12	12	24	12	12	24	12	12	0.573	NS	*	*

Idling: any period of time when the animal is not ruminating or eating, and includes behaviours such as licking, fighting, drinking water, scratching and sleeping.

PRQ: poor roughage quality; LH: lucerne hay; TSE: time spent eating; TSR: time spent ruminating; TSC: time spent chewing; TSIS: time spent idling whilst standing; TSIL: time spent idling whilst lying; DEB: duration of eating bouts; DRB: duration of ruminating bouts; NEB: number of eating bouts; NRB: number of ruminating bouts; Period: day and night; D × P: diet × period interactions; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4.6 Effect of varying levels of protein supplementation using lespedeza and sunflower meal on duration of 10 h day-time feeding behaviour patterns in Damara sheep (Exp 4)

Behaviour	60% MSM + 40% SFM	60% MSM + 40% LSP	40% MSD + 60% SFM	60% GH + 40% SFM	RMSE	p value
		Diets			Significance	
Time spent (min)						
Eating	219[ab]	290[a]	156[b]	189[ab]	44.32	0.0305
Ruminating	131[a]	163[a]	115[a]	140[a]	25.14	0.2104
Chewing	350[b]	454[a]	271[c]	330[b]	26.37	0.0002
Idling – standing	77[ab]	43[b]	139[a]	78[ab]	34.96	0.0535
Idling – lying	174[a]	104[b]	190[a]	193[a]	28.25	0.0149
Duration of bouts (min)						
Eating	11[b]	15[a]	9[b]	11[b]	1.322	0.0048
Ruminating	6[b]	9[a]	6[b]	7[ab]	1.118	0.0309
Number of bouts						
Eating	6[a]	7[a]	6[a]	6[a]	0.7071	0.3999
Ruminating	6[a]	6[a]	6[a]	7[a]	1.0408	0.7006

Idling: any period of time when the animal is not ruminating or eating, and includes behaviours such as licking, fighting, drinking water, scratching and sleeping; MSM: maize stover at milk stage, MSD: maize stover at dry stage; SFM: sunflower meal; LP: lespedeza; GH: grass hay; LH: lucerne hay.

[a, b] Means in a row with different superscripts are significantly different ($P < 0.05$).

4.4 Discussion

Diurnal feeding behaviour in ruminant herbivores is not seen as a way of predicting feed intake, but rather as a way of explaining intake (Emmans and Kyriazakis 2001). The influence of diet and roughage qualities on eating, ruminating and idling behaviour, and roughage intake in ruminant animals fed low quality roughages in subtropical and tropical Africa have been overlooked. Thorough understanding of intake in ruminants involves studying the major aspects of feeding behaviour; eating, ruminating, and idling (Abijaoude *et al*. 2000). From the current study, it is clear that roughage quality has profound effects on diurnal feeding behaviour patterns in goats and sheep. Consistent with our expectations (in Exp 1) and findings by Wanapat *et al*. (2009) and Gunun *et al*. (2013), sheep fed IRQ (urea treated hay) ate more than those fed PRQ (untreated hay), although Chermiti *et al*. (1994), Trach *et al*. (2001) and, Mesfin and Ledin (2004) reported lower dry matter intake of urea treated teff and barley straw in cattle. Unexpectedly goats fed IRQ, SIRQ and PRQ (Exp 2) ate statistically equal amounts these

feeds, though the tendency was IRQ>SIRQ>PRQ, confirming that urea treatment is more than just additional CP. Sheep and goats are sensitive to the four primary tastes: sweet, salty, bitter and sour (Baumont *et al.* 2000) and odoriferous compounds (Arnold *et al.* 1980). Improvement of roughage quality using urea may have altered one of the four tastes leading sheep to consume more (Exp 1), but not goats (Exp 2). Urea-treated hay is characterised by a strong pungent odour, which is expected to deter animals from eating (Mesfin and Ledin 2004). However, it seems that sheep (Exp 1) preferred eating more of the hay with a pungent odour than goats (Exp 2). Sensory perception of these compounds might be different in goats and sheep. Thus, research should assess whether the pungent odour, colour and taste of urea treated hay is partly responsible for changing intake in sheep (Exp 1), goats (Exp 2) and cattle (Mesfin and Ledin 2004). Furthermore, the effect of scent on feeding behaviour and intake warrants research. Unexpectedly, improving diet quality by increasing levels of lucerne hay, and supplementation with fish and sunflower meals did not alter feed intake in sheep.

Table 4.7 Effect of different inclusion levels of fish meal and sunflower meal on duration of day-time and night-time feeding behaviour patterns in Merino sheep (Exp 5)

Diets	Period	Behaviour (min)							
		TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Experiment 5a									
TTH + 16% FM	Day	154	219	373	346	19	15	9	16
	Night	66	276	342	376	8	19	9	9
	24 h	220	495	715	722	12	19	18	25
TTH + 20% FM	Day	180	233	414	305	23	16	9	15
	Night	57	333	390	329	6	23	10	10
	24 h	237	566	804	634	12	23	19	25
TTH + 24% FM	Day	164	198	362	357	20	14	9	15
	Night	66	286	352	367	8	19	9	9
	24 h	230	484	714	724	13	20	18	24
TTH + 28% FM	Day	186	215	400	318	23	15	9	15
	Night	62	333	395	323	8	23	9	9
	24 h	248	548	795	641	14	23	18	24
Significance	RMSE	27.33	40.64	51.79	51.70	7.330	4.799	2.798	2.820
	Diet	NS	*	*	*	NS	NS	NS	NS
	Period	***	***	NS	NS	***	***	NS	***
	Diet × Period	NS	NS	NS	NS	NS	NS	NS	NS
Experiment 5b									
TTH + 16% SFM	Day	156	198	354	365	19	14	9	15
	Night	65	293	358	361	8	19	9	9
	24 h	221	491	712	726	12	35	18	14
TTH + 20% SFM	Day	168	187	355	364	21	12	9	16
	Night	57	289	347	372	7	20	9	9
	24 h	225	476	702	736	13	19	18	25
TTH + 24% SFM	Day	168	184	352	367	20	13	9	15
	Night	60	276	336	383	8	18	9	9
	24 h	228	460	688	750	13	19	18	24
TTH + 28% SFM	Day	168	183	352	367	20	13	10	14
	Night	63	293	356	362	8	18	9	9
	24 h	231	476	708	729	12	21	19	23
Significance	RMSE	33.70	41.87	53.59	53.49	6.384	3.571	2.874	2.788
	Diet	NS	NS	NS	NS	NS	NS	NS	NS
	Period	***	***	NS	NS	***	***	NS	***
	Diet × Period	NS	NS	NS	NS	NS	NS	NS	NS

Idling: any period of time when the animal is not ruminating or eating, and includes behaviours such as licking, fighting, drinking water, scratching and sleeping.

TTH: *Themeda triandra* hay; TSE: time spent eating; TSR: time spent ruminating; TSC: time spent chewing; TSIS: time spent idling whilst standing; TSIL: time spent idling whilst lying; DEB: duration of eating bouts; DRB: duration of ruminating bouts; NEB: number of eating bouts; NRB: number of ruminating bouts; Period: day and night; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4.8 Pearson correlation of feed attributes and feeding behaviour parameters in Exp 1, 2, 3 and 5

DMI	TSR	TSE	TSC	IRgmin	IRgbout	DM	CP	NDF	ADF	HEM	
	0.47 (<.0001)	0.21 (0.022)	0.50 (<.0001)	0.70 (<.0001)	0.77 (<.0001)	-0.11 (0.24)	0.11 (0.2335)	0.33 (0.0003)	0.28 (0.0031)	-0.03 (0.7510)	DMI
		0.10 (0.272)	0.89 (<.0001)	0.32 (0.0004)	0.29 (0.0015)	-0.24 (0.0099)	0.25 (0.0081)	-0.07 (0.4484)	0.15 (0.1083)	0.25392 (0.0064)	TSR
			0.54176 (<.0001)	-0.50 (<.0001)	0.09 (0.3564)	0.09 (0.3589)	-0.28 (0.0026)	0.48 (<.0001)	0.47969 (<.0001)	-0.22 (0.0173)	TSE
				0.05 (0.6290)	0.28827 (0.0019)	-0.16 (0.0822)	0.08 (0.3915)	0.16 (0.0935)	0.09 (0.3416)	0.11 (0.2274)	TSC
					0.59 (<.0001)	-0.11 (0.2256)	0.27 (0.0034)	-0.01 (0.8869)	-0.08 (0.4214)	0.16 (0.0980)	IRgmin
						0.30 (0.0012)	-0.21 (0.0217)	0.50 (<.0001)	0.38 (<.0001)	0.06 (0.5215)	IRgbout
							-0.56 (<.0001)	0.47 (<.0001)	0.25 (0.0066)	0.38 (<.0001)	DM
								-0.64 (<.0001)	-0.61 (<.0001)	0.23 (0.0127)	CP
									0.94 (<.0001)	-0.34 (0.0003)	NDF
										-0.62 (<.0001)	ADF
											HEM

n = 114 and 22 diets.

TSR: time spent ruminating; TSE: time spent eating; TSC: time spent chewing; IRgmin: intake rate g/min; IRgbout: intake rate g/bout; DM: dry matter; CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; HEM: hemicellulose.

In this study, sheep and goats across all experiments maintained similar intake rates, thus differences in feed intake in any of the experiments would only be due to differences in time spent eating, bite frequency and bite size. Unfortunately, bite frequency and size were not measured in this study. Similar conclusions were drawn by Penning *et al*. (1995) and Rutter *et al*. (2002). In accordance with Rutter *et al*. (2002) who worked on sheep fed on rye grass and clover, dry matter intake rates were not affected by dietary treatments. This suggests that under any dietary condition intake rates are under the control of the animal's physiological status in

ruminant animals fed indoors. Under grazing conditions, intake rates are affected by feed factors such as leaf size and sward height (Prache 1997), which are non-existent indoors.

Ruminant animals reduce intake rates and increase eating time, and vice versa, so as to maintain desired feed intake levels through management of grazing or eating time (Baumont *et al*. 2004). This motivation to eat depends on the animal's needs and, day and night time feeding patterns. Hay treatments used in our study (Exp 1 and 2) were of the same grass species with their quality differing as a result of treatment with urea only, although, there was a possibility of slight differences in organoleptic properties between these treatments, intake rates for IRQ, SIRQ and PRQ hays were expected to be similar. Intake rates for feeds and diets in this study are similar to those obtained by Baumont *et al*. (1997) with sheep fed lucerne hay, but different from those by Dominigue *et al*. (1991). Initial intake rates accounted for most differences in daily feed intake (Baumont *et al*. 1997), but unfortunately it was not measured in these studies. Contrary to results from Exp 1 and 2, Chermiti *et al*. (1994) and Trach *et al*. (2001) reported increased intake rates in cattle fed urea treated straw. Intake rates in cattle were approximately 3 times higher in the study by Chermiti *et al*. (1994), and Trach *et al*. (2001) than in sheep in Exp 1.

So, from the above, it seems possible that roughage intake may be controlled using two methods that are antagonistic: by either increasing eating time whilst maintaining constant intake rates (Baumont *et al*. 2004), or by increasing intake rates whilst maintaining constant eating time; both of these warrants further study. Differences in rumen fill levels at any given time between sheep and goats on all treatments may govern feed intake by partially controlling intake rates and time spent eating. The lower the rumen fill levels the more receptive space in the rumen to accommodate more feed and eventually the greater the intake rate and time spent eating. Rumen fill levels and fatigue as a result of increasing eating time to compensate for low intake rates can barely be used to explain the overall time spent eating and ultimately intake in ruminant animals (Penning *et al*. 1995). Additionally, most studies, including the current study have failed to focus on and account for the effect of the number of hedonic feeding sessions and their duration as a factor that increases time spent eating. Studies have reported different frequencies of small meals across different types of hay, and although durations of small meals were not reported, small meals increased time spent eating by sheep (Baumont *et al*. 1997) and increased feed intake in goats (Abijaoude *et al*. 2000). The challenge lies in setting a time range for feeding bouts to be classified as hedonic. It is worthwhile to determine how roughage and diet quality improvement techniques (such as urea, lime and ash treatment of hay,

supplementation using protein concentrates) and period of the day influence frequencies and duration of hedonic bouts in pen fed and grazing ruminants.

Generally, ruminants spend more time ruminating compared to eating. This is in line with our findings from all experiments, although findings by Abijaoude *et al.* (2000) have shown that there is a tendency to spend more time eating than ruminating in goats fed on different diets. Daily time spent ruminating, and the duration of ruminating sessions generally increased for sheep fed hay of poor quality (Exp 1) and sheep fed increasing levels of SFM and FM (Exp 5), which is similar to results by Jalali *et al.* (2012) in sheep, goats and llamas. In Exp 2, eating time in goats was not a function of roughage quality, which is different for sheep fed same feeds (Exp 1) and sheep fed increasing levels of lucerne (Exp 3). These results suggest that eating time in goats is based on the desire to eat or hedonic eating. As anticipated, time spent eating and chewing decreased with increased levels of lucerne hay (increased diet quality). Overall chewing time in goats (Exp 2), number of eating and ruminating sessions (all experiments), and duration of eating bouts in sheep (Exp 1) were not affected by diet quality.

This may suggest that these are physiologically controlled behaviours in goats and sheep. No significant changes in ruminating time as a result of improving feed or diet quality have been reported in cattle fed urea treated hay (Trach *et al.* 2001), in agreement with results for goats (Exp 2) and sheep (Exp 3 and 4). In support of our findings (in Exp 1), Chermiti *et al.* (1994) reported that cattle spent more time ruminating per unit intake of untreated straw (PRQ). Urea treatment of forages breaks lignocellulose bonds between plant cells reducing their physical strength (Chenost and Kayouli 1997). Urea-treated hay is expected to be soft and easy to chew, thus reducing ruminating time. Improvement of hay quality using urea treatment reduced ruminating index (Chermiti *et al.* 1994; Trach *et al.* 2001), however, not in goats (Exp 2).

Unexpectedly, ruminating indices decreased with increasing levels of sunflower meal, and were lower for sunflower meal compared to fish meal (Exp 5). Given the high NDF content of sunflower meal compared to fish meal it was expected that sheep spend more time ruminating per unit intake of sunflower meal than fish meal. Ruminating indices in Exp 1 and 2 were approximately between 2 - 5 times as high as for cattle fed on urea treated straw. These results suggest that goats and sheep would be less efficient in rechewing the cud than cattle, probably due to a smaller total surface area of the molars than cattle as tooth surface area is isometrically scaled to $BW^{0.67}$ (Shipley *et al.* 1994). Chewing efficiency in mammalian herbivores is influenced by morphological adaptations in the dental design (Fritz *et al.* 2009). Data from Kaske *et al.* (2002) suggests that sheep need 10-fold more chews per unit of NDF

intake to equal efficiency in ruminating cattle, hence, goats and sheep are likely to spend more time rechewing digesta per unit DM and NDF intake. All but one of the ruminating times reported in this study are consistent with Welch's (1982) proposed physiological daily rumination upper limit of 600 min/day. Daily ruminating time in Exp 1 was above the proposed physiological upper limit for sheep fed PRQ, which is similar to findings by Deswysen and Ehrlein (1981) in sheep fed silage (607 and 653 min/day), Kaske and Groth (1997) in pregnant ewes (679 min/day) and by Minervino *et al*. (2014) in sheep fed coast-cross hay (668 min/day). There are general suggestions that high levels of feed intake increase time spent ruminating. It is possible that over time ruminants have adapted to storing more roughage in the rumen when consuming poor quality roughages in the tropics. Hence, sheep in Exp 1 spent more time ruminating digesta of a diet that was consumed in lower quantities. It is clear that longer ruminating times were a result of low roughage quality but not high intake levels, thus rumination time is a function of roughage quality rather than just the level of intake. However, correlation results suggest that rumination time is a positive function of intake (Table 4.8) and is likely to increase with rumen 'fill' which is higher in animals after prolonged adaptation to roughage diets (Nsahlai *et al*. 1996). Observed rumen fill levels (kg fibre/100 kg weight) of greater than 2.2 were seen in goats (Adebayo 2015) when 1.7 is expected for temperate ruminants (Mertens 1973). A value greater than 1.7 should be applied to ruminants fed on tropical roughages in Africa.

Due to the impending reduction in roughage quality of most tropical grasses as a result of climate change, ruminants will likely adapt to improve utilisation of poor quality roughages by storing more roughage in the rumen and increasing rumination time. Further studies are needed to elucidate how ruminant animals have adapted their eating and ruminating behaviours, and intake rates to changes in reproductive status and forage quality as a result of climatic factors such as global warming, especially in the subtropical and tropical areas. In semi-arid, low rainfall areas of Africa there are very short growth periods for grasses causing early maturity. Rapid attainment of maturity would reduce lignification and lowers crude protein levels slightly in grasses. Based on the positive relationship between crude protein content and intake rate (g/min) obtained in this study, crude protein may play a role in influencing feeding behaviour through intake rate. The generally low crude protein levels of mature tropical grasses led to goats maximising nutrient intake rates during the wet seasons when feeds of high nutritional quality (high crude protein levels) are abundant so as to build up enough reserves to survive the dry season (Sebata and Ndlovu 2012). Effects of crude protein levels on feeding behaviour raised in the above discussion are strengthened based on

the Pearson correlation of CP with time spent eating and ruminating, hence, more studies are needed to ascertain the extent to which different crude protein levels in feeds affect feeding behaviour in ruminants under grazing conditions in tropical Africa.

The absence of differences in the daily duration of eating sessions, and number of eating and rumination periods across the dietary treatments is in line with a general consensus that the number of eating and rumination periods are not affected by roughage quality and kind of feed (Warly *et al*. 1994; Baumont *et al*. 1997). Where animals have similar daily feed intake levels, the individual number of eating sessions may vary up to fourfold (Emmans and Kyriazakis 2001). Control of the number of eating sessions may be under biological control as determined by the desire to eat.

Photoperiod played a huge role in influencing daytime and night-time feeding behaviours measured in the current study, except for the duration of eating sessions and time spent idling whilst lying in sheep (Exp 1), chewing time in goats and sheep (Exp 2 and 5, respectively), and idling time in sheep (Exp 5). The effect of period of day on the number of eating and ruminating sessions, time spent eating and ruminating, and duration of rumination sessions only strengthens the fact that sheep and goats fed only on roughage diets eat during the day and ruminate at night. Ruminants fed varying levels of roughage and concentrate may not follow a similar trend, as shown in sheep (Exp 3) that ruminated more during the day than at night when given increasing levels of lucerne hay. Instead, goats evenly distribute number of meals between the day and night so as to avoid digestive and metabolic upsets such as acidosis (Abijaoude *et al*. 2000) when fed diets containing concentrates, but the number of meals were higher during the day than at night when fed a roughage alone (Exp 2). Time spent eating at night accounts for approximately 10–15% of the total daily eating time (Gregorini 2012), which is fairly lower than 19–30% (Exp 1, 2 and 5) and 39–42% (Exp 3) reported in this study.

It is doubtless that goats and sheep in this study followed a strict circadian rhythm of idling whilst standing, ruminating and eating. The concept of predation and instinct may explain some of these adherences to strict circadian cycles. Fear and perception of threat of predation influences feeding behaviour patterns in herbivores (Newman *et al*. 1995). There exists a certain degree of fear of predation in domesticated ruminant animals kept indoors. It is generally assumed that predation risk is greater during eating than ruminating because animals maintain poor levels of vigilance when eating as their heads are positioned downwards, hence, animals may limit the amount of time spent grazing or eating (Rutter *et al*. 2002). On the other hand, predation risk is at its highest at night than during the day because most predators use the

cover of the night to stalk on their prey. This suggests that due to instinctive fear of predation, ruminants will alter their feeding behaviour patterns with respect to period of the day, but maintain a balance between levels of vigilance in each feeding behaviour to the risk status of that particular period of day. As a result, ruminants will spend more time grazing or eating during the day than at night, and spend more time ruminating than eating at night as shown in this study. To make up for the reduced vigilance on the threat of predation posed by spending more time eating during the day, goats and sheep (Exp 1, 2 and 3) in our study spent more time idling whilst standing during the day than at night. Idling whilst standing during the day balances the total time of engaging in behaviours that maintains good levels of vigilance during the day. Sheep (in Exp 3) displayed a unique way of reducing the risk of predation. Ruminating time, number and duration of rumination sessions was greater during the day than at night and so was eating time, the number and duration of eating sessions. This means that these sheep were aware that predation risk is higher at night and hence did everything during the day. As such they spent more time idling whilst standing at night than during the day so as to stay vigilant over the night. However, idling time lying was greater at night than during the day. This means that at night these sheep spend more time lying and standing than during the day.

In Exp 5 a and b, daytime and night-time behaviours only peculiar to sheep supplemented with increasing levels of protein concentrates was observed in this study. Frequencies of ruminating sessions were greater during the day than at night with number of eating bouts independent of period of the day. This suggests that sheep took regular breaks to ruminate so as to increase vigilance levels following eating during the day. This may be observed by the small difference between times spent ruminating at night and during the day (<8 min across all diet qualities). More research is needed to clarify issues on the circadian control of feeding behaviour patterns in different ruminant species and genotypes that co-exist and graze tropical grasslands in relation to the concept of predation.

Consistent with our findings (from Exp 1 alone), Baumont *et al*. (1997) reported significant effects of type of hay x period of day interactions on time spent eating and ruminating. Von Engelhardt *et al*. (2006) and Minervino *et al*. (2014) also reported similar results for ruminating activities in camels and sheep over various diet qualities, although studies by Hailu (2003 cited by Von Engelhardt *et al*. 2006) on camels showed that rumination activities were evenly distributed throughout the day and night. Minervino *et al*. (2014) observed higher rumination activity occurred during the day than at night (similar to results from sheep in Exp 3) and eating times were evenly distributed throughout the day and night for sheep fed high concentrates diets. For some mysterious reason, duration of eating bouts was

not affected by diet quality (all experiments) nor by period of day (Exp 1). These findings tend to suggest the existence of a physiological limit for eating time per session, irrespective of diet quality and period of day. Fatigue due to exceedingly long hours ruminating per day was expected to result in longer time being spent idling whilst lying in sheep fed PRQ hay (Exp 1). Contrary to these expectations, and similar to findings by Rutter *et al*. (2002), sheep in our study increased ruminating time at the expense of time spent idling. Chewing time was evenly distributed during the day and night within each treatment. The absence of the influence of period of day on chewing behaviour in sheep and goats (Exp 1, 2 and 5), strongly indicates that chewing time is mainly a function of roughage quality, although results from sheep (Exp 3) showed that chewing time is dependent on roughage quality, period of day and their interaction. Genotype, season and daytime affected feeding behaviour of goats and sheep on the rangeland, and time spent grazing was strongly influenced by seasonal variations (Bakare and Chimonyo 2011). It would be worthwhile to determine how diurnal feeding behaviour patterns (eating, ruminating, and idling) of goats and sheep are affected by season of the year, where the lengths of the photoperiods and scotoperiods are different, in tropical Africa.

As expected, positive correlations of times spent eating, ruminating and chewing, and intake rates to intake suggest that there are possibilities of using feeding behaviour to predict intake (Table 4.8). Based on these correlation results, time spent eating and chewing, and intake rate (g/min) are behavioural parameters to include in intake prediction models.

Due to a low nitrogen (crude protein) content (Exp 1 and 2) and less time spent eating by sheep fed PRQ (Exp 1), feed intake was low, resulting in goats and sheep failing to eat enough feed to meet their nutritional needs. Back-fat reserves were mobilised to supply energy for maintenance cost due to increased time re-chewing PRQ in Exp 1. Although sheep fed IRQ lost just little weight, they barely managed to maintain themselves partly due to higher crude protein levels and improved digestibility. Sheep supplemented with protein concentrates recorded body mass gains. Protein content in the diets was in excess of maintenance requirements.

In summary, as seen by the influence of feed and diet quality on feeding behaviour, there are possibilities of using mathematical models to predict feeding behaviour (eating, ruminating and idling time) in ruminant animals using feed attributes. These models may incorporate diet or roughage quality and period of the day as major predictor variables for feeding behaviour. Prediction of feeding behaviour in ruminant animals may be used to improve prediction power of models that seek to predict digesta passage rate through the rumen provided that the feed intake, frequency of rumen contractions and the amounts of digesta that

passes out at each contraction are known, with the assumption that what is eaten is what is actually passed out of the rumen. A simultaneous evaluation of roughage intake, rumen fill levels, passage rates, digestibility and feeding behaviour will be key for understanding the evolutionary adaptation of ruminant digestive physiology.

4.5 Conclusion

Goats and sheep fed on roughage alone ruminate at night and eat more during the day but those fed a roughage and supplemented with lucerne hay spent more time ruminating than eating. Time spent eating and ruminating were affected by diet quality and time of the day. Ruminants adjust their feeding behaviour patterns with respect to period of the day, but maintain a balance between levels of vigilance in each feeding behaviour to the risk status of that particular period of the day. Roughage intake is limited as a result of increased rumination time of low quality roughages. Mathematical models that seek to predict roughage intake in sheep and other ruminant should incorporate factors that affect intake rates and time spent eating, ruminating and chewing. Feeding behaviour patterns during the day and night followed similar trends to those of grazing domestic and wild ruminant animals.

Chapter 5
Digesta passage rates and rumen digesta load at various times post-feeding termination in sheep fed on two different roughage qualities

Abstract

The objective of the current study was to ascertain the effects of roughage quality and time lapse following meal termination on the trend of digesta load disappearance in the rumen. The study also determined the effects of roughage quality on digesta passage rates and hindgut digesta load after feeding stopped in sheep. In one diet treatment, roughage quality was improved by urea treatment of veld hay to produce hay of improved quality (IRQ) and the other treatment was untreated veld hay (PRQ). In Trial 1, four rumen fistulised sheep were used to determine in-sacco degradability of IRQ and PRQ. After the 1st run of degradability, sheep were interchanged across diets and degradability was measured, making n=4 for both diet treatments. In Trial three, 12 sheep were randomly allocated to IRQ (n=6) and PRQ (n=6) to determine solid and liquid passage rates. In Trials two and four, sixteen sheep were randomly allocated to IRQ and PRQ. Apparent digestibility of IRQ (n=4) and PRQ (n=5) was determined for 7 days. In order to determine post feeding rumen fill levels, 2 sheep were slaughtered for each sampling time in each diet treatment at 0, 6, 12 and 24 h after eating stopped. Fractional passage rates of liquid and solid material were higher for IRQ than PRQ. Apparent digestibility was not affected by roughage quality. Rate of degradation and ED were enhanced by improvement of roughage quality. On evaluation, models accounted for 30% (solid passage rate) and 20% (liquid passage rate) of the variation in unseen data in prediction. Roughage quality had no effects on wet and dry digesta load in the foregut and hindgut compartments, except on abomasum dry matter load. Time lapse post feeding had no effects on rumen digesta load in the foregut and hindgut compartments, except on the dry and wet digesta load in the omasum. NDF load for sheep fed on PRQ and IRQ were 2.3 and 2.8 kg/ 100 kg BM, respectively. There was a linear decrease in proportion of rumen load with time up to 24 h post feeding termination for both roughage qualities. However, the slope for PRQ was significantly lower than that for IRQ. The average final fractional clearance rate of rumen digesta at 24 h post feeding termination was approximately 0.018/h (IRQ) and 0.006/h (PRQ) using linear regression. Rates of clearance of digesta from the rumen after feeding stopped were 0.023/h and 0.007/h for IRQ and PRQ, respectively, using the exponential model. In summary, it seems that passage rate had negligible effects on emptying of rumen load post feeding termination. Digestibility had negligible effect on hindgut fill. The implications of a linear decrease in

rumen digesta load after eating stops are that subsequent feed intake after sheep are deprived of feed for up to 24 gradually increases linearly with time.

Additional keywords: Diet quality, digestibility, fractional passage rate, model evaluation, rumen fill.

5.1 Introduction

Ruminant production in tropical and subtropical regions of Africa is mainly characterised by grazing livestock animals on tropical grasslands. There is an impending reduction in ruminant performance in Africa due to a decrease in forage quality and availability as a result of global warming (Rust and Rust 2013). Marginal increments in global temperatures are projected to cause a decrease in forage quality and digestibility by increasing the highly indigestible lignin content of plant cell walls. Hay and straw derived from tropical grass species is generally described as of poor quality, bulky and "high methane" roughages that elicit low feed intakes (Osuji *et al*. 1995). In most cases, low feed intake of hay derived from tropical grasses by grazing ruminants is a result of slow movement of solid digesta out of the rumen, causing rumen "fill". Ruminants eat to meet their nutritional needs (Emmans and Kyriazakis 2001), unless constrained not to by factors such as rumen capacity. Rumen fill levels vary throughout the day and are a function of digesta clearance rate from the rumen governed by rates of passage and degradation. Adaptation of tropical ruminants to store more feed of poor nutritional quality may be implicated in high rumen fill levels (Nsahlai *et al*. 1996).

Mathematical models have been developed to predict the rates of digesta passage out of the rumen. Passage rate model evaluation studies should seek to ascertain performance of prediction models with changes in forage quality (digestibility) as impacted by changes in climate patterns. This will ascertain the usefulness of current passage rate prediction models in dynamic nutritional conditions due to climate change.

Long unprecedented starvation (period between successive eating sessions) is a common occurrence in communal ruminant production systems in Africa. The influence of starvation on subsequent feed intake depends on the rumen digesta load post feeding termination. Rumen digesta load at various times after termination of feeding bouts determines the amount of available or receptive space in the rumen at the time of measurement. Little is known on the effect of improving tropical hay quality on the pattern and extent of decrease in digesta load in the rumen with time after sheep stop eating. Given the capacity to predict rumen digesta load using artificial neural networks (Adebayo 2015), this knowledge may be useful in determining subsequent intake post feeding necessitating prediction of roughage intake.

The objectives of the current study were: (1) to determine the effects of improvement of roughage quality on digesta passage rates, total tract digestibility and in-sacco degradability; (2) to evaluate the performance of passage rate prediction models developed in chapter 3; and (3) to ascertain the trend of digesta disappearance from the rumen at various times following meal termination. This study tested the hypothesis that: (1) roughage quality has no effect on digesta passage rates and digestibility; and (2) digesta in the rumen disappeared in a nonlinear fashion based on the rate of degradation and passage after feeding has stopped.

5.2 Material and Methods

5.2.1 Study site

The experiment was conducted with the approval of the University of KwaZulu-Natal Ethics Committee, the Animal Ethics Sub-Committee (ref. AREC/072/2015M). The experiment was conducted at the University of Kwazulu-Natal's Ukulinga Research Farm, Pietermaritzburg, in the subtropical hinterland of KwaZulu-Natal Province, South Africa. Study site lies on the geographical coordinates 30°24'S and 29°24'E at an altitude of 700m. Mean annual rainfall in the study site is approximately 735 mm, falling mostly in summer, between October and April. Maximum and minimum mean annual temperatures are 25.7 and 8.9°C, respectively. In extreme weather conditions, summer temperatures may reach highs of above 32°C with minimum temperatures as low as 3°C at night in winter.

5.2.2 Animals, housing, feeding and experimental design

Four adult wether sheep with an average body mass of 58.3 ± 4.9 kg (Trial 1 and 3), fitted with permanent rumen cannulas of 120 mm internal diameter (passage rate and rumen degradability trial) and 8 adult wether sheep (Trial 3) with an average mass of 55.25 ± 4.1 kg (passage rate trial only) were used. In Trials 2 and 4, 16 wether sheep with an average mass of 36.47 ± 9.46 kg were used to determine digestibility and post feeding rumen fill levels. Sheep were dosed for internal parasites and placed in individual pens with access to clean water for the whole duration of the trial. In one dietary treatment, roughage quality was enhanced by treating veld hay with 4% urea for 40 days to give hay of improved roughage quality (IRQ) and the other treatment was untreated veld hay with poor roughage quality (PRQ). Sheep were allocated approximately 2 kg DM of either IRQ or PRQ at 1000 h and 1500 h daily. Hay was fed milled to pass through a 12 mm screen using a hammer mill (Scientec hammer mill 400, Lab World Pty Ltd, Johannesburg, RSA). Sheep were randomly allocated to IRQ and PRQ. Hay left in the feeders was weighed daily before new hay allocation was done. Daily roughage intake was

calculated by subtracting feed left from feed allocated (Roughage intake = feed in – feed out). Trial 1 and 3 lasted 48 days, comprising of a 14-day period for adaptation to the experimental feeds, followed by 7 and 20 days of faecal sample collection and rumen degradation sample incubations, respectively. The 4 fistulated sheep were interchanged across diets on day 10 and a 14-day diet adaptation period was adhered to, thereafter a second run of nylon bag degradability of the IRQ and PRQ was carried out. Trial 2 and 4 lasted 34 days, comprising of a 14-day period for adaptation to the experimental diet followed by 7 and 20 days of measuring digestibility and rumen fill by slaughtering, respectively.

5.2.3 Trial 1: In-sacco degradability study

Degradability of roughages was determined using the nylon bag technique. Roughage samples were milled to pass through a 2 mm screen using a hammer mill (Scientec hammer mill 400, Lab World Pty Ltd, Johannesburg, RSA). Approximately 3 g of each ground roughage sample was weighed into labelled nylon bags (ANKOM Co, Fairport, New York, USA; internal dimensions: 5 cm x 9 cm; pore size 50 μm). Bags were tied to a stainless steel disc with 10 evenly spaced small holes drilled through the periphery of the disc serving as anchor points. Bags were sequentially incubated (in triplicates per time interval) in the rumen for 120, 96, 72, 48, 24, 9, 6, and 3 hours (Osuji *et al*. 1993). IRQ samples were incubated in the rumen of animals fed IRQ, while PRQ samples were incubated in animals fed on PRQ. Immediately after removal from the rumen, bags were washed with clean running water until the water ran clear. Thereafter, the incubated bags, including the zero hour bags were washed for 30 minutes (6 cycles each lasting 5 minutes) using a semi-automatic washing machine. Washed bags were dried in an oven at 80˚C for 48 hours, cooled in a desiccator and weighed.

5.2.4 Trial 2: Digestibility study

In-vivo digestibility of IRQ (n=4) and PRQ (n=5) was determined over a 7-day period. Faecal bags were attached to the sheep's hindquarters 3 days before collection of faecal samples so as to allow the sheep to adapt to carrying the bags. Faecal bags were emptied daily throughout the experiment. Immediately after collection, the faecal samples were dried in an oven at 60ºC for 48 hours. Dry faeces were weighted. Apparent digestibility (AD) was determined by subtracting total faeces from total intake divided by total intake over a 7-day period (AD $= \frac{\text{total intake} - \text{total faeces}}{\text{total intake}}$).

5.2.5 Trial 3: Passage rate study

5.2.5.1 Preparation of Ytterbium labelled roughages

Ytterbium marked roughages were prepared according to Hartfield *et al*. (1990). Roughage samples to be marked were ground to pass through a 12 mm screen. 150 g each of IRQ and PRQ 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 litres of distilled water. Ytterbium labelled roughages were prepared by soaking roughages in 2.5 g/l $YbCl_3.6H_2O$ solution at a rate of 50 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 dried in an oven at a temperature of 50°C for 48 hours. Labelled roughage was kept in plastic bottles pending administration.

5.2.5.2 Preparation of Co-EDTA

Cobalt-EDTA was used as a liquid marker. The fluid marker was prepared according to Uden *et al*. (1980). 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 7g NaOH was added. The solution was allowed to cool to room temperature, after which 160 ml H_2O_2 was added. 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 crystallisation. 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 dried in an oven at 90°C for 24 hours and stored in plastic bottles pending administration.

5.2.5.3 Administration of markers

Sheep were starved overnight. 20 g ytterbium labelled roughages were offered to each sheep. 120 g of Co-EDTA crystals were dissolved in 720 ml water and each sheep was drenched 60 ml of solution containing Co-EDTA. Eleven sheep readily consumed >95% of the ytterbium marked roughages. One sheep did not readily consume the marked roughage but finally consumed all of the marked roughage after it was mixed with 10 g lucerne hay in 10 minutes.

5.2.6 Trial 4: Rumen load post feeding

After the digestibility trial, sheep were slaughtered to determine post feeding rumen fill levels. A day prior to slaughter, feed was removed at 1500 hrs such that all animals were starved for

17 hours before the next feed allocation. On the day of slaughter, sheep were allowed to eat their daily allocation of hay from 0800 hrs until each animal voluntarily stopped eating. An animal that had a break of greater than 5 minutes after an eating session was regarded to have stopped eating. Time after feed termination was recorded immediately. One sheep had feed removed after it ate for more than 100 minutes without taking a break greater than 5 minutes. The amount of feed consumed on the day of slaughter and time spent eating were recorded. Sheep were weighed 20 minutes prior to slaughter. Rumen digesta load was determined by slaughtering sheep 0, 6, 12 and 24 hours after meal termination.

During the period leading to slaughter, animals were transported from Ukulinga farm livestock section to the Ukulinga farm abattoir. Two animals were slaughtered for each sampling time for each dietary treatment. Sheep were slaughtered by electrical stunning to make them unconscious and the jugular vein slit with a sharp knife and bled (exsanguination). The entire animal guts were removed and each compartment emptied and weighed to determine the mass of wet digesta in each section of the gut. Lengths of the small intestines, caecum, and large intestines were measured for each sheep.

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

In Trial 3, 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 7 days after administration of markers by rectal palpation and extraction of sizeable rectal faecal samples by hand on each sheep. Faecal sampling times were: 0, 1, 4, 7, 10, 13, 21, 24, 27, 29, 48, 53, 72, 77, 96, 101, 120,144 and 168 hours post marker administration. Faecal samples from each sheep were dried in an oven at a temperature of 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 airtight plastic bags pending analysis. 2 g of air dried rumen and faecal samples were weighed, 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 HNO_3 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 deionised water. Solution was diluted to volume with deionised water and mixed well. 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 4, rumen digesta and faecal samples were collected and dried to a constant mass in an oven at 60°C to determine the dry matter content. The digesta were analysed for neutral detergent fibre using an ANKOM A220 fibre analyser (ANKOM Technology, New York, USA).

5.2.8 Chemical analysis of experimental feeds

Table 5.1 Chemical composition of experimental feeds used in trials

Chemical composition (g/kg DM)							
Trial 1 & 3	DM	CP	NDF	ADF	HEM	Ash	CF
IRQ	923	91	746	417	330	86	12
PRQ	926	40	735	391	344	67	13
Trail 2 & 4							
IRQ	864	83	873	503	370	56	12
PRQ	907	43	826	466	360	55	13

IRQ: improved roughage quality; PRQ: poor roughage quality

Moisture, dry matter, organic matter and ash were analysed using procedures described by the Association of Official Analytical Chemists (AOAC 1999). Nitrogen content in IRQ and PRQ was determined using an automatic protein determinate machine, LECO TruSpec nitrogen analyser FP2000 (LECO, Pretoria, South Africa). Crude protein content was calculated by multiplying the nitrogen content by a factor of 6.25 (Crude protein = nitrogen content × 6.25). Neutral detergent fibre and acid detergent fibre were analysed using an ANKOM A220 fibre analyser (ANKOM Technology, New York, USA). Hemicellulose content was determined by subtracting acid detergent fibre content from neutral detergent fibre content (Hemicellulose = neutral detergent fibre – acid detergent fibre). Crude fat content was determined using the Soxhlet method on the Soxhlet Buchi 810 fat analyser (Soxhlet Buchi, Switzerland).

5.2.9 Mathematical procedures
5.2.9.1 In-sacco degradability study

Degradability of roughage samples were determined using the dry matter loss in the 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.

5.2.9.2 Passage rate study

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 $t \geq TT$, where: Y and A are the adjusted marker concentration in the faecal DM, k_1 and k_2 – 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 Statistical Analysis System 9.3 (SAS Institute Inc., Cary, NC, USA). The regression coefficient (k_1) gave the slowest rate constants that correspond to the rate of passage in the rumen and y-intercept as A_1. Estimation of fitted values for collection times that correspond to the ascending phase and the peak portions was done using the regression equation for the natural log of the descending slope. Residual 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 (k_2) that corresponds to the rate of passage in the hindgut and y-intercept as A_2. The selectivity factor (SF) was calculated as $SF = MRT_{particles} \div MRT_{liquid}$ (Clauss and Lechner-Doll 2001).

5.2.9.3 Validation of passage rate prediction models previously developed

Liquid and solid prediction models were evaluated using passage rate and degradability results from this study. Body weight changes (kg/d) used in calculation of APL were reported in Chapter 3. Mature body weight of Dohne Merino sheep was 90 kg (Snyman 2014). For all evaluations, regression analyses of observed against predicted passage rates, residuals against observed passage rate and residuals against predicted passage rates were carried out using the linear regression procedure. Coefficients of determination were used to evaluate the precision of regression lines in approximating real data points. Root mean square error (RMSE) was used to determine accuracy of these models. To evaluate the linear and mean biases in model predictions, the residuals (observed minus predicted passage rates) were regressed against predicted passage rates. The intercept and slopes of these regression lines were tested against 0 and 1, respectively, to determine any linear or mean bias (St-Pierre 2003).

5.2.9.4 Modelling of post feeding rumen load

Modelling of rumen fill levels was done using the linear regression procedure. In determining the trends of decrease in rumen load levels with time post feeding, 2 outliers were removed from data for the poor roughage quality fed sheep slaughtered 12 hours post feeding. Actual slaughter times were used to recalculate the real time of slaughter after feeding was terminated. Rumen fill levels against real slaughter times post feeding were regressed using the linear regression procedure and used to determine the equation of the curve. The equation of the curve was extrapolated to determine rumen fill level at time 0 h post feeding. Based on this recalculated rumen fill at time zero post feeding, the proportions of rumen load at each time post feeding relative to rumen fill load at time zero were calculated. Proportions of rumen fill levels relative to rumen fill at time zero post feeding were regressed against time post feeding, separately for each roughage quality. Differences in slopes of these 2 curves were tested using the regression procedure.

Rumen fill levels were also fitted into a linear model with a natural logarithm function. The Genmod procedure was used to determine the linear model with a natural log link function for the proportion of rumen fill levels with time post feeding. This model takes a linear form with a log link function, a function that associates the regressors with the response variable as: $Ln\ Prop = Ln\ Prop_0 + (rate \times time)$. This model was used to determine the rate of disappearance of digesta from the rumen at various times after eating stopped. The final model was: $Prop = Prop_0 \times e^{rt}$, where $Prop_0$ is the initial proportion, Prop – proportion of rumen load at any time after eating stopped, t – time and r – rate of disappearance.

5.2.10 Statistical analysis

The correlation procedure was used to establish the Pearson correlation coefficients between wet and dry digesta load in the various compartments of the gastrointestinal tract. Experimental datasets were statistically analysed using the General Linear Model (GLM) procedure to determine the effect of roughage quality on degradability, passage rate, wet matter, dry matter and NDF load in the foregut. The effect of time after feed termination on wet matter, dry matter and NDF load in the foregut were determined. The Student-Newman-Keuls (SNK) test was used to identify sample means that are significantly different from each other at $P < 0.05$. The experimental model for Trial 1-3 was: $Y_{ij} = \mu + R_i + BM_j + e_{ijk}$, where: Y = degradability, digestibility and passage rate, μ – overall mean, R_i – roughage quality effect (i = IRQ; PRQ), BM – body mass, e_{ijk} – experimental error. The model for Trial 4 was: $RF_{ijk} = \mu + R_i + P_j +$

$BM_k + \varepsilon_{ijkl}$, where: RF = rumen fill level (wet matter, DM, NDF), μ – overall mean, R_i – roughage quality effect (j = IRQ; PRQ), P_j – period of sampling effect (k = 0; 6; 12; 24 h), BM – body mass, e_{ijk} – experimental error.

5.3 Results

5.3.1 In-sacco degradability trial

Improvement of roughage quality enhanced effective degradability (ED) by +86 g/kg and increased rate of degradation by approximately 2-fold (Table 5.2). Dry matter intake and intake per unit of body mass during Trial 2 was +0.127 kg and 0.006 kg/kg BM greater for the IRQ compared to PRQ. Roughage quality had no influence on apparent digestibility of dry matter.

5.3.2 Digesta passage rate trial

Fractional passage rate and mean retention time of solid digesta in the rumen were -0.004 per h lower and +9.8 h greater, respectively, for sheep fed PRQ than those fed on the IRQ. Fractional passage rate and mean retention time of liquid in the rumen were not affected by roughage quality. As expected fractional passage rates and mean retention time for solid and liquid digesta in the hindgut were not affected by roughage quality. Selectivity factor was approximately 1.5-fold lower for sheep fed IRQ compared to those fed on PRQ (Table 5.3).

5.3.3 Evaluation of passage rate prediction models
5.3.3.1 Solid passage model

The regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) in model evaluation was: Y = 0.01 ($\pm$ 0.004) + 0.388 ($\pm$ 0.187) X (n = 6, RMSE = 0.003), accounting for 30% of the variation in prediction. The intercept (p = 0.03) and slope (P = 0.009) were different from 0 and 1, respectively (Fig 5.1.a). Predicted solid passage rate for both roughage qualities clustered in close proximity to the ideal prediction line. A plot of residual solid passage rate against predicted solid passage rate assessing the mean bias (intercept) and linear bias (slope) of the model in predicting solid passage rate (Fig 5.1.b) is given in this equation: Y = 0.01 ($\pm$0.0039) – 0.63 ($\pm$0.182) X (R^2 = 0.54, RMSE = 0.0025). The intercept (P = 0.03) and slope (P = 0.009) were different from 0 and 1, respectively. Residuals were high for IRQ compared to PRQ.

5.3.3.2 Liquid passage model

The regression relationship between the observed (Y) and predicted (X) liquid passage rates (per h) in model evaluation was: Y = 0.09 ($\pm$ 0.0038) – 0.63 ($\pm$ 0.399) X (n = 6, RMSE =

0.007), accounting for 20% of the variation in prediction. The intercept ($P = 0.02$) and slope ($P = 0.002$) were different from 0 and 1, respectively (Fig 5.1.c). A plot of residual liquid passage rate against predicted liquid passage rate assessing the mean bias (intercept) and linear bias (slope) of the model in predicting liquid passage rate (Fig 5.1.d) is given in this equation: $Y = 0.09 \ (\pm0.031) - 1.63 \ (\pm0.399) \ X$ ($R^2 = 0.63$, RMSE = 0.007). The intercept ($P = 0.02$) and slope ($P = 0.0001$) were different from 0 and 1, respectively. Residuals tended to be high for IRQ compared to PRQ.

Table 5.2 Effect of improving roughage quality of veld hay on in-sacco degradability (Trial 1) and in-vivo digestibility (Trial 2) in sheep

	Diets		Significance	
	IRQ	PRQ	RMSE	*P* value
	Degradability (g/kg DM)			
a	146	144	14.2	0.15
b	533	520	64.1	0.78
PD (a+b)	679	664	64.1	0.94
ED	440[a]	354[b]	23.8	0.01
c (per h)	0.042[a]	0.020[b]	0.001	0.03
L (h)	1.4	-4.8	7.02	0.34
	Apparent digestibility			
Intake (kg)	0.778[a]	0.651[b]	0.092	0.0003
Intake(kg/kg BM)	0.020[a]	0.014[b]	0.002	0.0005
DMD (g/kg DM)	0.451	0.369	0.07	0.106

IRQ: improved roughage quality; PRQ: poor roughage quality; a: rapidly degradable water soluble fraction; b: slowly degradable portion of the insoluble fraction; PD: potentially degradable fraction; ED: effectively degradable fraction; c: rate of degradation of the "b" fraction; L: time lag; DMD: dry matter digestibility; OMD: organic matter digestibility.

[a,b] Means in a row with different superscripts are significantly different ($P < 0.05$)

Table 5.3 Effect of improving roughage quality on solid and liquid digesta passage rates in the rumen, hindgut and whole gastrointestinal tract of sheep (Trial 3)

	Diets		Significance	
	IRQ	PRQ	RMSE	*P* value
Fractional passage rate (per h)				
RR (k_p)	0.020[a]	0.016[b]	0.002	0.02
HG (k_p)	0.038	0.145	0.209	0.39
RR (k_l)	0.035	0.043	0.008	0.13
HG (k_l)	0.057	0.089	0.031	0.10
Mean Retention Time (h)				
RR_p	51.6[b]	61.4[a]	4.20	0.01
HG_p	28.1	27.2	11.17	0.84
RR_l	28.8	24.2	4.64	0.12
HG_l	19.6	12.7	5.5	0.05
Selectivity Factor				
RR	1.8[b]	2.6[a]	0.517	0.03
HG	1.7	2.4	1.43	0.39

IRQ: improved roughage quality; PRQ: poor roughage quality; RR: reticulorumen; HG: hindgut; GIT: gastrointestinal tract; k_p: fractional passage rate of solid particles; k_l: fractional passage rate of liquid RR_p: rumen solid particles; HG_p: hindgut solid particles; RR_l: rumen liquid; HG_l: hindgut liquid.

[a,b] Means in a row with different superscripts are significantly different (*P* <0.05).

Table 5.4 Effect of roughage quality on intake, intake rate and duration of feeding bout of first eating session after an 18 hour starvation period in sheep (Trial 4)

	Diets		Significance	
	IRQ	PRQ	RMSE	*P* value
Intake (kg)				
DM	0.326[a]	0.188[b]	0.078	0.001
NDF	0.285[a]	0.155[b]	0.07	0.001
Feeding behaviour				
DEB (min)	67[a]	47[b]	17.85	0.04
IR (g/min)	4.97[a]	4.08[a]	1.129	0.06

DEB: duration of eating bout; IR: intake rate

[a,b] Means in a row with different superscripts are significantly different (*P* <0.05)

5.3.4 Rumen digesta load trial

Dry matter intake and NDF intake during the first eating session on morning of Trial 4 was +0.138 kg and +0.13 kg greater, respectively, for sheep fed IRQ compared to those fed on PRQ.

Duration of the first eating session on the morning after an 18 h starvation period was +20 min greater for sheep fed on IRQ compared to those fed on PRQ. Sheep fed on PRQ ate -0.88 g/min less than sheep fed on IRQ during the first eating session on the morning after an 18 h starvation period (Table 5.4).

Generally, wet digesta load in the rumen, omasum and abomasum was 92.2, 4.1 and 3.7% of the total foregut wet digesta load, respectively, for sheep fed on IRQ. Sheep fed on PRQ had 89.9, 3.6 and 6.5% of the total foregut wet digesta load in the rumen, omasum and abomasum, respectively. A similar trend was observed with the dry matter load. The compartmental distribution of total dry digesta load in the foregut was 89.8% (rumen), 6.8% (omasum) and 3.4% (abomasum) for sheep fed on IRQ, and 83.7% (rumen), 7.2% (omasum) and 9.1% (abomasum) for sheep fed PRQ (Table 5.5). Roughage quality had no effect on wet digesta load in all foregut compartments. Time post-meal termination had an effect on wet matter load in the omasum. Wet omasal load decreased gradually with time from 0 to 12 h post feeding, but increased at 24 h post feeding. The 24 h wet omasal load was +0.353 and +0.319 kg/100 kg BM greater than the 12 h and 6 h wet omasal digesta load, respectively.

Roughage quality had no effects on dry digesta load in the foregut except in the abomasum. Dry digesta load in the abomasum was +0.138 kg/100 kg BM greater for sheep fed on PRQ compared to those fed on IRQ. Time post-meal termination had an effect on dry matter load in the omasum. The 24 h dry omasal load was +0.068 and +0.059 kg/100 kg BM greater than the 12 h and 6 h dry omasal digesta load, respectively. Rumen fill for NDF was 26% higher for sheep fed on IRQ compared to those fed on PRQ. There was a general tendency for NDF load to increase with time post meal termination. NDF was significantly higher (1.5 fold) at 24 h post meal termination compared to 0 h after meal termination.

Roughage quality and time post feeding termination had no effects on the wet and dry matter digesta load in the hindgut. Time post-feeding termination had an effect on the dry matter load per unit compartment length in the colon. Dry colon load (kg/mCL/100 kg BM) decreased gradually with time from 0 to 12 h post feeding, but increased at 24 h post feeding. At 12 h post feeding termination the dry colon digesta load was -0.135 kg/mCL/100 kg BM lower than the load at 0 h post feeding termination (Table 5.6).

Correlations between wet and dry digesta load in all compartments were weak ($R < 0.5$) except for strong correlations between wet digesta load in the rumen and large intestines, large intestines and abomasum, large intestines and small intestines, and small intestines and colon. Strong correlations ($R > 0.5$) between wet and dry digesta load were observed between the dry omasum to the wet abomasum and wet large intestine loads, the dry large intestine to the wet

small intestine and wet large intestine load, and dry omasum to the wet abomasum load (Table 5.7).

The regression relationship between the dry rumen load (Y) and time post feeding termination (X) (h) was: $Y = 3.285 (\pm 0.0775) - 0.0583 (\pm 0.00570) X$ (n = 4, RMSE = 0.0999) for sheep fed IRQ (Figure 5.2.a). The model accounted for 98% of the variation. The regression relationship between dry rumen load (Y) and time post feeding termination (X) (h) was: $Y = 2.33 (\pm 0.034) - 0.0142 (\pm 0.0024) X$ (n = 3, RMSE = 0.04) for sheep fed PRQ. The model accounted for 98% of the variation. The slope of the curve for PRQ was significantly different from that for IRQ ($P = 0.03$).

The regression relationship between the proportion of dry rumen load (Y) and time post feeding termination (X) (h) was: $Y = 1.00 (\pm 0.015) - 0.018 (\pm 0.0013) X$ (n = 5, RMSE = 0.0248) for sheep fed IRQ (Figure 5.2.b). The model accounted for 99% of the variation. The regression relationship between the proportion of dry rumen load (Y) and time post feeding termination (X) (h) was: $Y = 1.00 (\pm 0.008) - 0.006 (\pm 0.0006) X$ (n = 4, RMSE = 0.0126) for sheep fed PRQ. The model accounted for 96% of the variation. The slope of the curve for PRQ was significantly different from that for IRQ ($P = 0.003$). At 24 h post feeding, sheep lost 42.6% (IRQ) and 18.8% (PRQ) of digesta load at termination of feed intake. The average final fractional clearance rate of rumen digesta at 24 h post feeding termination was approximately 0.018/h (IRQ) and 0.006/h (PRQ).

The exponential relationship between the proportion of rumen load (Y) and time post feeding termination (X) (h) was: $Y = 1.008e^{-0.023X}$ (IRQ) and $Y = 1.0006e^{-0.007X}$ (PRQ) (Figure 5.2.c). Rates of clearance of digesta from the rumen after feeding stopped were 0.023/h and 0.007/h for IRQ and PRQ, respectively. Improving roughage quality resulted in a 3-fold increase in the rate of disappearance of digesta from the rumen post feeding. The clearance rates obtained from the linear regression model are similar to those obtained from the exponential model for both roughage qualities.

5.4 Discussion

5.4.1 Passage rate, apparent digestibility, degradability and reticulo-rumen digesta load

Passage of solid digesta from the rumen relies on the extent and how fast solid digesta is fermented by microbial populations in the rumen. In this study, high fractional passage rate of solids through the rumen due to an improvement of roughage quality were expected. The IRQ supplied extra non-protein nitrogen from urea compared to the PRQ. These were used for

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proliferation of microbial populations that caused higher effective degradability and rate of degradation of the IRQ. This means that particles from IRQ reached the critical particle size quickly to allow solid particles to pass out of the rumen compared to PRQ. Hence, solid digesta passage out of the rumen was faster for the IRQ. Generally, solid passage rates for both roughage qualities were lower than those of Schlecht *et al*. (2007) in Sahelian sheep fed tropical bush hay. Differences may be attributed to the negative energy balance and animal production level lower than unity in sheep in this study. There are general suggestions that starving ruminants may withhold solid digesta for extended periods of time. Undernutrition which may be correlated to starvation may have caused the sheep to retain solid digesta for a long time. More work needs to be done to ascertain the effects of prolonged starvation on solid and liquid fractional passage rates in ruminants grazing on poor quality roughages in subtropical and tropical regions. However, mean retention times in the rumen for solid digesta in bush hay fed sheep (Schlecht *et al*. 2007) were similar to those of sheep fed PRQ. Similar to this study, Nsahlai *et al*. (1998) observed low fractional passage rates of solid (0.011-0.03 per h) in Ethiopian Menz sheep fed on a poor quality roughage.

Selectivity factors (SF) in the rumen observed in this study for both roughage qualities are within the range of 1.6-3.8 for grazing ruminants (Clauss and Lechner-Doll 2001). High SF for PRQ than IRQ strongly supports the view that grazing ruminants adapted to poor quality roughages retain solid digesta for extended periods of time. Selectivity factors are used to describe ruminant ecological differences and find application in classification of ruminants into different feeding types (Clauss and Lechner-Doll 2001). Rumen retention time is a function of roughage quality. In the context of this study, SF may be used to describe physiological differences in degree of adaptation of ruminants to different roughages qualities. This would suggest that ruminants with SF close to 3.8 would be well adapted to low quality roughages which is typical to ruminants that inhabit subtropical and tropical regions.

Figure 5.1. a Relationship between the observed (Obs) and predicted (Pred) solid passage rates (k_l) for model evaluation.
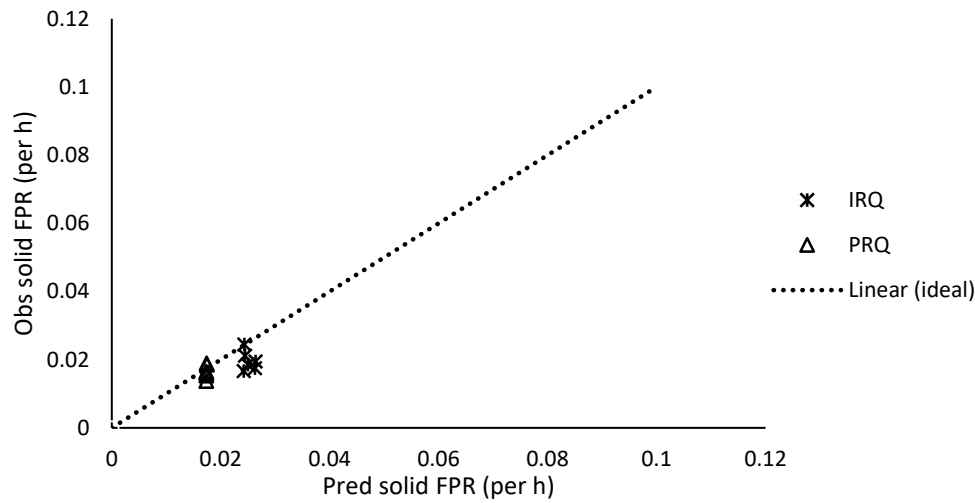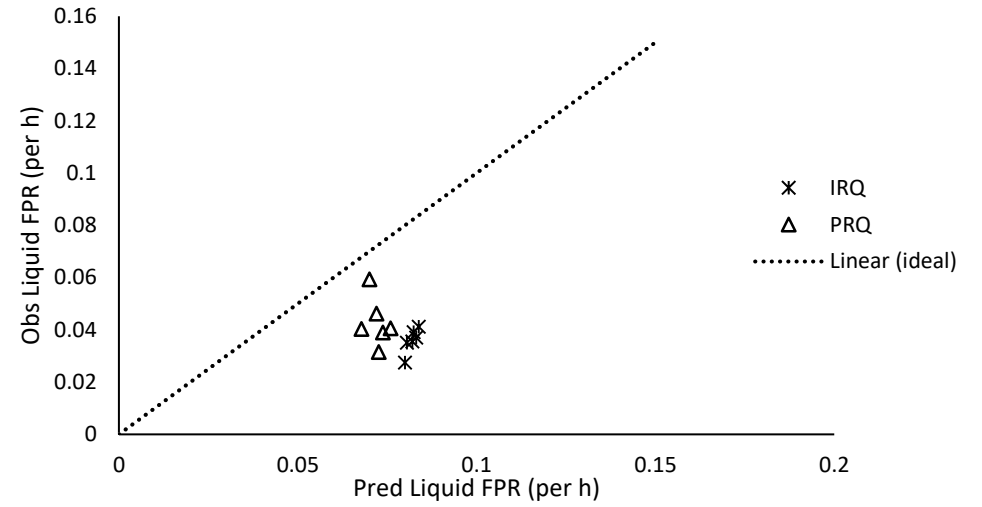

Figure 5.1. c Relationship between the observed (Obs) and predicted (Pred) liquid passage rates (k_l) for model evaluation.
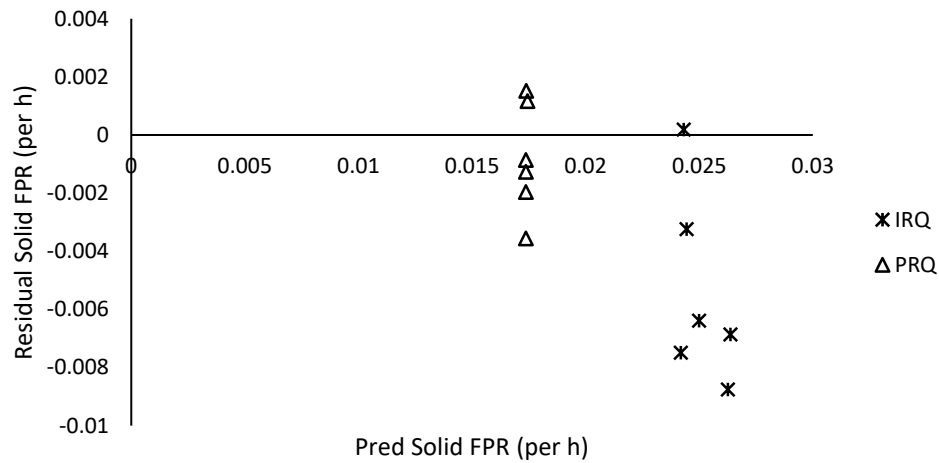

Figure 5.1. b Residual (Observed – Predicted) plot against predicted (Pred) solid FPR to test model bias in evaluation.
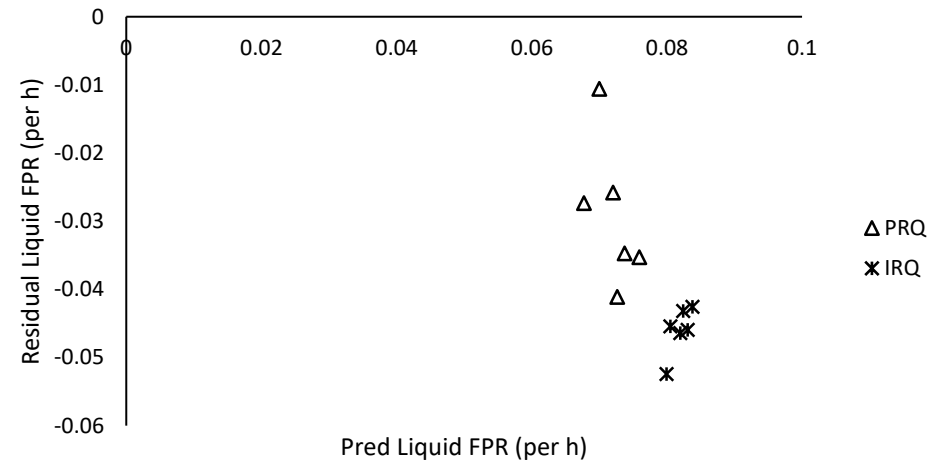

Figure 5.1. d Residual (Observed – Predicted) plot against predicted (Pred) liquid FPR to test model bias in evaluation.

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Table 5.5 Effects of roughage quality and post feeding time on digesta and nutrient load (kg/100 kg BM) in the foregut of Merino sheep (Trial 4)

Load (kg/100 kg BM)	Feed		Time post-feeding termination (h)				
Wet matter load	IRQ (n=8)	PRQ (n=8)	0 (n=4)	6 (n=4)	12 (n=4)	24 (n=4)	RMSE
Rumen	22.18	20.58	18.93	22.42	23.45	20.95	3.084
Omasum	0.971	0.824	0.962[ab]	0.781[b]	0.747[b]	1.10[a]	0.141
Abomasum	0.893	1.48	1.608	0.819	1.115	0.884	0.856
Dry matter load							
Rumen	2.68	2.16	2.48	2.58	2.71	1.91	0.731
Omasum	0.204	0.185	0.199[ab]	0.175[ab]	0.166[b]	0.234[a]	0.029
Abomasum	0.099[b]	0.237[a]	0.249	0.107	0.171	0.144	0.106
NDF load							
Rumen	2.88[a]	2.28[b]	1.94[c]	2.98[a]	2.41[b]	3.00[a]	0.202
Omasum	2.78[a]	2.15[b]	1.69[b]	2.67[a]	2.43[a]	2.87[a]	0.234
Abomasum	2.34	2.13	1.71[b]	2.43[a]	2.22[a]	2.52[a]	0.235

Feed × time interactions were not significant

[a,b] Means in a row with different superscripts are significantly different ($P <0.05$)

Table 5.6 Effects of roughage quality and post feeding time on digesta load (kg/100 kg BM) in the hindgut of Merino sheep (Trial 4)

Load (kg/100 kg BM)	Feed		Time post-feeding termination (h)				
Wet matter load	IRQ (n=8)	PRQ (n=8)	0 (n=4)	6 (n=4)	12 (n=4)	24 (n=4)	RMSE
Small intestines	1.45	1.32	1.44	1.51	1.14	1.51	0.295
Caecum	1.36	1.19	1.40	1.35	1.05	1.33	0.240
Colon	1.97	2.14	2.21	1.96	1.60	2.55	0.439
Dry matter load							
Small intestines	0.163	0.122	0.135	0.195	0.118	0.142	0.046
Caecum	0.208	0.181	0.204	0.221	0.162	0.188	0.058
Colon	0.370	0.420	0.446	0.422	0.305	0.423	0.071
Dry matter load (kg/mCL/100 kg BM)							
Small intestines	0.030	0.026	0.031	0.039	0.021	0.024	0.011
Caecum	2.402	2.013	2.657	2.061	1.848	2.346	0.845
Colon	0.252	0.301	0.343[a]	0.259[ab]	0.208[b]	0.296[ab]	0.047

Feed × time interactions were not significant; CL: compartment length; BM: body mass.

[a,b] Means in a row with different superscripts are significantly different ($P <0.05$).

Table 5.7 Correlation between wet (top-right) and dry (bottom-left) digesta load in various compartments and that of dry and wet matter in each compartment (extreme right) in the gastrointestinal tract of Merino sheep (Trial 4)

Comp.	R	O	A	SI	LI	C	Var.	WR	WO	WA	WSI	WLI	WC
R		-0.08	-0.12	-0.49	-0.53	-0.03	DR	0.30	-0.05	0.08	-0.36	-0.14	-0.48
		(0.77)	(0.71)	(0.07)	(0.05)	(0.92)		(0.28)	(0.87)	(0.81)	(0.21)	(0.62)	(0.10)
O	-0.14		-0.41	0.20	0.37	-0.10	DO	-0.17	0.86	-0.13	0.04	0.45	0.07
	(0.61)		(0.19)	(0.49)	(0.20)	(0.76)		(0.56)	(0.00)	(0.71)	(0.90)	(0.12)	(0.82)
A	-0.04	-0.07		0.31	0.62	0.10	DA	-0.24	-0.28	0.96	0.43	0.79	0.26
	(0.90)	(0.83)		(0.33)	(0.03)	(0.77)		(0.48)	(0.40)	(0.00)	(0.18)	(0.01)	(0.44)
SI	0.03	-0.04	-0.38		0.80	0.73	DSI	0.31	0.19	-0.34	0.19	-0.08	0.10
	(0.93)	(0.91)	(0.22)		(0.00)	(0.01)		(0.28)	(0.51)	(0.32)	(0.51)	(0.80)	(0.77)
LI	-0.45	0.40	0.48	0.16		-0.17	DLI	-0.33	0.28	0.41	0.58	0.71	0.06
	(0.12)	(0.20)	(0.12)	(0.60)		(0.58)		(0.27)	(0.36)	(0.21)	(0.05)	(0.01)	(0.84)
C	0.05	0.26	-0.44	0.46	0.24		DC	0.01	-0.14	-0.54	0.27	-0.23	0.57
	(0.87)	(0.39)	(0.14)	(0.12)	(0.44)			(0.99)	(0.65)	(0.09)	(0.40)	(0.45)	(0.04)

Comp.: compartment; Var.: variable; WR: wet rumen; WO: wet omasum; WA: wet abomasum; WSI: wet small intestines; WLI: wet large intestine; WC: wet colon; DR: dry rumen; DO: dry omasum; DA: dry abomasum; DSI: dry small intestine; DLI: dry large intestine; DC: dry colon; R: rumen; O: omasum; A: abomasum; SI: small intestines; LI: large intestines; C: caecum.
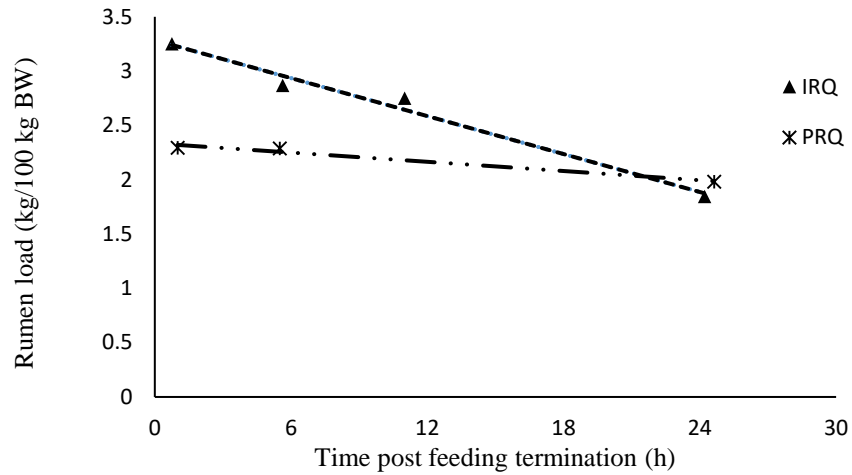
Figure 5.2. a Effect of time post feeding termination on actual dry rumen digesta load in sheep.
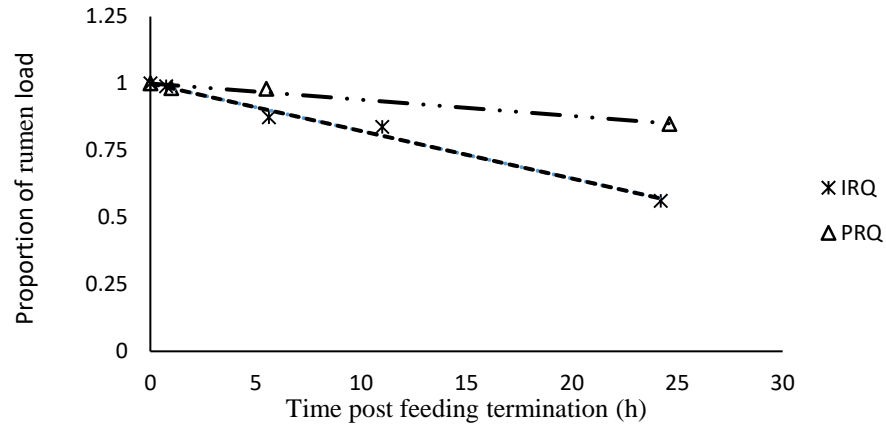
Figure 5.2. b Effect of time post feeding termination on proportion of dry rumen digesta load relative to the dry rumen load at time zero hours post feeding using a linear fit.

Figure 5.2. c Simulation of effect of time post feeding termination on proportion of dry rumen digesta load relative to the dry rumen load at time zero hours post feeding using an exponential model.

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Technically, proportions of rumen digesta load that disappear at various times post meal termination represent fractional passage rate of digesta from the rumen. On average the proportion of fluid digesta to total digesta in the rumen lies within the ra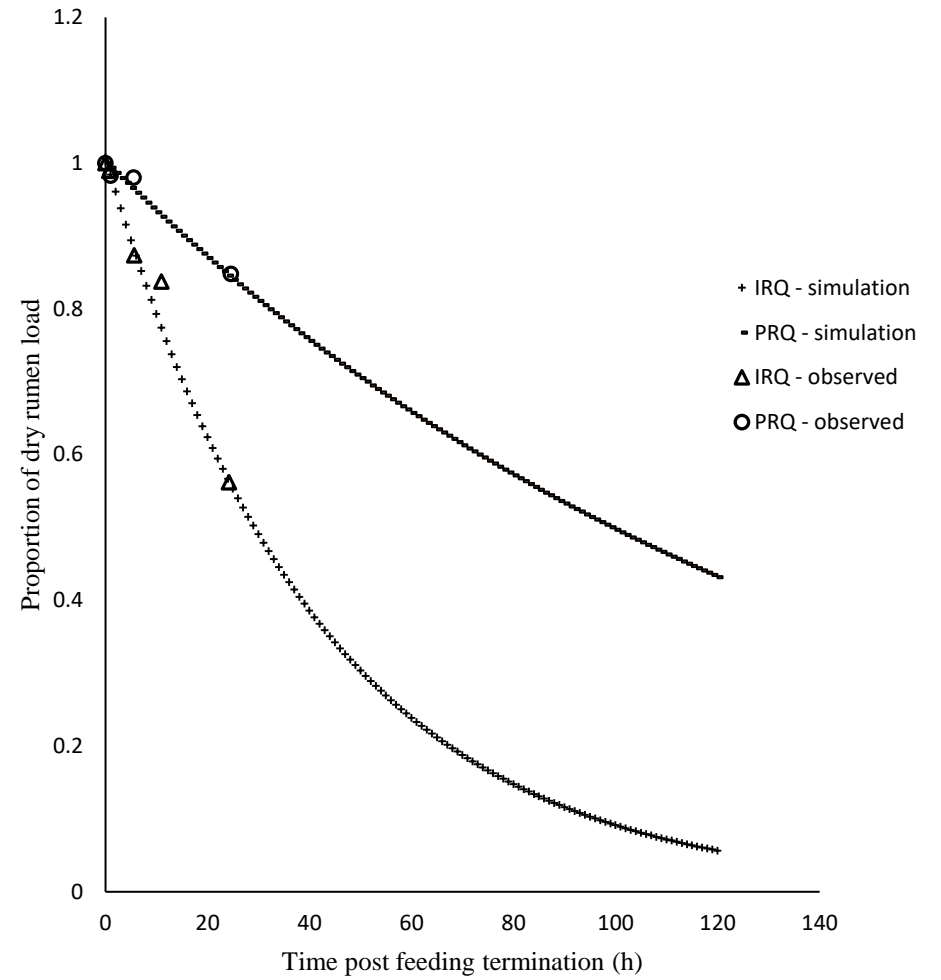nge of 80-90% (Fuller *et al*. 2004), which is similar to results obtained in this study. Contrary to findings of this study, wet and dry rumen digesta load decreased consistently with time (3>7.5>12 h) after feeding stopped in buffalo fed on alfalfa hay (Yansari *et al*. 2007). Rumen and reticulum digesta load for wet and dry matter at 0 h were significantly higher than digesta load 10 h post-feeding in sheep fed alfalfa hay regardless of intake levels (Waghorn *et al*. 1986). Oshita *et al*. (2008) reported 39-43% reductions in rumen dry matter load over a 21 h period post feeding in cattle. However, similar to findings of this study, Sekine *et al*. (1991) reported null effects of time after meal termination on wet and dry rumen digesta load in sheep. Lack of differences in rumen load in this study may have been due to starving sheep for a 17 h period prior to start of the rumen fill trial. Again, providing feed for one feeding bout that lasted on average of not more than 1 h and removing the feed ("a second starving") for up to 24 h depending on slaughter time may have caused these discrepancies.

Firstly, ruminants that anticipate long periods of hunger may develop special inbuilt passage rate control mechanisms. These mechanisms may aim to slow down rates of emptying of digesta from the rumen to maximise nutrient utilisation and to prevent rapid attainment of critically low rumen fill levels. Overnight starvation of 16.6 h reduced the rumen dry matter and NDF digesta load by -58 and -56%, respectively, with reference to the fill level prior to starvation (Chilibroste *et al*. 1998). Long starvation periods may cause very low fill levels. Thus, starvation may have caused sheep to have similar fill levels regardless of time post feeding in this study. Secondly, based on in-sacco degradability obtained in this study, dry matter loss at 24 h was approximately 35% (PRQ) and 46% (IRQ). This suggests that after "2 starvation periods" amounting up to 41 h caused rumen fill levels to be low for sheep slaughtered 6, 12 and 24 h post feeding. Starvation may have resulted in most of the sheep having rumen fill levels that are similar and close to a residual rumen fill. When rumen fill levels reach this residual value, the rate of emptying of digesta load through passage would be expected to be very low, and under the control of the animal's physiological status. This implies that effects of roughage quality and time post feed termination would have no effect on rumen fill levels in this study. Whether digesta passage rate preceding a starvation period in ruminants is under voluntary or involuntary control still remains unknown and warrants further research.

Digesta clearance due to passage rate is mainly determined by reticulorumen contractions. Frequencies of rumen contractions per minute are greater during eating than

idling, with a general tendency of eating>ruminating>resting (Frandson 1981). It is expected that the intensity and frequencies of these contractions would decrease with time post feeding. It seems that passage rate had negligible effects on emptying of rumen load post feeding due low frequencies of rumen contractions. Degradability rate which is less influenced by animal factors was to a greater extent responsible for digesta clearance. More studies need to ascertain the control of digesta clearance from the rumen in response to prolonged starvation.

Based on the regression of dry rumen fill load post feeding, digesta load decreased gradually with time in sheep fed improved quality roughage. For some mysterious reason, the 12 h post feeding rumen fill levels for 2 sheep fed on the poor quality roughage were unexpectedly higher than the 0 and 6 h post feeding rumen fill levels. These results suggest that the dynamics of rumen digesta kinetics post feeding is still not entirely understood. Firstly, these 2 outlying points reveal that individual ruminants adapt differently to roughages of poor quality (Nsahlai *et al*. 1996). Implicitly, rumen fill levels fluctuate greatly in individual ruminant animals and are dependent on the amount of receptive space in the rumen that can accommodate more feed. Fluctuations in rumen "fill" are determined by feed intake based on the desire to eat and are generally governed by rates of passage and degradation. Secondly, all rumen digesta loads were scaled to 100 kg of body mass at slaughter. Use of body mass as a scaling factor for rumen dry matter load may be unsuitable and its use limited to specific situations. Rumen digesta load was not affected by diet treatments when scaled to body weight at slaughter, but were significant when scaled to total stomach weight (Moolchand *et al*. 2013). The degree of maturity and animal production level may well be used as alternative scaling factors. Knowledge of rumen fill levels based on animal production level and degree of maturity may be importance in this context.

Despite the anomality discussed in the previous paragraph, the best regression fit showed a linear decrease in proportion of rumen load with time post feeding termination for both roughage qualities. The rate of decrease of dry matter load and proportion of dry matter load with time post feeding was greater for the IRQ compared to PRQ. Cellulolytic bacterial populations were presumably greater in the rumen of sheep fed on the IRQ due to a higher CP and energy content provided by urea. Hence, there was a higher rate of cellulose degradation of IRQ compared to PRQ. Strikingly similar to findings in this study, Huhtanen *et al*. (1993) reported a linear trend in the disappearance of rumen digesta load from 3 h to 12 h post feeding in cattle (29% decrease).

The higher disappearance rate of the improved roughage compared to the poor roughage was due to a faster rate of degradation of the improved roughage. It was expected

that the decrease would take an exponential decay trend rather than a linear trend. Linear decreases in the proportion of digesta load from the rumen after feeding stops do not conform to the proposed concept of the existence of a residual rumen fill value. Trends that follow an exponential decay curve for the proportion of fill with time lapse post feeding would have a point where the proportion of digesta load left in the rumen decreases at a decreasing rate. At this juncture the proposed residual fill level would have been reached. It is possible that the observed linear trend represents the straight segment of the exponential curve. This suggests that the trend is linear only up to 24 h. This study did not include rumen sampling times beyond the 24 h mark due to ethical considerations. However, simulation of the digesta load trend beyond 24 h showed the attainment of an exponential decay trend. Similarly, disappearance of neutral detergent fibre and digestible neutral detergent fibre from the rumen post feeding was exponential Huhtanen *et al*. (1993). This suggests that reductions in digesta load post feeding occurs in two distinct phases (Huhtanen *et al*. 1993), with an initial linear phase (0-24 h post feeding) and a gradual exponential "decay" phase (occurring beyond 24 h post meal termination).

Fractional passage rates at 24 h post feeding termination for sheep fed on IRQ conform to the range of 0.012-0.030 per hour for solids (McDonald *et al*. 2010). However, sheep fed on PRQ had a slightly lower fractional passage rate. The slower fractional passage rate of sheep fed PRQ conform to the view that ruminants fed on poor roughage qualities in the tropics may have longer mean retention times (MRT) in the rumen. Longer MRT's give adequate time for particle size reduction of the PRQ to occur allowing digesta to pass out of the reticulo-omasal orifice. Long MRT's of PRQ complements its slower degradation rate. Passage rates would play a negligible role in digesta clearance in starved ruminants fed poor quality roughages. The rate parameter on the exponential curve in this study may represent the degradation rate of the slowly degradable fraction of fibre rather than its rate of passage. Based on the exponential curve, the high rate at which the proportion of IRQ disappears is supported by the observed higher degradation rate of IRQ than PRQ.

Rumen fill levels for NDF (kg fibre/100 kg weight) are 1.7 for ruminants feeding on temperate roughages (Mertens 1973). This fill level may be higher than 2.2 for ruminants feeding on low quality tropical roughages (Adebayo 2015) due to slow digesta degradation and passage rates. The average rumen load for NDF in this study were greater than 2.2 for both roughage qualities. These results are similar to those of Adebayo (2015) in goats fed on urea treated, urea sprayed and untreated hay. These results suggest that ruminants adapt differently

to roughages of poor quality (Nsahlai *et al*. 1996) and that larger rumen fill for NDF are expected for ruminants in the tropics compared to those in temperate regions.

5.4.2 Omasum, abomasum and hindgut digesta load

Similar to findings of this study, Adebayo (2015) did not obtain significant effects of roughage quality on omasum (*P*=0.092) dry digesta loads in goats. The effect of diet on dry abomasum load is similar to Álvarez-Rodríguez *et al*. (2010) and Adebayo (2015). Lambs fed alfalfa had lower abomasal digesta load compared to those fed concentrate (Álvarez-Rodríguez *et al*. 2010). Goats fed on IRQ had lower abomasum digesta load than those fed on PRQ (Adebayo 2015), which is a similar trend observed in this study. However, there was a tendency of the wet and dry digesta load in the rumen, omasum, small intestines and caecum to be higher in IRQ than PRQ, which is contrary to Adebayo (2015) whose values followed the order: IRQ<PRQ<SIRQ. The higher compartmental fill load for IRQ compared to PRQ in this study was solely due to high feed intake of IRQ. The observations of low digesta load in the rumen, omasum, small intestines and caecum seen in goats (Adebayo 2015) were due to high digestibility of the IRQ compared to the PRQ. Higher digesta passage rate and digestibility of IRQ may have resulted in lower digesta load in the omasum and abomasum compartments in sheep fed IRQ. The decrease in omasum digesta load with time up to 12 h post feeding is similar to Waghorn *et al*. (1986). Similar to findings in this study, time post feeding had no effects on digesta load in the abomasum (Waghorn *et al*. 1986).

Similar to goats (Adebayo 2015), an improvement of roughage quality did not affect the wet digesta load in the hindgut of sheep. The lack of dietary effects on dry digesta load in the hindgut is similar to results obtained for the small intestines (Álvarez-Rodríguez *et al*. 2010; Adebayo 2015), colon (Adebayo 2015) and caecum (Álvarez-Rodríguez *et al*. 2010) in lambs and goats. Contrary to findings in this study, dry digesta load in the colon was influenced by diet (Álvarez-Rodríguez *et al*. 2010). In this study, dry matter load (kg/mCL/100 kg BM) in the colon was affected by time post feeding termination only after scaling to compartment length and body weight.

The implications of a linear decrease in digesta load in the rumen after eating stops are that subsequent feed intake after sheep were deprived of feed for up to 24 gradually increases linearly with time. Models that seek to predict rumen fill levels should take into account the effects of starvation and time lapse post feeding termination on rumen digesta load.

5.4.3 Model evaluation

Both solid and liquid passage rate prediction models were developed based on assumptions that animals were in a positive energy balance or at maintenance level of feeding. Hence, animal production level (APL) values ranged from 1-2.4 in model development. In model development there were no observations from animals that were in a negative energy balance due to unavailability of data. With the exception of 2 sheep (fed on IRQ) which were at maintenance level, all other sheep in the passage rate study were in a negative energy balance as seen in APL values less than 1. The solid model had better precision in predicting solid passage rate compared liquid passage rate in sheep that were losing weight. Based on these findings it is possible that negative energy balance affects passage rate of liquid to a greater extent than of solids. Hence, both solid and liquid prediction models need to be improved by capturing data on ruminants that have an APL less than 1. Scarcity of this kind of data may limit model improvement.

5.5 Conclusion

Improvement of roughage quality increased solid passage rate but did not affect liquid digesta passage rates from the rumen. Proportions of digesta load in the rumen decreased linearly up to 24 h post feeding termination regardless of roughage quality. There is a possibility that this trend shapes into an exponential "decay" curve after 24 h post feeding termination.

Chapter 6
General discussion, knowledge gaps and recommendations

6.1 General discussion

There is abundant literature on digesta passage rates in ruminant herbivores. There exists a wide variation among studies in passage rate data collected. This variation is mainly due to differences in feed, animal and environmental factors in studies that report digesta passage rates. There is very little application of empirical measures of rumen digesta passage rates. The main purpose of this study was to make productive use of empirical measures of passage rates by developing dynamic and robust passage rate prediction models.

The specific objectives of this study were to: (1) develop solid and liquid passage rate prediction models for nutritionally and climatically diverse ruminant herbivores, (2) to ascertain how diurnal feeding behaviour of small ruminant herbivores in a subtropical region is affected by diet quality and period of the day, and (3) to ascertain the effects of roughage quality on digesta passage rates and time lapse post meal termination on the trend of decrease in rumen digesta load in sheep.

In chapter 3, a total of 17 and 23 factors were used as input variables to develop 2 prediction models for liquid and solid passage rate, respectively. The study tested the hypothesis that it is possible to develop a single passage rate prediction model for diverse ruminant herbivores. Both models achieved acceptable levels of accuracy and precision in prediction of digesta passage rates for dietary and genetically diverse ruminant herbivores. The hypothesis is accepted based on the view that models developed in this study accounted for more variation in unseen data for 17 species of ruminant for which most studies had failed to achieve using a single model. It was concluded that the predictive potential of both models could be improved by indexing for environmental temperature and feeding behaviour. Feeding behaviour was reviewed to be part of data variables which in subsequent models could be included for intake prediction. However, unavailability of feeding behaviour measures in all studies that reported passage rates eliminated its use in model development in this study.

Chapter 4 ascertained whether feeding behaviour of small ruminants fed on a variety of diet qualities would be different. It was hypothesised that roughage/diet quality affects times spent eating, ruminating and idling. Generally, improved feed quality increased eating time during the day but not at night, and reducing feed quality tripled the difference in daytime chewing the curd at night. Generally, goats and sheep fed on roughage alone ruminated at night and ate more during the day but those fed on roughage supplemented with lucerne hay spent

more time ruminating than eating. Perception and fear of predation explained differences in daytime and night time feeding behaviours. Acceptance of the hypothesis suggested that there is a potential of modelling feeding behaviour using feed compositional attributes and period of the day as the major input variables. In conclusion, modelling of feeding behaviour is critical in improving predictive potential of digesta passage rate models.

In Chapter 5, the influence of roughage quality on passage rates and time lapse after meal termination on rumen digesta load was investigated. It was hypothesised that: (1) diet quality has no effect on digesta passage rate; and (2) fractional clearance rate of rumen digesta after meal termination would remain constant with time governed by passage and degradation rates [RF=f(k_d; k_p)]. Improvement of roughage quality increased solid passage rate but not liquid passage rate. Roughage quality had an effect on the rate of digesta clearance with time. Regression of the proportion of rumen load with time post meal termination ascertained that the fractional clearance rate of rumen digesta was linear up to 24 h after sheep stopped eating. However, simulation of the proportion of dry digesta load after 24 h post meal termination took an exponential decay trend. Based on the observed rate of disappearance using the exponential model it was concluded that passage rate had a negligible effect on digesta clearance following meal termination when preceded by starvation. So, degradation appeared to be the major factor responsible for digesta clearance post meal termination when preceded by starvation. The 1st hypothesis was accepted for liquid passage rates and rejected for solid passage rates. The 2nd hypothesis was rejected based on the view that passage rate seemed to have a negligible influence on digesta clearance rate. Thus, in this study following a brief starvation, RF could have been largely governed after meal termination by degradation rate (RF=f(k_d)). In conclusion, time post meal termination should be indexed in models that seek to predict rumen fill levels. The effects of starvation on digesta passage rates and the role of passage rates in accounting for digesta clearance warrants further study.

6.2 Knowledge gaps

More research is needed to get full understanding of the dynamics of roughage intake in ruminant herbivores. Firstly, very few impact studies on roughage intake are conducted in African grasslands. It is known that increasing ambient temperatures are likely to reduce forage quality and availability (Dzama 2016). However, the quantitative impacts of temperature changes on the availability and quality of pasture in these grasslands are unknown. This makes it virtually impossible to determine sustainable grazing practices in arid and semi-arid areas of Africa to prevent overgrazing and pasture depletion. Simulation of intake in grazing ruminants

is vital in providing a tool for implementation of grazing practises to sustainable use of pasture resources and improvement of ruminant production. Prediction of passage rates has provided a noble start to prediction of intake. Secondly, for ruminants to survive, they need to eat enough forage to maintain the vital metabolic processes that keep them alive. Most ruminant livestock animals indigenous to subtropical and tropical Africa are well adapted to harsh environments in communal areas (Dzama 2016) and high temperatures beyond the thermoneutral zone. It is common scientific knowledge that extremely high temperatures cause drastic reduction in roughage intakes. It is perplexing how ruminants maintain roughage intake levels that allow them to survive in warm semi-arid to arid regions of Africa in areas where temperatures go way above the thermoneutral zone, remains relatively undocumented. Ability to maintain adequate intake is an important survival trait. Determination of how livestock have survived in the environments they are well adapted to and match their genetic makeup to their environment would be pivotal to improving livestock production in the subtropics and tropics. Evaluation of the wealth of animal genetic resources so as to understand the match between livestock populations, breeds and genes with their physical, biological and economic landscape is vital for the survival of ruminant livestock and improved food security. Landscape genomics would help clarify the genetic basis of adaptation of genotype to the environment. Genetic basis of adaptive mechanisms such as feeding behaviour and feeding type may open new avenues for determining the genetics behind roughage intake. There are suggestions that passage rates of digesta in the rumen being under genetic control. This only strengthens the view that roughage intake may be under some degree of genetic control.

6.3 Recommendations for future research

With an ultimate goal of developing a roughage intake prediction model, there is need for expansion of work on the major anatomical and physiological factors that affect intake; rumen fill, passage rates and degradation. Based on the potential for the use of artificial neural networks (ANN) in prediction of rumen fill (Adebayo 2015) and digesta passage rates (Chapter 3 of this study); there is great potential on the use of ANN to predict roughage intake in ruminant herbivores. However, accuracy and precision in prediction of passage rates need to be improved. Proposed research pathways include:

1. Indexing for liquid passage in solid passage prediction model
2. Indexing for ambient temperature in liquid and solid passage rate prediction models
3. Modelling of feeding behaviour
4. Modelling of degradability parameters

5. Modelling of microbial protein yield

6. Modelling of intake

7. Ruminant livestock landscape genomics

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Appendix

Literature used in creation of passage rate datasets

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Ethical clearance certificate

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KWAZULU-NATAL
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YAKWAZULU-NATALI

28 July 2015

Mr Mehlull Moyo
Discipline of Animal and Poultry Science
School of Agricultural, Earth and Environmental Sciences
Pietermaritzburg Campus

Dear Mr Moyo

Protocol reference number: AREC/072/2015M
Project title: Post-feeding rumen fill, rate of passage of solid and liquid through the rumen of cattle, sheep and goats fed on tropical roughages

Full Approval – Research Application
With regards to your revised application received on 23 July 2015. 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 28 July 2016.

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

Yours faithfully

....
Dr Shahidul Islam
Chair: Animal Research Ethics Committee

/pm

Cc Superivsor: Professor IV Nsahlai
Cc Dean / Head of School: Professor A Modi
CcActing Registrar: Professor Deo Jaganyi
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